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Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy–canopy vegetation patch type rivals that occuring vertically by soil depth

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ABSTRACT

Soil moisture integrates and drives ecohydrological processes in dryland ecosystems. However, despite the central importance of soil moisture, relevant field studies have not holistically assessed key inter-related aspects of ecohydrological spatiotemporal variation: the threshold-like manner in which soil texture controls the frequency at which soil water is readily available for plants, assessment of horizontal heterogeneity associated with vegetation patches in addition to vertical heterogeneity associated with depth, seasonal variation associated with precipitation type (snow vs rain) and inter-annual variation spanning notably wet and dry periods. We measured soil water content by neutron probe in a semiarid piñon-juniper woodland (*Pinus edulis* and *Juniperus monosperma*) in northern New Mexico, USA, over 15 years and evaluated an ecohydrological metric–plant-available water, estimated as the percentage of time that soil water content was sufficiently wet to be generally available to plants. The frequency of plant-available water varied significantly across all variables assessed: precipitation amount (across years or seasons), precipitation type, vertically with soil depth and horizontally with vegetation patch type (canopy patches beneath trees, intercanopy patches between trees and edges between the two patch types). Notably, in many cases, horizontal heterogeneity in plant-available water associated with vegetation patch was as substantial as vertical heterogeneity associated with depth, yet such horizontal heterogeneity is not included in most ecological or hydrological models. Our results highlight spatiotemporal variation in the frequency of plant-available water that is substantial, often overlooked, and may need to be explicitly considered for predicting dryland vegetation responses to land use and climate change. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS drought; juniper; pinyon; piñon; soil water heterogeneity; moisture; semiarid woodlands; Walter's two-layer hypothesis

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INTRODUCTION

Global vegetation patterns are constrained and in large part determined by how climate patterns translate into soil water content, and in turn how soil water content translates into the availability of water to plants (e.g. Walter, 1973; Woodward, 1987; Neilson, 1995; VEMAP, 1995). Such relationships are a central theme of ecohydrology, particularly in dryland ecosystems, where soil moisture is viewed as a key, integrating variable (Rodríguez-Iturbe, 2000; Porporato *et al.*, 2001; Rodríguez-Iturbe and Porporato, 2004). Spatiotemporal variation in soil moisture distribution can result in differential availability of water to co-located plant functional types such as trees, shrubs and grasses (Jackson *et al.*, 1996; Schenk and Jackson, 2002a,b) and can underlie vegetation assemblages and associated ecosystem structure across grasslands, shrublands, savannas, woodlands and forests (Belsky and Canham, 1994; Neilson 1995; Aguiar *et al.*, 1996; Peters, 2002; House *et al.*, 2003; Breshears, 2006). In particular, variability of soil water vertically with soil depth has been used to predict the ratio of woody to herbaceous vegetation across regional gradients (Walter, 1971, 1973; Coffin and Lauenroth, 1990; Sala *et al.*, 1997; Breshears and Barnes, 1999; Caylor and Shugart, 2006). A larger amount of deeper soil moisture is generally viewed as being favourable for supporting a larger proportion of woody plant biomass, although there are many situations where this relationship is either insufficient to explain or does not apply to observed patterns (Scholes and Walker, 1993; Le Roux *et al.*, 1995; House *et al.*, 2003; Ryel *et al.*, 2008). More recently, differences in the frequency of soil moisture availability related to shallow and deeper 'pools' have been highlighted as a potential driver of vegetation dynamics in drylands (Ryel *et al.*, 2008).

In addition to the vertical heterogeneity with depth, soil water can also vary horizontally with respect to vegetation patches (Loik *et al.*, 2004). Soil water content can differ between the canopies of woody plants and the inter-canopies that separate them (Joffre and Rambal, 1988, 1993; Belsky *et al.*, 1989a,b; Dawson, 1993; Ryel *et al.*, 1996; Breshears *et al.*, 1997; Bhark and Small,

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2003; Lebron *et al*., 2007 see also Loik *et al*., 2004), with canopy patches being either drier or wetter than intercanopy patches, and patch types differing perhaps most dramatically in those with banded vegetation patterns (e.g. Cornet *et al*., 1992). In addition, edges between canopy and intercanopy patches can be important transition zones that, in some cases, may have the most soil moisture due to canopy drip (Breshears *et al*., 1997; Madsen *et al*., 2008). Importantly, both the vertical and the horizontal aspects of soil moisture heterogeneity may be important in determining the distribution and abundance of plant functional types and their responses to land use change (e.g. desertification; Schlesinger *et al*., 1990), yet until recently both factors have been rarely considered simultaneously in this context (Breshears and Barnes, 1999; Scwhinning and Ehleringer, 2001; Schenk and Jackson, 2002a; Loik *et al*., 2004).

Despite the fundamental importance of soil water availability to dryland vegetation dynamics, there are astonishingly few data sets of sufficient duration to quantify aspects of soil water distributions and temporal variability (e.g. Scott *et al*., 2000), in contrast to the longer data sets that are available for some more mesic grassy fields associated with meteorological monitoring sites or for agricultural sites (Robock *et al*., 2000). Given the large inter-annual variability in climate that occurs in dryland ecosystems, longer-term data sets spanning several years are needed to evaluate soil water variability. Vertically, soil water varies with depth among different ecosystem types (Lauenroth *et al*., 1993), and modelling studies have highlighted the importance of vertical heterogeneity in soil water over longer time frames (Sala *et al*., 1992; Paruelo and Sala, 1995; Rodríguez-Iturbe and Porporato, 2004). However, horizontal variability is not usually considered. In addition, a component of the vertical soil profile that is usually ignored is plant use of water in bedrock, a process inferred in recent studies but for which soil water dynamics have not been evaluated directly (Jones and Graham, 1993; Anderson *et al*., 1995; Zwieniecki and Newton, 1996; Hubbert *et al*., 2001a,b).

The ecohydrological importance of spatiotemporal variation in soil moisture (expressed as volumetric soil water content) is highly dependent on its non-linear relationship with soil water potential. This relationship has a relatively pronounced inflection point that is dependent on soil texture and determines a threshold-like response after which soil moisture rapidly becomes much less available to plants. Importantly, this relationship reflects a first-order constraint that soil texture imposes on water availability for plants. Of course, different plant species—and the different plant functional groups that they may be categorized with respect to—can differ physiologically with respect to plant-available water in that some species can access and utilize soil water under drier conditions than can other species. Nonetheless, soil texture imposes a fundamental constraint on how readily available soil water is in a given location, and yet how this constraint varies spatially, with respect to horizontal as well as vertical heterogeneity, and temporally, for snow- versus rain-dominated seasons and for more extreme wet or dry periods versus intermediate periods, has generally not been assessed and remains largely unknown. Accounting for this fundamental differentiation between when soil water is readily available from when it is not has been integral to several key concepts of soil–plant water relationships that include 'wilting point', 'non-limiting water range', 'least limiting water range', 'available water', 'plant-available soil water' and 'readily available water' (e.g. da Silva *et al*., 1994; Kramer and Boyer, 1995; Sadras and Milroy, 1996; Zou *et al*., 2000; Kirkham, 2005), as well as more generally proposed 'growth' versus 'maintenance' pools of soil moisture (Ryel *et al*., 2008). Indeed, the converse—how often plant-available water is lacking in a given period—may be a key determinant of the major vegetation change associated with drought-induced plant mortality (McDowell *et al*., 2008; Breshears *et al*., 2009; Adams *et al*., 2009). Using a single threshold value to differentiate when soil water is relatively available is an oversimplification for a relationship that is actually continuous and does not account for other factors such as hysteresis in drying versus wetting, or, as noted, for physiological differences among species of different plant functional types that allow some species to acquire water at lower soil water potentials than other species. Despite these limitations, soil texture remains a fundamental first-order control on spatiotemporal variation in soil moisture availability that constrains ecohydrological relationships in ways that, when explicitly considered, may aide in developing improved predictions.

In short, field studies of soil water content are generally lacking in one or more key aspects: (1) translation of soil water content into simple but ecohydrologically relevant metrics of probability of plant water status, (2) horizontal heterogeneity associated with woody plant cover in addition to vertical heterogeneity associated with depth and (3) duration of sufficient length to enable assessment of how patterns differ inter-annually for notably wet or dry years in addition to assessment of how those patterns vary seasonally with precipitation type (snow versus rain). Holistic assessment of these aspects of soil moisture are lacking (Figure 1), despite their potentially fundamental ecohydrological importance for vegetation dynamics. Here we report on a 15-year time series of soil water content measurements from a semiarid piñon-juniper woodland and their translation into ecohydrological metrics based on the frequency of time that water is relatively available to plants. More specifically, our objectives were to assess (1) vertical heterogeneity in plant-available water with depth, specifically for three functional layers: shallow soil (20 cm), deeper soil (>20 cm to bedrock) and bedrock; (2) horizontal heterogeneity in plant-available water as a function of patch type (canopy and intercanopy patches, as well as the edges between them); and (3) seasonal and annual patterns in vertical and horizontal heterogeneity in plant water availability. We discuss the relative magnitudes of these aspects of soil moisture heterogeneity and their

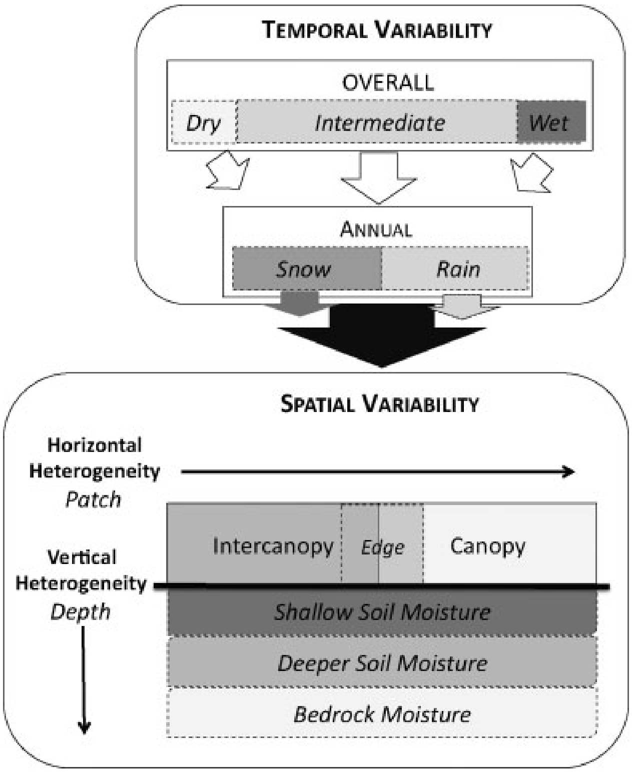

Figure 1. Key inter-related aspects of ecohydrological temporal and spatial variability in soil moisture and associated water availability for plants. Assessing overall temporal variability requires a sufficiently long time series, lacking from most studies, to assess wet and dry periods. Annual trends can be partitioned between snow- and rain-dominated months. Spatial variability can include vertical heterogeneity associated with depth and horizontal variability associated with vegetation patch type—canopy locations beneath woody plants and intercanopy patches that separate them, and potentially the edge locations between canopy and intercanopy patches as well.

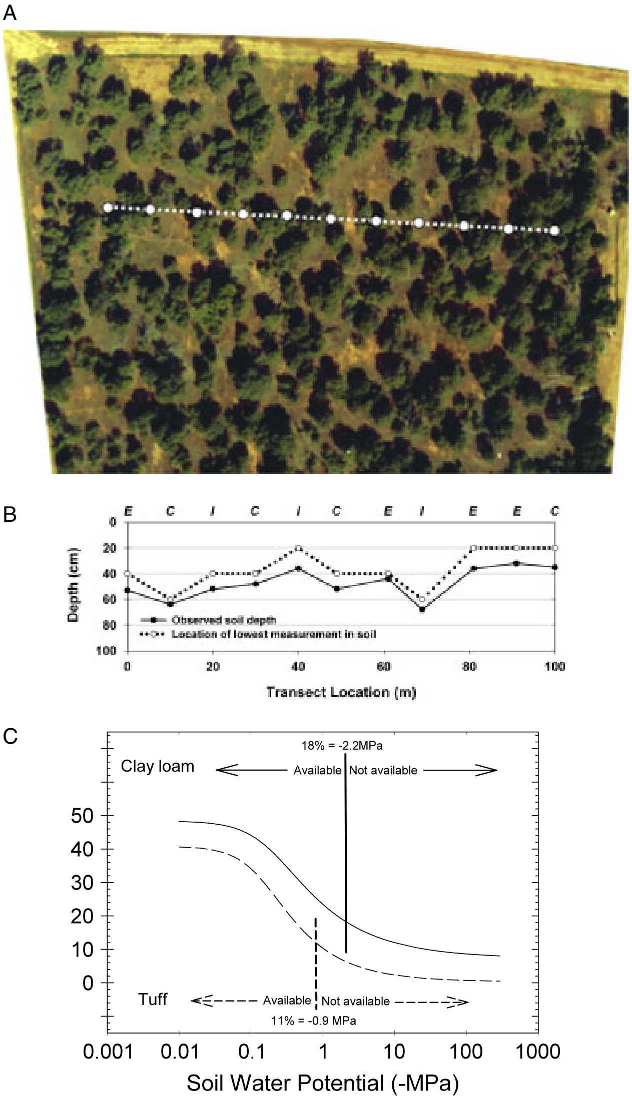

Figure 2. Mesita del Buey field site soil moisture locations and associated soil characteristics. (a) Orthophoto with location of 100-m transect with measurement locations indicated (note darkest parts of image are shadows from trees). (b) Vegetation patch types (C, canopy; I, intercanopy; E, edge) and corresponding soil depth (open circles) for each location; solid circles indicate depth to which the soil calibration curve was used; the tuff bedrock curve was used for deeper depths. (c) Soil characteristic curves relating soil water content to soil water potential for clay loam soil and tuff bedrock. The upper 75% of the range of effective water-holding capacity (as defined by van Genuchten, 1980) is indicated as an approximation of the inflection point of the characteristic curve and an indication of soil-texture-controlled differentiation between water that is readily available versus not readily available for plants (18% water content by volume and −2·2 MPa water potential for the clay loam soil, and 11% water content and −0·9 MPa for tuff bedrock).

potential implications for vegetation dynamics of different plant functional types.

METHODS

Study site

The study was conducted at the Mesita del Buey piñon-juniper woodland (Figure 2a), located on a mesa top (slope <5%) at an upper elevation (2140 m) in northern New Mexico, USA, within Technical Area 51 of the Los Alamos Environmental Research Park (latitude 35° 50′ N, longitude 106°16′ W: the site of numerous related ecohydrological studies: see Breshears, 2008 and references therein). The area has a temperate montane climate, with annual precipitation of ~400 mm, mainly in the form of winter snowfall and late-summer precipitation (Bowen, 1990, 1996). Over the course of the study, daily precipitation was measured continuously at meteorological stations on study plots adjacent to the site (Nyhan *et al.*, 1990) using a weighing gauge and a long-term event recorder (Weathermeasure Corp., Sacramento, CA). The soils at the site are predominantly sandy loam or loam at the surface, but graded to an argillic horizon in texture with a clay loam underlying in the Bt horizon (Davenport *et al.*, 1996); soils of the area encompassing the study site are described as Hackroy clay loam, derived from volcanic tuff (Nyhan *et al.*, 1978). Soil depths ranged from 32 to 68 cm for the specific locations at which soil water content was measured (Figure 2b) and from ~30 to 125 cm at Mesita del Buey more generally (Davenport *et al.*, 1996). The dominant overstory species through the duration of this study were piñon pine, *Pinus edulis* Engelm., and one-seed juniper, *Juniperus monosperma* (Engelm.) Sarg, with an overstory canopy coverage of 50%, near equal densities of the two species, just over 500 woody individuals per hectare, and a clumped distribution of individual crowns (Padien and Lajtha, 1992, also see Martens *et al.*, 1997, 2000). Ground cover in intercanopy areas adjacent to the study site was about 85% with ~50% from cryptogamic crust, 13% from grass [primarily blue grama: *Bouteloua gracilis* (H.B.K.) Lag.], 2% semi-shrub, 1% forb and 18% litter (Wilcox, 1994); canopy areas were covered with litter and contained a few herbaceous plants (Reid *et al.*, 1999). Canopy patches were not obviously mounded relative to intercanopy patches at this site. The study period culminated in a severe drought that resulted in extensive vegetation changes: >90% mortality of *P. edulis* trees >1 m tall (Breshears *et al.*, 2005); therefore, the data set spanned a period with extreme enough conditions to trigger major changes in vegetation.

Soil moisture measurements

Soil water content (% volume) was measured by neutron attenuation along a 102-m transect running approximately SW to NE (bearing 113°/33°) at 11 access tubes spaced ~10 m apart (varying from 8 to 11 m, due to access problems encountered near some trees when drilling holes for access tubes; Figure 2). Each location was categorized in 1992 as 'canopy', 'intercanopy', or 'edge' based on whether woody overstory was present or absent directly above the measurement location. Of the four canopy locations, two were under piñons and two were under junipers. Intermediate 'edge' locations were within 50 cm inside or outside of a canopy/intercanopy boundary. This categorization was used for the duration of the study; a reevaluation near the end of the study in 2001 indicated that only one intercanopy location was transitioning into an edge location, and one edge location was transitioning into a canopy one (by only a few centimeters in both cases). As noted above, in 2002, a severe drought and associated insect outbreak resulted in extensive mortality of *P. edulis* near the end of the study in 2002 (Breshears *et al.*, 2005, 2009). However, foliage remained on the branches of most dead trees through October 2002, and therefore effects of shading and interception due to the tree canopies likely did not change during this final phase of the study.

Soil water content was measured from November 1987 through October 2002, generally at 2-week intervals (the longer intervals corresponded to winter months prior to snowmelt and May 2000, when the study site was closed due to the Cerro Grande Fire). The measurements were calibrated using site-specific soils (Nyhan *et al.*, 1994) during each use to ensure consistency in measurement; a consistent protocol and measurement by only a few trained personnel over the course of the study further minimized measurement bias and error. For each access tube, depth to the soil–tuff interface was ascertained on the basis of a soil core obtained in 2002 located ~80 cm from the access tube within the same overstory type as that for the access tube. Soil water content readings were calibrated for our specific neutron probe (#5079) for each depth at each probe location using either clay loam for soil depths or crushed tuff for the underlying bedrock tuff (Nyhan *et al.*, 1994).

Estimates of plant-available water

We estimated a threshold at which soil water was relatively available to plants based on soil characteristic curves for topsoil (clay loam) and for tuff. The soil characteristic curves were developed in the laboratory via measurements of soil water tension (head, in centimeters, and later converted to soil water potential in megapascal) as a function of soil water content from a combination of hanging column suction, pressure plate pressure, or thermocouple potential (with different techniques being applied at different tensions; unpublished report by D. B. Stevens and Assoc., April 1994. *Laboratory analysis of soil hydraulic properties of protective barrier landfill cover demonstration samples.* LAB-94(1)\4800\LANL-RPT.494). We selected a point on the soil characteristic curve to represent a threshold—approximately located at the inflection point—separating water that was relatively available to plants from that that was not. Although we recognize that such a value is not actually a discrete cut-off point and that a range of values could be selected for this purpose, this value nonetheless is reflective of the fundamental way in which soil texture constrains plant water availability and is important in partially determining periods during which transpiration and other photosynthetic activity can occur, as discussed above. The threshold value was selected to be the upper 75% of the range of the effective water-holding capacity (as defined by van Genuchten, 1980), which is near the inflection point of the characteristic curve, and corresponded to 18% water content by volume and −2·2 MPa water potential for the clay loam soil, and 11% water content and −0·9 MPa for the tuff bedrock. Although other metrics could also be used, this one strongly reflects a value near which the soil water potential, and consequently general availability of soil water to plants, changes greatly. These thresholds were then compared with soil water content measurements (% volume) to classify availability of water based on estimates of plant water uptake thresholds at a given location, depth and time.

Analyses

Our analysis design included factors related to vertical heterogeneity (depth), horizontal heterogeneity (vegetation patch type) and season (snow- vs rain-dominated months), all evaluated over 11 spatial replicates (tubes) and 15 annual replicates (years). Our division of seasonal periods here is based on the long-term trends (Bowen, 1990), indicating higher probabilities of snow than rain for November through April (hereafter designated as snow-dominated months) and higher probabilities of rain than snow for May through October (hereafter designated as rain-dominated months). The data for plant-available water were evaluated by year, subdivided within year into snow-dominated months (November–April), and rain-dominated months (May–October), by patch type (intercanopy, edge and canopy) and by depth, with soil type varying with depth by location. Soil water content measurements (% volume) were averaged for each combination of tube, depth, month and year to give each month equal weight in subsequent analyses. Percent plant-available water was calculated for each combination of year, season, patch and depth, using frequencies of soil moisture measurements exceeding plant-available water thresholds described above. We summarized these results with respect to several categories. For vertical heterogeneity, we summarized average variation by depth for all of the water year, snow- and rain-dominated months; and differences between dry, intermediate and wet periods as a function of depth for all of the year, snow- and rain-dominated months. Similarly, for horizontal heterogeneity, for each of the three patch types (intercanopy, edge, canopy), we summarized average variation for depth for all of the year, snow- and rain-dominated months; and differences between dry, intermediate and wet periods as a function of depth for all of the year, snow- and rain-dominated months. Notably dry water years (less than the 10th percentile) were 2000 and 2002. Notably wet years (greater than the 90th percentile) were 1991 and 1998. For snow-dominated months, the driest periods below the 10th percentile were in 1999/2000 and 2001/2002 and wet periods exceeding the 90th percentile occurred in 1992/1993 and 1994/1995. For rain-dominated months, the driest periods below the 10th percentile were in 2001 and 2002 and wet periods exceeding the 90th percentile occurred in 1988 and 1991. Mean plant-available water and 95% confidence intervals were used in graphical summaries.

We conducted an analysis to evaluate source contributions to the overall variation in plant-available water. We estimated variance components associated with patch type, month and year for presence/absence of plant-available water with a generalized linear mixed model for binary variables (PROC GLIMMIX, SAS, 2001). Variance components are on the logit scale with the residual variance fixed at $\pi^2/3$ for the standard logistic distribution.

RESULTS

Vertical heterogeneity in plant-available water

Soil water content varied substantially by depth, both within and across years (Appendix Figure 1). Notably, precipitation generally translated into soil water content in 2, 1 or 0 major integrated pulses within a water year, depending on the year. Not surprisingly, soil water content was more variable at shallower depths (in the top 100 cm) than for deeper depths, and content generally decreased from the 40 to 60 cm, the depth interval associated with the soil-to-tuff transitions. Soil water contents at depths between 80 and 100 cm were substantial (15–20%) and dynamic, whereas soil water content at 150 cm was relatively static at about 5% volumetric water content. Soil water content at depths greater than 150 cm (200, 250 and 300 cm; data not shown) was very similar to that at 150 cm.

The frequency of plant-available water averaged over the year increased with depth from 20 to 80 cm (Figure 3). There was little or no plant-available water at depths greater than 150 cm. For snow-dominated months, there was a greater frequency of plant-available water at 20 and 40 cm depths, and hence less variation with depth between 20 and 80 cm. For rain-dominated months, the frequency of plant-available water increased with depth from 20 to 80 cm in a manner similar to that for the entire water year. The depth distributions for

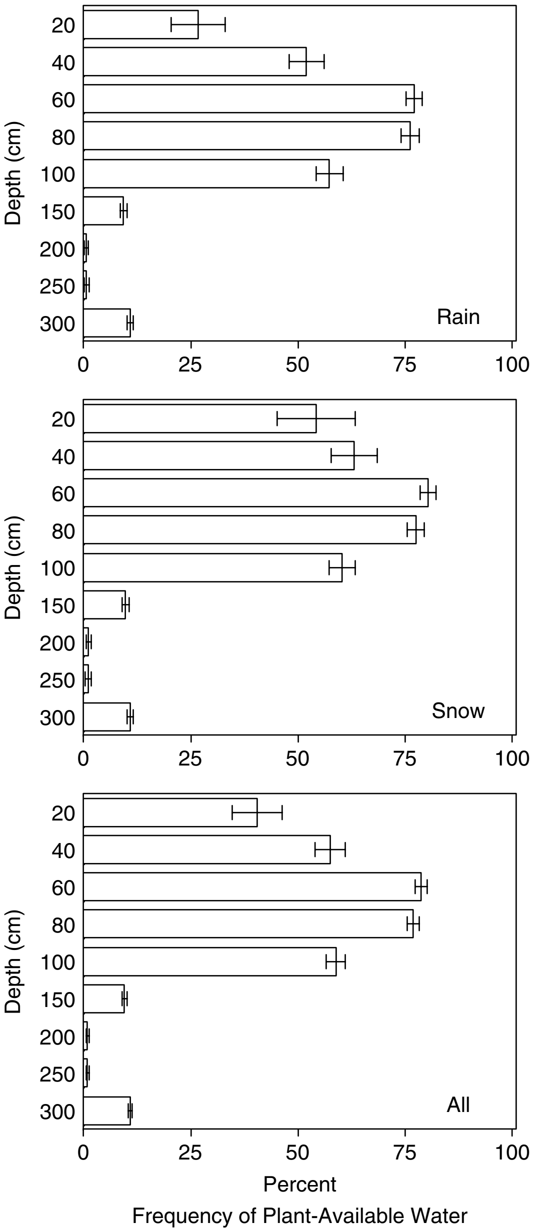

Figure 3. Relative frequency of plant-available water over the water year (November–October) as a function of depth for the entire year (All), snow-dominated months (Snow) and rain-dominated months (Rain). Error bars represent 95% confidence intervals associated with temporal variation.

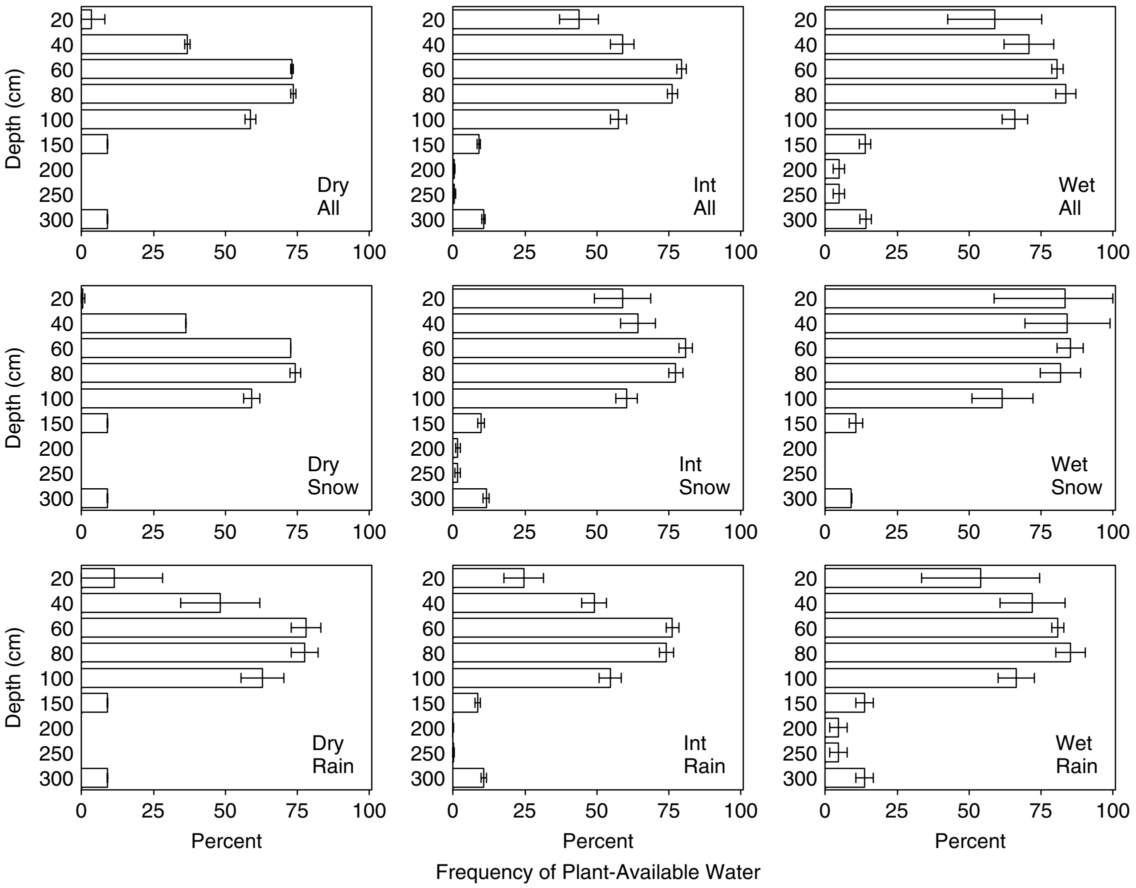

Figure 4. Relative frequency of plant-available water as a function of depth for the entire water year (All) and seasonally for snow-dominated months (Snow), and rain-dominated months (Rain), each evaluated for dry (Dry), intermediate (Int) and wet (Wet) periods annually or seasonally. Error bars represent 95% confidence intervals associated with temporal variation.

the frequency of plant-available water differed annually between dry, intermediate and wet years (Figure 4—All row), exhibiting increases at 20 and 40 cm and, to a lesser extent, 60 and 80 cm when comparing dry, intermediate and wet years. In dry years, the frequency of plant-available water increases with depth from 20 to 80 cm, whereas in wet years water is available to plants more than 50% of the time at all depths from 20 through 80 cm. Snow-dominated months (Figure 4—Snow row) were more variable between wet versus dry periods than were rain-dominated months (Figure 4—Rain row) and nearly always had available water in the soil depths in wet years (Figure 4—Wet, Snow).

Horizontal heterogeneity in plant-available water

Soil water content varied with patch type—intercanopy, edge, canopy—in a dynamic manner that varied with depth and time (Appendix Figure A2), as highlighted in examples for a year that was dry overall and in both snow- and rain-dominated months (2000), an intermediate year (1997), a year with a wet winter (1993) and a year with a wet summer (1991). Canopy patches differed from intercanopy patches by as much as −7·6 to 10·2% volumetric water content at upper (20 cm) depths and by as much as −6·6 to 14·1% at deeper (80 cm) depths. The differences between intercanopy and canopy patches varied with season (e.g. Appendix Figure A2, 40 cm in 1997). The large differences between canopy and intercanopy at deeper depths (80 and 100 cm) were dynamic (e.g. Appendix Figure A2, 1993). Edge locations were often intermediate in soil water content between canopy and intercanopy locations, and occasionally were the wettest locations.

The spatiotemporal variability of soil water content produced substantial variation in plant-available water as a function of patch type, depth and season (Figure 5). For 20–80 cm depths, water was most frequently available in edge locations rather than in canopy or intercanopy patches. Plant-available water was more frequently available at 20 cm in canopy than in intercanopy patches and at 40 cm in intercanopy than in canopy patches. Plant-available water in tuff at 80 and 100 cm showed a clear and significant increase in the frequency moving from intercanopy to edge to canopy locations (Figure 5; $p < 0.0001$, Cochran–Armitage trend test). Edge locations at 150 cm had plant-available water 26% of the time, whereas canopy or intercanopy locations rarely had plant-available water at this depth. Large differences also existed between patch types at these depths for both snow- and rain-dominated months.

The patterns of horizontal heterogeneity among patch types also varied annually among dry, intermediate and wet years (Figure 6). In intercanopy patches, moving from dry to wet years, the frequency of plant-available

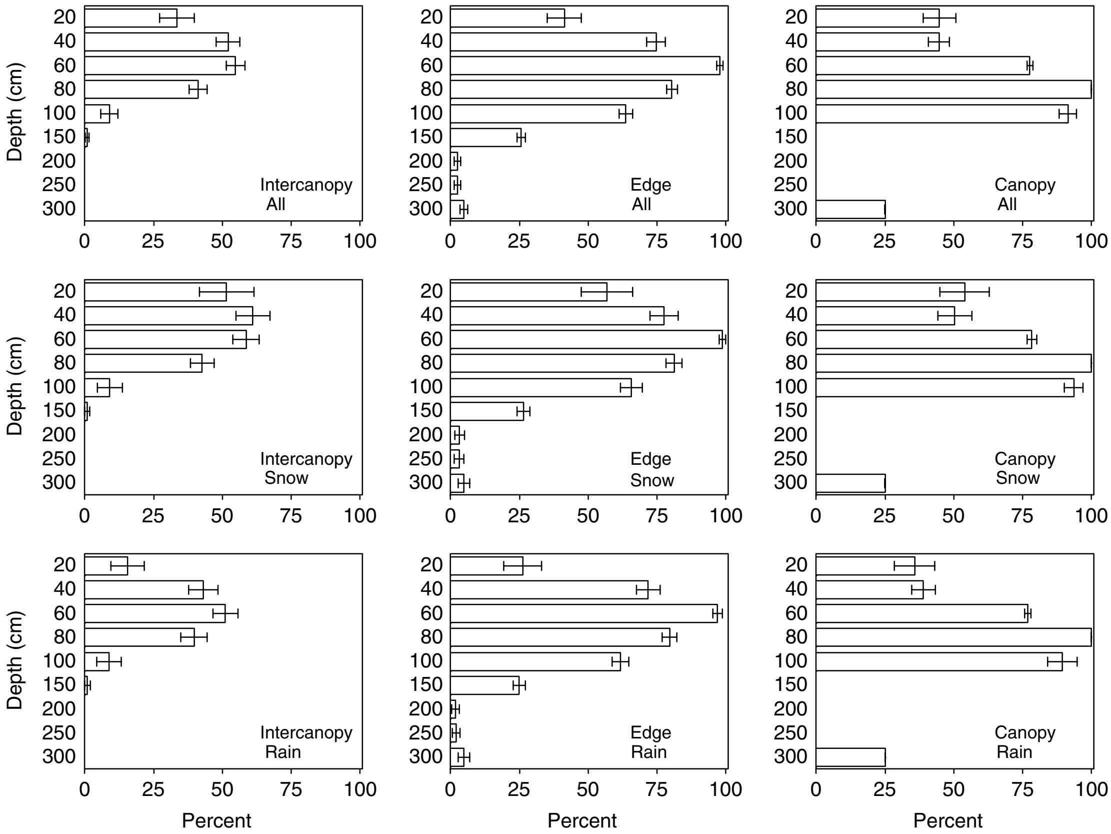

Figure 5. Relative frequency of plant-available water for each of three patch types (intercanopy, edge, and canopy) for the entire water year (All), snow-dominated months (Snow) and rain-dominated months (Rain). Error bars represent 95% confidence intervals associated with temporal variation.

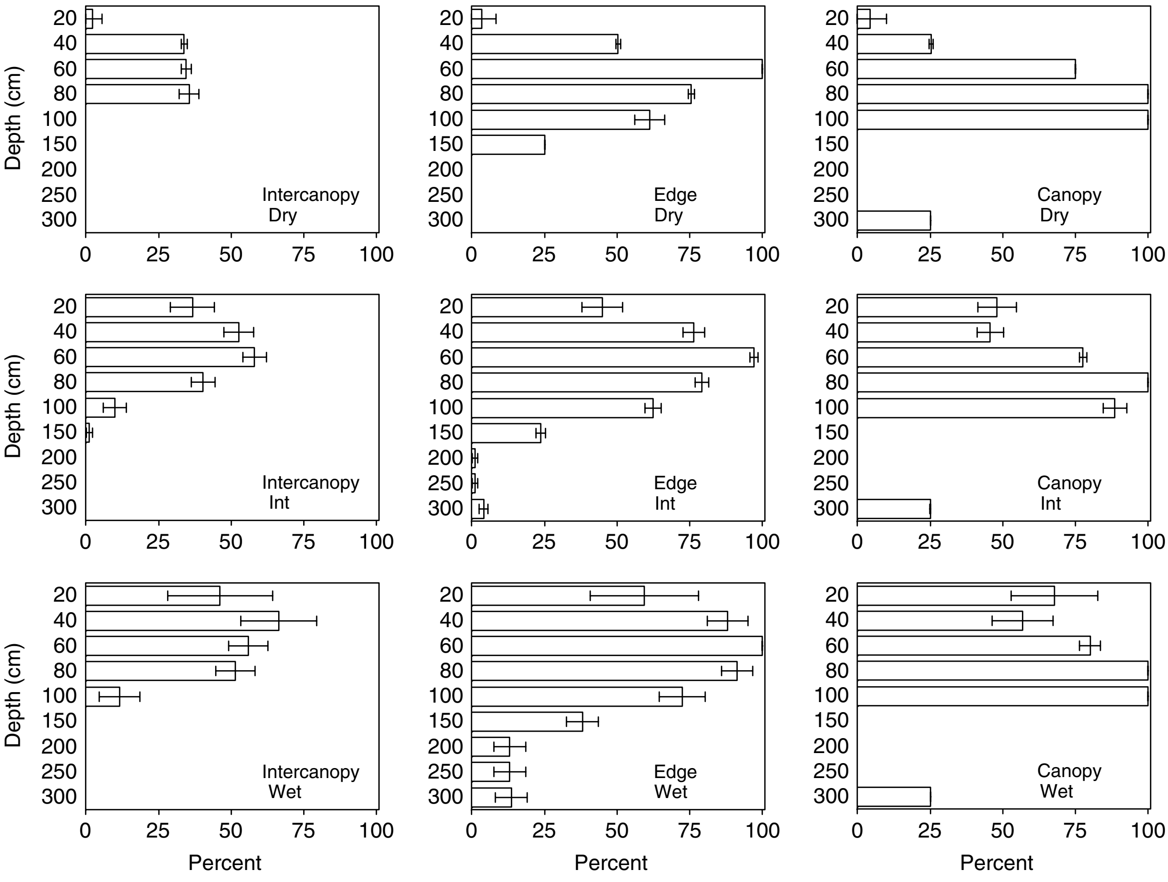

Figure 6. Relative frequency of plant-available water for each of three patch types (intercanopy, edge, and canopy) over the water year for dry (Dry), intermediate (Int) and wet (Wet) years. Error bars represent 95% confidence intervals associated with temporal variation.

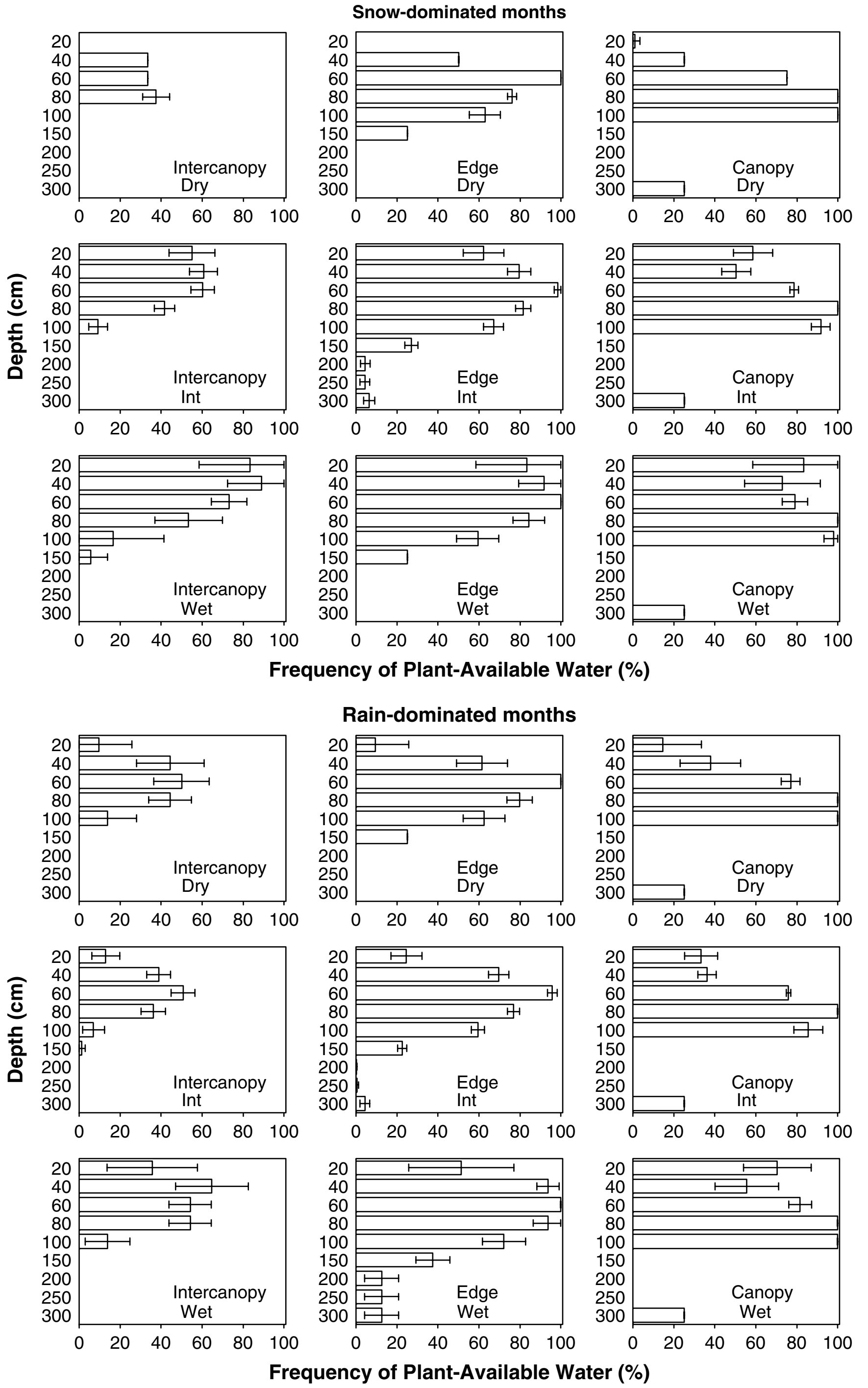

Figure 7. Relative frequency of plant-available water for three patch types (intercanopy, edge and canopy) for seasonal periods that were (Dry), intermediate (Int) and wet (Wet), presented for snow- and rain-dominated months. Error bars represent 95% confidence intervals associated with temporal variation.

water increased with water shifting from being most frequently available at 60 cm in dry years to 40 cm in wet years. There was a more dramatic shift in the depth profile of the frequency of plant-available water between dry years and wet years for canopy than intercanopy patches. In wet years, the frequency of availability was relatively constant from 20 to 60 cm, with water nearly always available at 80–100 cm. In dry years, plant water availability increased with depth from 20 to 60 cm, being available about 70% of the time at 20 cm. These results indicate that the frequency of plant-available water responded differently in canopy versus intercanopy patches to changes in type of precipitation. The frequency of plant-available water at all depths increased in edge locations, moving from dry to wet years.

Substantial variations also existed in the frequency of plant-available water within a season for wet versus dry periods (Figure 7). Snow-dominated months exhibited the greatest patch-scale variations across dry, intermediate and wet periods, most notable at shallow depths

(Figure 7—Snow section). During snow-dominated months, high inter-annual variability in the 20 cm depth overwhelmed between-patch variation. Rain-dominated months also exhibited patch-scale variations across dry, intermediate and wet years (Figure 7—Rain section). During rain-dominated months, canopy patches had a higher frequency of plant-available water than intercanopy patches. Canopy patches were more likely to have plant-available water than intercanopy patches in rain-dominated months at all depths to 150 cm except for that at 40 cm.

Overall spatiotemporal variability in plant-available water

Patch-scale variation was an important component of the overall spatiotemporal variability in plant-available water. The relative importance of different factors affecting plant-available water varied with depth: annual and monthly variation exceeded patch variation in the top 20 cm, whereas patch-scale variation exceeded annual and monthly variation at 60–150 cm (Figure 8). On the basis of this finding, we summarized our results with respect to key components of spatiotemporal variation in plant-available water that might be most applicable to improving ecohydrological predictions (Figure 9), considering six compartments (four in soil and two in bedrock tuff) that were differentiated on the basis of the two main cover types (canopy and intercanopy) and three functional soil layers (shallow soil in which evaporation occurs, 20 cm; deeper soil, >20 cm to the soil–tuff interface, the depth interval of which varied with tube location; and tuff bedrock from the soil–tuff interface down to 100 cm). In previous summaries, we had differentiated results by depth alone, even though both soil and bedrock occurred across the transect at some depths (40 and 60 cm); in contrast, here, to place results in a more ecohydrologically relevant context, we differentiate by soil layer (upper, lower and bedrock) rather than strictly by depth. Under mean conditions, the frequency of plant-available water in intercanopy patches was greater in the lower soil layer than that in the upper soil layer, whereas in canopy patches the frequency was greater in the upper soil layer than that in the lower soil layer, by a factor of >2·0. In the upper soil layer, the frequency of plant-available water is greater in canopy than in intercanopy patches, whereas in the lower layer the frequency is greater in intercanopy than in canopy patches. Heterogeneity among the four soil compartments varied substantially between wet and dry years. In wet years, the frequency of plant-available water in all four compartments increased, with the increases being proportionally larger in canopy than in intercanopy patches. Vertical heterogeneity in wet years remained about the same as in mean years for both intercanopy patches and canopy patches. In wet years, horizontal heterogeneity in the upper soil layer, where water is more frequently available in canopy than in intercanopy patches, becomes slightly amplified. Conversely, horizontal heterogeneity in the lower soil layer, where water is more frequently available in intercanopy than in canopy patches, becomes substantially dampened in wet years. In dry years, plant-available water was almost never present in any of the four soil compartments (<5%), diminishing the magnitude of any remaining heterogeneity. Heterogeneity among the four soil compartments also differed substantially between snow- and rain-dominated months. For snow-dominated months, water was more frequently available than for mean conditions for all four soil compartments and heterogeneity was nearly eliminated vertically in intercanopy patches and horizontally in the upper soil layer. Canopy locations in the lower soil layer are drier than those in the other three soil compartments for snow-dominated months. For rain-dominated months, water in all four soil compartments was less frequently available than that under mean conditions and vertical heterogeneity became amplified, particularly in intercanopy patches. Heterogeneity also increased horizontally in rain-dominated months, particularly in the upper layer. Our results also indicate that edge locations (Figures 5–7, but omitted from Figure 9 for simplicity's sake), which although small in area can at times have the greatest frequency of plant-available water, could be included to represent further refinement of horizontal patch-scale heterogeneity.

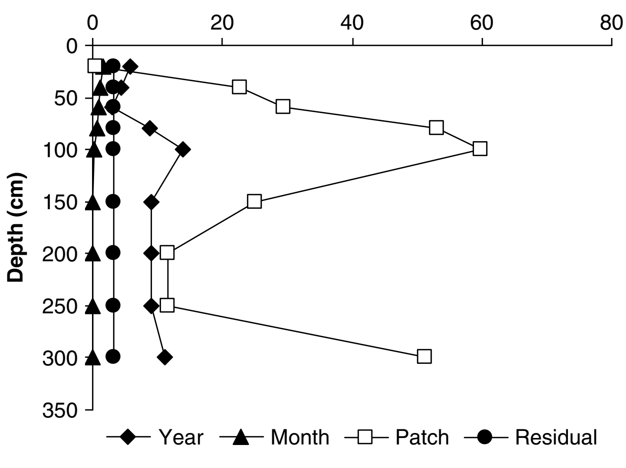

Figure 8. Variance components of plant-available water (PAW) at each depth as a function of year, month, patch type, and residual.

DISCUSSION

Vertical and horizontal heterogeneity in plant-available water

Our results highlight several key dimensions of spatiotemporal variation in the frequency of plant-available water. In general, overall heterogeneity in the four soil compartments was least in dry years, with substantial heterogeneity for mean conditions, wet years, rain-dominated months and—but to a lesser extent—snow-dominated months. Notably, most studies of soil moisture and related plant-available water in drylands are not of sufficient duration to differentiate conditions associated with more extreme wet or dry years from those for

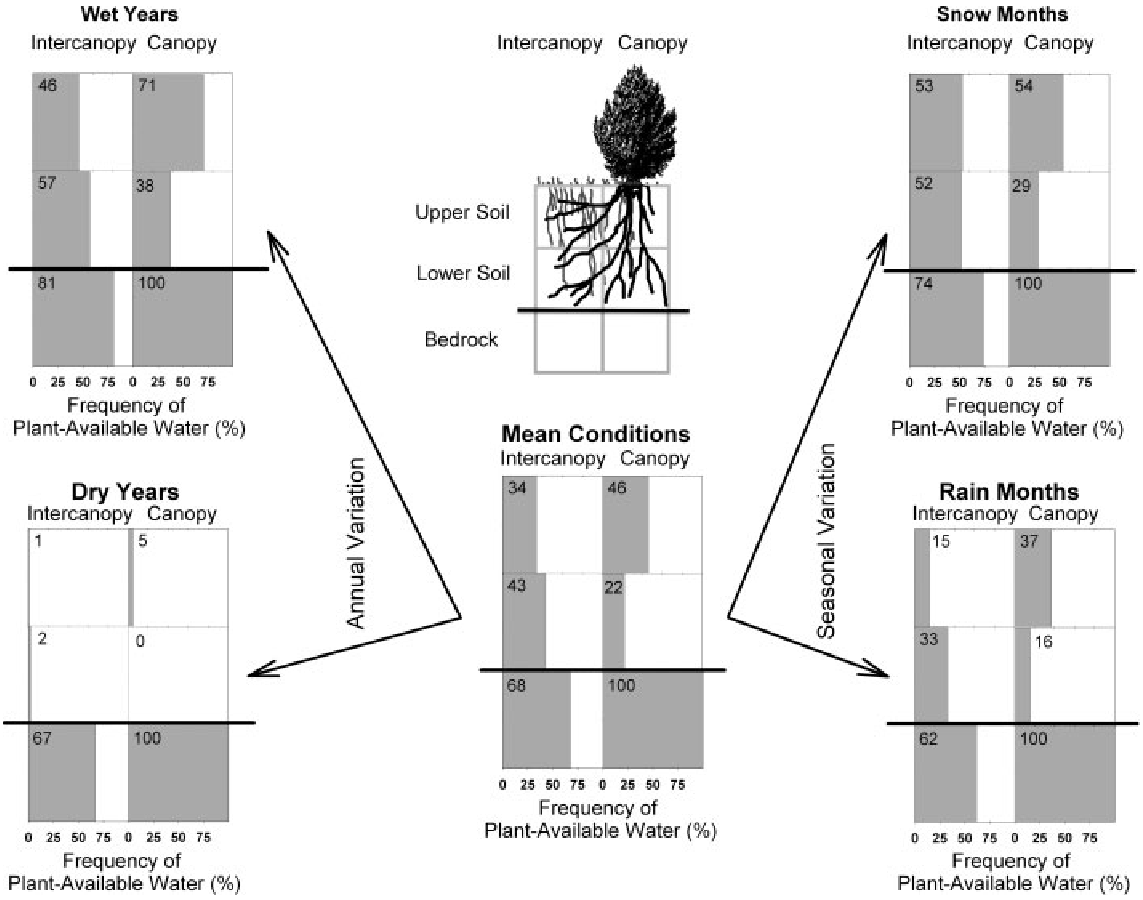

Figure 9. Relative magnitudes of frequency of plant-available water summarized relative to six compartments [canopy vs intercanopy horizontally and by shallow soil (20 cm), deeper soil (>20 cm to tuff), and bedrock (tuff down to 100 cm)] for mean conditions, wet years, dry years, snow-dominated months and rain-dominated months, d: dry years, e: wet years, highlighting that differences associated with horizontal heterogeneity can in many cases be of similar magnitude to vertical heterogeneity. Root access to bedrock could be via root growth in fissures or a root mat at the soil–bedrock interface.

intermediate years. Here, even though we are limited to only two relatively wet or dry years (within the 10th percentile on either end of the distribution), substantial differences in the amount and spatial distribution of frequency of plant-available water are readily apparent. Also note that the frequency of plant-available water in canopy locations was always greater in the upper rather than in the lower soil layer, whereas conversely, in intercanopy patches, the frequency was always greater in the lower rather than in the upper soil layer (except in snow-dominated months, when vertical heterogeneity was lacking). One surprising result was the high frequency of plant-available water in the tuff (e.g. 60–80 cm). This high value could be due to the fact that the characteristic curve for tuff is from crushed tuff, while the field measurements take place in in-tact tuff. Water may be more tightly bound in the intact tuff than in the crushed tuff, and hence we may have overestimated the actual frequency of plant-available water in tuff. Nonetheless, our data document that soil water does vary temporally at these depths, which are below the zone of soil evaporation (as determined in isotopic studies, Newman *et al.*, 1997). Consequently, these dynamics are likely due at least in part to plant water use, perhaps either due to root penetration into bedrock fissures and/or due to the presence of a root mat at the soil–bedrock interface. Bedrock underlying soils has been identified as a potentially important component of plant-available water in semiarid ecosystems (Jones and Graham, 1993; Anderson *et al.*, 1995; Zwieniecki and Newton, 1996; Hubbert *et al.*, 2001a,b), although the dynamics of soil water content and associated plant-available water have been rarely quantified. These dynamics could also be associated in part with the hydraulic redistribution of water from shallower depths (Burgess *et al.*, 1998), a possibility that requires future testing.

Our study documents that there is substantial horizontal heterogeneity—between canopy and intercanopy patches, as well as for the edges between them—in soil moisture and associated frequency of plant-available water, in shallow soil, deeper soil and bedrock tuff. Key limitations of our study include that our results are only from one site and that our sample sizes for patch types are relatively small; nonetheless, our study is notable in that it is based on a long-term data set that provides insights into spatiotemporal variation—spatially both horizontally and vertically, and temporally both seasonally and across a range of years that includes wet and dry extremes temporally. Because the effects of woody plants on water budget may be greater when foliage is of higher density, evergreen and extending closer to the ground surface, we hypothesize that our results may be applicable to other piñon-juniper woodlands and potentially other savanna and woodland systems that share similar foliar characteristics (Breshears and Ludwig, 2009). Horizontal heterogeneity in soil water content at shallow depths has been documented in a variety of systems (Joffre and Rambal, 1988, 1993; Belsky *et al*1989a,b; Breshears *et al.*, 1997; Guo *et al.*, 2002; Kropfl *et al.*, 2002; Madsen *et al.*, 2008), with soil moisture being greater in canopy than in intercanopy patches at some times or places, and the converse occurring at other times or places. Our results here are noteworthy in that they translate this heterogeneity into plant-available water, quantify the large differences at the patch scale (Figure 9) and provide probabilities of occurrence. In addition, our results extend those above in that they document a large amount of heterogeneity at deeper depths, including in the bedrock tuff.

Limitations associated with neutron probe precluded detection of soil water dynamics at more shallow depths than our shallowest measurement at 20 cm depth. Soil water content at more shallow depths can be quite dynamic, as highlighted by continuous measurements obtained in unvegetated soils adjacent to our study site (Nyhan *et al.*, 1997). Nonetheless, these smaller, more dynamic pulses are unlikely to obscure the major variability in soil water content seasonally, annually, vertically, or horizontally that we document here. As automated data sets of soil water content obtained with time-domain reflectometry develop into long-term data sets, the importance of smaller, shorter pulses can be further evaluated. However, time-domain reflectometry is unlikely to provide meaningful data on bedrock water, and hence measurements by neutron probe may also be an important part of improved future sampling strategies.

Determinants of spatiotemporal variation in plant-available water. The heterogeneity that we quantified in plant-available water, both vertically and horizontally, varies interactively and over time. These differences are presumably inter-related with differences in components of the water budget. As noted previously, soil moisture is viewed as an integrating factor of ecohydrological processes (Rodríguez-Iturbe and Porporato, 2004) because it reflects the net effects of water balance components (e.g. interception, runoff, soil evaporation, plant water uptake), but consequently it is also difficult to evaluate the roles of those components based on soil moisture data alone. Horizontal heterogeneity in plant-available water does not appear to be driven by heterogeneity in soil properties themselves: excluding the presence and effects of the litter layer associated with canopy patches, soil properties (Davenport *et al.*, 1996) and infiltration rates (Wilcox *et al.*, 2003b) at the site do not differ between canopy and intercanopy patches (data on potential horizontal heterogeneity between canopy and intercanopy patches at depths within the tuff are lacking and requires future evaluation). Several aspects of the water budget that do differ between canopy and intercanopy patches likely are contributing to the observed horizontal heterogeneity in plant-available water. Canopy patches generally receive reduced precipitation inputs due to foliar interception of precipitation (Skau, 1964; Collings, 1966; Owens *et al.*, 2006), and this likely affects heterogeneity in soil water content (Breshears *et al.*, 1997; Madsen *et al.*, 2008), particularly in association with interception-related differences in snow cover (Breshears *et al.*, 1997). The large reduction in plant-available water from the upper to the lower soil layer of canopy patches (Figure 9) is likely due in part to interception effects. Stemflow associated with intercepted precipitation could also influence differences between patch types (Skau, 1964; Martinez-Meza and Whitford, 1996; Owens, *et al.*, 2006), particularly for dense evergreen canopies (Breshears and Ludwig, 2009). The effects of interception are also reflected in patch-scale differences in runoff, which is much greater in intercanopy than in canopy patches (Reid *et al.*, 1999). In many semiarid ecosystems, runoff is often redistributed from canopy to intercanopy patches (Ludwig *et al.*, 2005), although within piñon-juniper woodlands much of the redistribution of runoff appears to be from bare to grassy-covered locations within intercanopy patches (Reid *et al.*, 1999; Wilcox *et al.*, 2003a). Soil temperature and evaporation also differ at the patch scale (Everett and Sharrow, 1985; Breshears *et al.*, 1998; Lebron *et al.*, 2007), and this likely contributes to the greater frequency of plant-available water in the lower rather than upper soil layer of intercanopy patches (Figure 9). Although not clearly documented here, we expect that plant water uptake and use likely differ between the two patch types and with depth (Breshears and Barnes, 1999). Soil moisture in shallow intercanopy locations is likely influenced by plant water uptake by both herbaceous and woody plants (Breshears *et al.*, 1997), whereas that in canopy locations is likely influenced primarily by woody plants because the density of herbaceous plants under canopies is generally low (Arnold, 1964; Armentrout and Pieper, 1988) and herbaceous plants such as the dominant grass *B. gracilis* have limited lateral root spread (Coffin and Lauenroth, 1991). Overall, the different components of the water budget are probably most interactive in the upper part of the soil profile, where interception, runoff, soil evaporation and plant water use, including potential hydraulic redistribution, by both herbaceous and woody plants, are likely co-occurring. In addition, differences associated with edge locations may reflect increased water inputs near the canopy drip line and differential shading patterns associated with the intercanopy–canopy edge.

Ecohydrolgical implications of heterogeneity in plant-available water

The spatial heterogeneity in plant-available water that we document here could have potentially important implications for different plant functional types that need to be further assessed, particularly relative to the differentiation of woody and herbaceous plants, which has been a key focus for savanna, shrubland and woodland ecosystems (House *et al.*, 2003). Although other factors related to establishment factors, fire, soil, climate, grazing/browsing conditions and other disturbances certainly influence the ratio of woody to herbaceous plants at a site, the spatiotemporal distribution of plant-available water may underlie these factors in that soil moisture can constrain the amount and stature of woody plants at a site (House *et al.*, 2003; Breshears and Barnes, 1999). Several alternative conceptual and predictive models relate soil moisture and its heterogeneity to ratios of herbaceous to woody plants. Walter (1971, 1973) proposed that the ratio of herbaceous to woody plant biomass at a site is proportional to the ratio of shallow to deeper soil moisture, with the vertical layers differentiated on the basis of differences in rooting depths [see Emerson (1932) for an analogous hypothesis specific to piñon-juniper woodlands]. This simple model has been shown to be a useful predictor across broad gradients (Sala *et al.*, 1997; but see Ryel *et al.*, 2008) and is imbedded in more mechanistic models of vegetation dynamics among mixed lifeforms (e.g. Coffin and Lauenroth, 1990; Coffin and Urban, 1993; Peters, 2002) and of plant biogeography (Neilson *et al.*, 1985). Several more physically based soil water models are similar to those based on soil layers and factors in additional depth intervals (e.g. Walker and Langridge, 1996; Kemp *et al.*, 1997). Similarly, much research on plant functional types has focused on the vertical rather than horizontal differences in rooting depths between woody and herbaceous species (Jackson *et al.*, 1996). Some conceptual models note the potential importance of both vertical and horizontal heterogeneity in soil moisture in driving differential dynamics among plant functional types (e.g. Breshears and Barnes, 1999; House *et al.*, 2003; Caylor and Shugart, 2006; Ryel *et al.*, 2008). Both the vertical and horizontal aspects of heterogeneity in plant-available water are also considered in a more continuous representation under the ecological field theory (Sharpe *et al.*, 1986; Walker *et al.*, 1989). Field studies at sites such as the one we studied highlight that different plant functional types at our site have differing degrees of access to soil water vertically and horizontally. For example, in our system, *J. monosperma* is more effective at obtaining shallow intercanopy water than is *P. edulis*, differentiating them as shallow- versus deeper-rooted woody plants (Breshears *et al.*, 1997). Our results also suggest that soil water dynamics in bedrock, which is usually omitted or overlooked, may be important to consider in ecohydrological models of plant water use, although additional evaluation of this issue is needed. The soil water dynamics within the tuff are at depths below the soil evaporation zone (Newman *et al.*, 1997) and therefore suggest that tuff water is being utilized by plants. Some of the deeper soil water dynamics within tuff could be associated with hydraulic redistribution, with water from shallow layers, which are wetter following snowmelt, being translocated to deeper soil layers.

The spatiotemporal variability that we quantify is directly relevant to additional recent perspectives that consider 'thresholds', 'pulses' and 'pools' of soil moisture availability (Huxman *et al.*, 2004; Loik *et al.*, 2004; Ogle and Reynolds, 2004; Reynolds *et al.*, 2004; Schwinning and Sala, 2004; Schwinning *et al.*, 2004; Ryel *et al.*, 2008). Our data also document the extreme lack of plant-available water in very dry years. When multiple such years occur in near succession, extensive plant mortality can be triggered, as was observed in response to a severe regional drought in the 1950s (Betancourt *et al.*, 1993; Allen and Breshears, 1998) and near the conclusion of our study (Breshears *et al.*, 2005, 2009). Changes in seasonal variation in plant-available water may also have important implications for plant functional types (House *et al.*, 2003). Woody plants can potentially utilize this moisture immediately following snowmelt in warm periods in mid-winter, whereas herbaceous species cannot. Precipitation variability that influences snow- versus rain-dominated soil moisture could have important implications for C-3 versus C-4 species, and the nature of plant interactions may differ fundamentally between snow- versus rain-dominated months (Gebauer *et al.*, 2002; West *et al.*, 2008). Further, threshold amounts of summer precipitation may be required for the activity of water-absorbing roots at shallow depths (Williams and Ehleringer, 2000; Williams and Snyder, 2003). Our results do not directly link spatiotemporal variability in the frequency of plant-available water to the dynamics of different plant functional types, but they do highlight substantial heterogeneity that is not explicitly considered in most ecohydrological models and that should be further evaluated with respect to their importance for ecohydrological dynamics. For instance, the tree die-off that followed the dry year at the end of the study (Breshears *et al.*, 2005, 2009) indicates that the long-term spatiotemporal differences in the frequency of plant-available water that we quantified do indeed have important implications for vegetation dynamics. Similarly, site-specific studies show species differences in ability to exploit spatial heterogeneity in soil moisture (Breshears *et al.*, 1997).

CONCLUSIONS

Our results quantify not only large vertical heterogeneity in the distribution of plant-available water, which varies between dry versus wet years and between snow- versus rain-dominated months, but also substantial horizontal variation in plant-available water between intercanopy and canopy locations. Long-term measurements provided key insights on differences associated with wet or dry years relative to intermediate ones. Further, our results suggest an important interaction between water dynamics in the tuff bedrock and intercanopy patches (e.g. deeper 'pools'; Ryel *et al.*, 2008). Our results provide estimates, based on long-term field measurements, of the probabilities of water being available temporally (annually and seasonally) and spatially (vertically and horizontally). The differences that we quantify could have important implications for the dynamics of the mixed woody–herbaceous ecosystems of the terrestrial biosphere, particularly those with a dense evergreen canopy that has foliage extending down to near the ground (Breshears and Ludwig, 2009). Addressing challenges associated with land use and climate change for these extensive ecosystems may be enabled by an improved quantification of spatiotemporal variation in plant-available water.

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APPENDIX

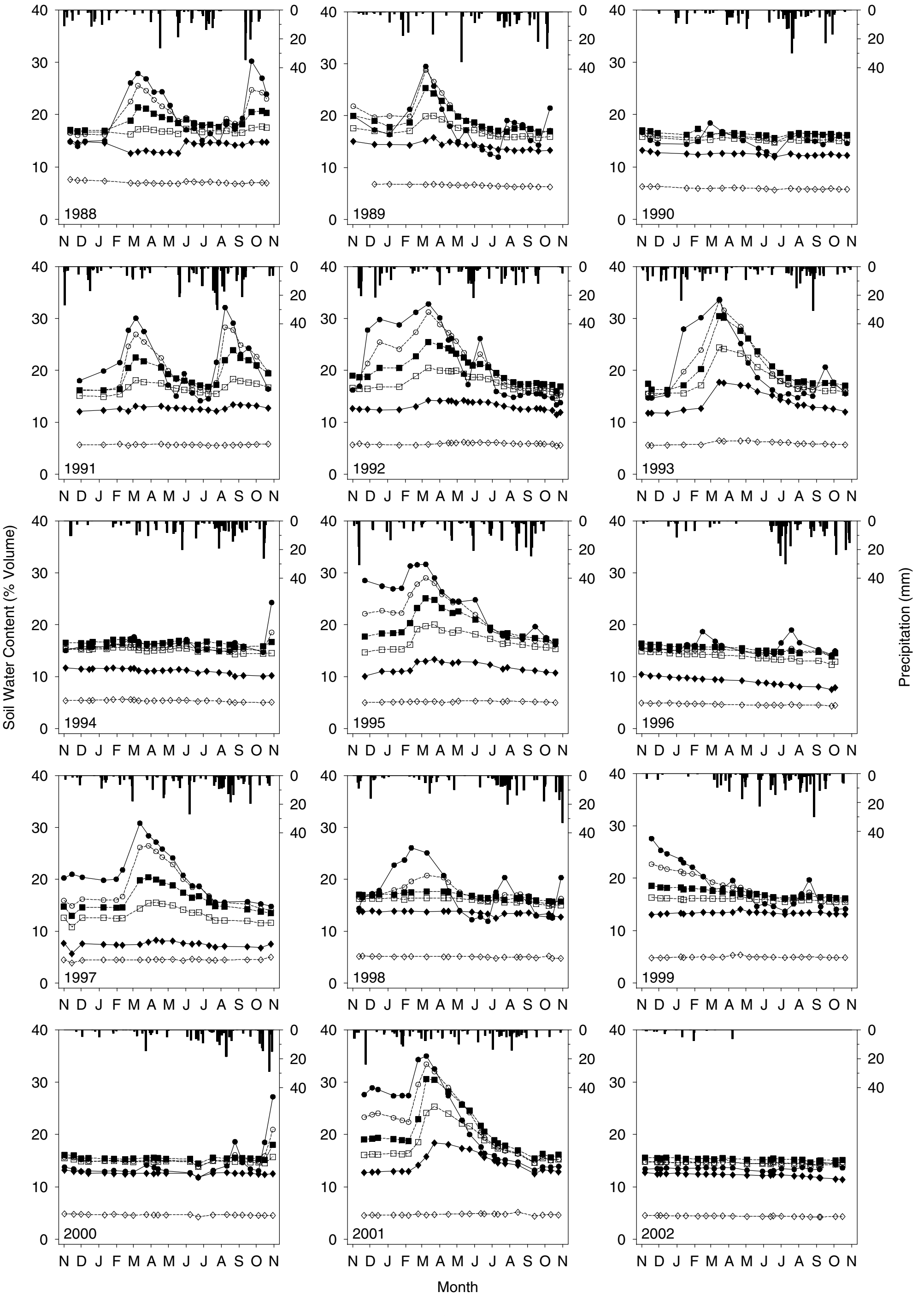

Figure A1. Daily precipitation (mm) and soil water content (% volume) for each water year spanning November through the following October (year listed is the one for January through October of that water year). Soil water contents are at depths (cm) of 20 (dot), 40 (circle), 60 (solid square), 80 (open square), 100 (solid diamond) and 150 (open diamond).

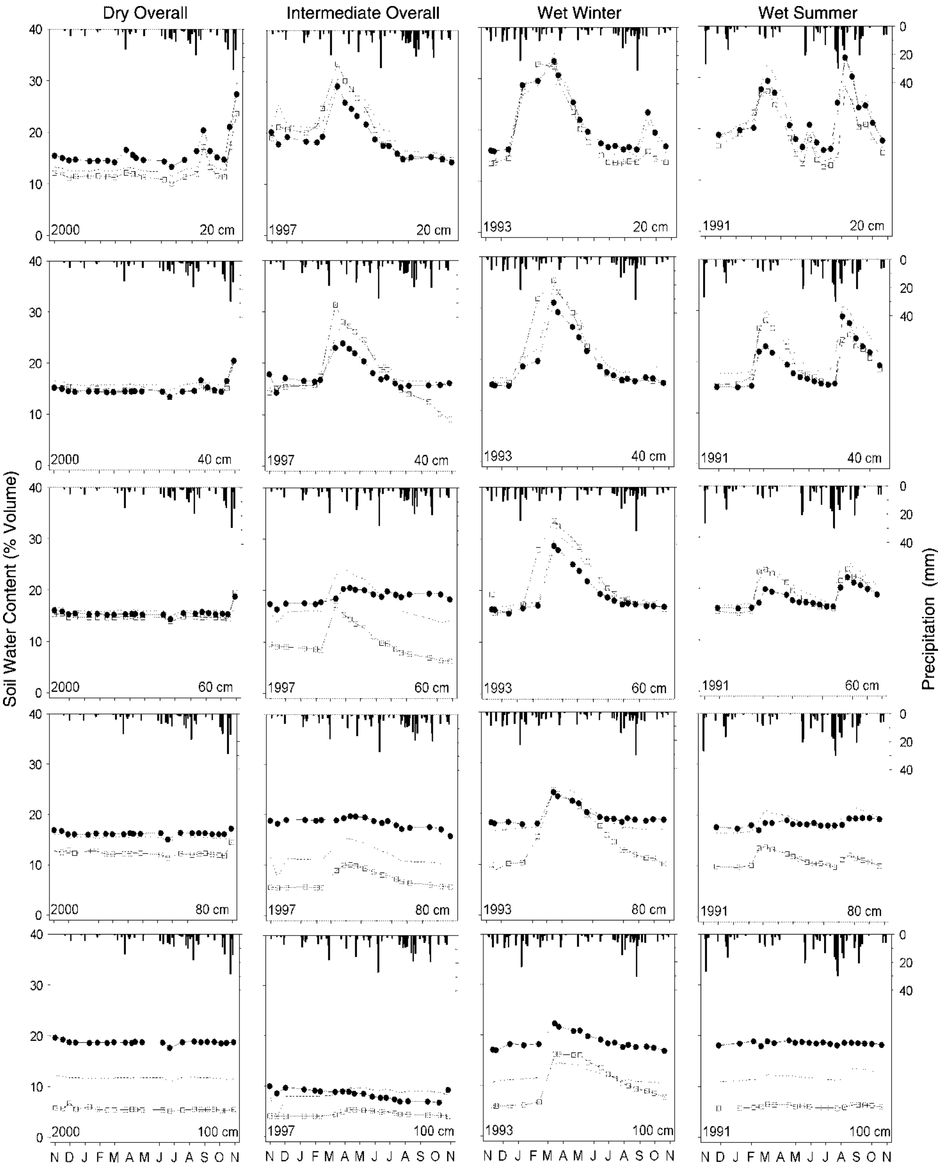

Figure A2. Daily precipitation (mm) and soil water content (%volume) for each of three patch types—intercanopy (open squares), edge (dashed line) and canopy (solid circles)—for water years spanning November through the following October (year listed is the one for January through October of that water year), for depths of 20, 40, 60, 80 and 100 cm. The example years correspond to a year that was dry overall and in both snow- and rain-dominated months (2000), an intermediate year (1997), a year with a wet winter (1993) and a year with a wet summer (1991).

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