Vegetation-infiltration relationships across climatic and soil type gradients

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[1] The enhancement of infiltration capacity in the presence of vegetation is well documented in arid ecosystems where it can significantly impact the water balance and vegetation spatial organization. To begin progress toward developing a theory of vegetation-infiltration interactions across a wide spectrum of climate regimes, three key questions are addressed: (1) Does vegetation also enhance infiltration capacity in mesic to hydric climates, and if so, what processes contribute to this enhancement? (2) Is there a canonical relationship between vegetation biomass and infiltration rate? and (3) How does the vegetation-infiltration feedback evolve across climatic gradients? To address these three questions, new field data examining biomass-infiltration relationships in different vegetation types in a humid climate and on loamy soils are combined with a meta-analysis of biomass-infiltration relationships from nearly 50 vegetation communities spanning a climatic gradient from hyperarid deserts to the humid tropics and representing a full spectrum of soil types. Infiltration capacity increased as a power law function of aboveground biomass in water-limited ecosystems, but vegetation biomass was not significantly correlated to infiltration capacity in humid climates. Across a climatic gradient from xeric to hydric, the slope of the power law relationship between aboveground biomass and infiltration capacity decreased.

1. Introduction

[2] Vegetation feedbacks to the water cycle have drawn increased interest in the past 30 years [*Bosch and Hewlett*, 1982; *Jackson et al.*, 2000; *Gerten et al.*, 2004]. Processes such as stomatal optimization with respect to water availability [*Cowan*, 1978, 1986; *Makela et al.*, 1996]; hydraulic lift [*Richards and Caldwell*, 1987; *Dawson*, 1993; *Caldwell et al.*, 1998]; and the constraints imposed by water stress on carbon allocation [*Porporato et al.*, 2001; *Schwinning and Ehleringer*, 2001; *Givnish*, 1986] have become foci of research and theoretical development, and their consequences are now being upscaled from the leaf, root and plant level to communities and catchments [*Schymanski et al.*, 2009; *Caylor et al.*, 2004]. There are, however, feedbacks between vegetation and the water cycle that do not directly result from plant activity. One such feedback is the alteration of the infiltration capacity of soils through biotic processes. This positive feedback (i.e., the presence of vegetation increases infiltration capacity) is well documented in arid ecosystems where it can lead to spatial organization [*Bromley et al.*, 1997; *Couteron and Kokou*, 1997; *D'Herbes*

et al., 2001; *HilleRisLambers et al.*, 2001; *Rietkerk et al.*, 2002; *D'Odorico et al.*, 2006; *Saco et al.*, 2007]. The processes that generate vegetation-infiltration capacity feedbacks have been widely explored in drylands [*Lyford and Qashu*, 1969; *Schlesinger et al.*, 1996; *Bergkamp*, 1998; *Dunkerley*, 2000, 2002a, 2002b; *Wainwright et al.*, 2002]. They include physical factors, such as protection of the soil surface, and biological factors, such as the creation of habitat for soil macrofauna. Vegetation-infiltration relationships are starting to be incorporated into hydrological models of arid ecosystems to predict rainfall-runoff partitioning, soil moisture distribution, vegetation dynamics and geomorphology of drylands [*Ludwig et al.*, 1999; *Couteron and Lejeune*, 2001; *Mauchamp et al.*, 2001; *Ursino*, 2005; *Zeng et al.*, 2005; *Bracken and Croke*, 2007; *Mayor et al.*, 2008]. Unlike stomatal conductance, infiltration capacity is not under the direct control of plants on short timescales. However, water can be the limiting resource for plant growth and consequently reproduction, and infiltration into the soil is unquestionably a key process that replenishes the root-zone soil moisture. Regardless of climate or soil type, many plant systems have a marginal safety factor when the minimum observed leaf pressure is compared with pressures needed to induce cavitation in the plant hydraulic system [*Sperry*, 2000]. That is, the hydraulic apparatus of the soil-plant system appears to function near the "edge." On long timescales, it is therefore plausible that plants have evolved strategies that enhance infiltration of water. It is logical to ask whether vegetation-

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Table 1. Species, Soil, and Meteorological Properties of the Duke Forest Infiltration Locations

	Hardwood[a]	Pine[b]	Grass[c]
Mean annual rainfall	1145 mm	1145 mm	1145 mm
Mean annual pan evaporation	1076 mm	1076 mm	1076 mm
Mean annual temperature	15.5° C	15.5° C	15.5° C
Soil series	Iredell (sandy clay loams)	Iredell (sandy clay loams)	Iredell (sandy clay loams)
Dominant species	*Quercus* (oak) and *Carya* (hickory) sp	*Pinus taeda*	*Festuca arundinacea*
Other species	*P. taeda* and *Juniperus virginiana*	diverse understorey	Forbs, other grasses
Canopy height	30 m	19 m	0–1.5 m, harvested annually

[a]Data from *Pataki and Oren* [2003], *Palmroth et al.* [2005], and *Stoy et al.* [2005].
[b]Data from *Oren et al.* [2001] and *Stoy et al.* [2006].
[c]Data from *Novick et al.* [2004].

infiltration relationships represent the cumulative effects of plant strategies that affect water availability in the root zone. Before this question can be effectively explored, several key uncertainties regarding vegetation-infiltration feedbacks must be addressed, specifically: (1) Does vegetation modify infiltration capacity at the soil surface in mesic and hydric climates, and if so, what processes contribute to this modification? (2) Based on available data, is there a canonical relationship that describes the interaction between vegetation indices and infiltration rates (in arid and humid climates)? (3) How does this relationship change across climates?

[3] These questions are important in the predictive modeling of runoff-infiltration partitioning and water balance as well as in addressing the question of plant strategy. The first question explores the generality of the postulated vegetation-infiltration feedback, which has not been established either in humid climates, nor generalized between multiple arid sites. It is unclear if and how vegetation alters infiltration capacity in wetter climates. Given the relative scarcity of vegetation and infiltration studies in these climates, new field results are needed that can delineate the role of vegetation when water is not necessarily limiting.

[4] The second question asks if it is reasonable to express infiltration rates as a function of vegetation biomass or cover. Such an expression, if identified, is not intended to negate the complexity of the feedbacks between vegetation and soil that result in a vegetation-infiltration relationship. Instead, it parameterizes the cumulative effect of these feedbacks, allowing general and large scale predictions to be made without requiring detailed site specific parameters. The nature of the nonlinearity of such a relationship is also important, and determines whether the relationship saturates or generates threshold-type responses with respect to vegetation cover. The third question relates to the strength of the relationship and its sensitivity to climatic drivers. Note that there is no expectation that infiltration capacity itself would respond to climate, but only the nature of the relationship between infiltration capacity and local vegetation.

[5] This work addresses these questions in two different ways. Firstly, infiltration capacity was measured in a humid field site in Duke Forest, North Carolina, where a pine plantation, a hardwood forest and a grass field are all colocated on the same soil series and experience the same climatic regime. Secondly the results from this field study were combined with a meta-analysis of studies measuring infiltration capacity and vegetation biomass. The meta-analysis gathered information from 21 studies spanning 32 different locations, 32 different soil types spanning the full range of texture classes, and 48 vegetation communities

across North and South America, Europe, Africa, Asia and Australia and ranging from hyperarid to tropical climates.

[6] To allow meaningful comparison between sites, aboveground biomass density (i.e., mass biomass per area of ground) was adopted as the independent variable. Unlike other measures such as percentage vegetation cover, biomass density does not saturate as climates become wetter and canopies close. Aboveground biomass is also likely to be correlated to important latent variables such as belowground biomass [*Clark et al.*, 1986; *Naidu et al.*, 1998] and leaf biomass [*McCarthy and Enquist*, 2007] that are expected to affect the vegetation-infiltration relationship but are not commonly measured in studies of infiltration.

[7] The three questions guiding this research may have different answers depending on the scale at which they are considered. We distinguish between biomass-infiltration relationships that arise within a single vegetation/ecosystem type ("within site variation") and those arising between vegetation/ecosystem types ("between site variation"). The former affects hillslope-scale processes such as runoff generation [*Bergkamp*, 1998; *Fiedler et al.*, 2002; *Ludwig et al.*, 2005; *Puigdefabregas*, 2005], while the latter is important for large-scale hydrological modeling over different land uses [*Kirkby et al.*, 2002; *Singh and Woolhiser*, 2002]. Accordingly, biomass-infiltration trends are assessed both within and between sites.

2. Methods and Materials

[8] The two components of the study, namely the field research and the meta-analysis are addressed separately.

2.1. Field Study

2.1.1. Site Description

[9] The study ecosystems are colocated in the Blackwood Division of the Duke Forest near Durham, NC (351980°N, 79180°W, 163 m asl). The study sites consisted of plots in three vegetation types: a grass field, a pine plantation and an 80–100 years old hardwood site. Details of the soil series, climate and species found in the study sites are provided in Table 1. The soil profile of all ecosystems is dominated by a clay pan at a depth of ca. 30–50 cm, which largely confines root growth to the surface soils [*Stoy et al.*, 2008]. Within each vegetation type three 20 × 20 m plots were subdivided into 2 × 2 m subplots. For each large plot, four subplots were selected at random to perform infiltration measurements, giving a total of 36 infiltration sites, 12 for each vegetation type. Each infiltration measurement required an undisturbed site 20 cm in diameter. An optimal site for

infiltration measurements was selected within each subplot, avoiding steep slopes, impermeable surfaces (i.e., rocks) and large trees.

2.1.2. Infiltration Measurements

[10] At each site, an infiltration measurement was made using a 20 cm diameter tension disk infiltrometer (Soil Measurement Systems, Arizona). Tensions were manually set using a Mariotte bottle at −8, −4, −1 and 1 cm. The infiltration rate was measured by monitoring the water level changes in the infiltrometer reservoir. The sites were prepared by placing a 20 cm diameter ring on the ground and trimming all litter and standing vegetation within the ring. Trimmed litter was removed and stored for determination of biomass. Care was taken to leave the soil surface intact during this removal. Where a thick O horizon was present (in the pine plantation), organic mulch was removed until the surface of the mineral soil was exposed. A thin layer of contact sand (Pavestone "all purpose") was used to create a level soil surface, and dampened with water. The infiltrometer was leveled against the sand pad prior to commencing the infiltration measurements. These measurements were made starting from the highest tension (−8 cm). Infiltration ran for a minimum of 30 min. If a steady state rate had not been reached at this time, infiltration continued until a near steady state was reached (typically 45 min).

2.1.3. Soil Coring

[11] Following the infiltration measurements, the contact sand was removed and four 5 cm diameter, 30 cm deep soil cores were taken from within the 20 cm diameter infiltration ring. The cores were separated into three components by depth: 0–5 cm, 5–15 cm, and 15–30 cm. Two of the four cores were bulked for estimating root density, and two were bulked for laboratory analysis. Rocky subsoils prevented a complete sample set from being obtained at every site. Within each vegetation type one infiltration site was trenched, rather than cored, and intact soil samples taken for further analysis (reported elsewhere).

2.1.4. Saturated Hydraulic Conductivity Estimation

[12] Wooding's solution for three dimensional infiltration was used to infer the saturated hydraulic conductivity of the soil [Wooding, 1968; Smettem and Smith, 2002]. Firstly, a curve was fitted to the measurements of infiltration rate to estimate the steady state infiltration value. Wooding's solution was applied to a pair of steady state infiltration values measured at two different tensions, which allowed an estimate of Gardner's parameter α (arising from a simplified exponential model of the unsaturated conductivity given as $K = K_{sat} \exp{(\alpha h)}$), where h is the tension. The saturated hydraulic conductivity we report is based on the estimates at the two lowest tensions, namely −1 and +1 cm. The formulation is given by:

$$K_{sat} = \frac{Q}{\pi r^2 \exp[\alpha h]\left(1 + \frac{4}{\pi r \alpha}\right)}, \qquad (1)$$

and

$$\alpha = \frac{\ln(Q(h_1)/Q(h_2))}{h_1 - h_2}, \qquad (2)$$

where Q is the measured steady state flow rate into the soil, h is the tension and r is the radius of the infiltrometer plate.

Theoretically, Gardner's parameter (α) should be constant across multiple tensions; however, we found that the estimates of α varied depending on which pairs of tensions were considered. Accordingly, we computed K_{sat} based on piecewise regression between successive data points [Smettem and Smith, 2002].

2.1.5. Macropore Flux Estimation

[13] The capillary equation determines the radii ($r_{\min}$) of conducting soil pores under a given tension based on the tension (h, cm), the contact angle θ (which may be estimated as 0), the density of water ρ (0.998 g/cm^2), the air-solid surface tension σ (0.0073 cm/s^2) and gravity g (0.0981 cm/s^2) [Batchelor, 1967] given as:

$$r_{\min} = -\frac{2\sigma \cos\theta}{\rho g h} \approx \frac{-0.15}{h}, \qquad (3)$$

for h in cm. The estimates of hydraulic conductivity obtained at different tensions increase as the tension applied approaches zero. If this increase in flow is attributed to the activation of macropores with radii too large to have been conducting under the previous (higher) tension, then the change in K_{sat} may be used as an estimate of the conductivity of macropores of a given radius "activated" at each reduction in tension [Watson and Luxmoore, 1986; Buttle and McDonald, 2000; Holden, 2009]. The additional flow arising due to the activation of these macropores is referred to as the "macropore flux," which is reported as a percentage of K_{sat} estimated at zero tension.

2.1.6. Hydrophobicity Estimation

[14] Infiltration measurements suggested that soils in the pine plantation were hydrophobic. To assess hydrophobicity, drop penetration tests were conducted in the field and on subsamples of oven dried soil. Drop penetration tests are conducted by placing a drop of deionized water on the soil surface and measuring the time interval in which it remains beaded on the soil surface. Penetration times of more than 1 s were taken as indicative of some degree of hydrophobicity (see Dekker et al. [1998], who used a threshold of 5 s). Three drop penetration tests were conducted per soil sample in the lab. Field drop penetration tests were undertaken in the pines following removal of the O horizon.

2.1.7. Root Measurements

[15] Root mass within the soil cores was estimated by washing each core in a 2 m water column through which compressed air was blown. Washed cores were decanted into 0.5 mm sieves and the roots removed with tweezers. Roots were picked out until at least 95% of the root mass was removed from the sample. Roots were washed clean of all soil particles, wrapped in absorbent paper and oven dried at 70°C for 48 h. Roots were weighed and the mass of all fragments greater than 2 mm diameter (coarse roots) recorded separately from the mass of smaller fractions (fine roots).

2.1.8. Laboratory Measurements

[16] Several standard soil analyses were performed in the laboratory. Bulk density measurements were made based on oven-dried weights of the bulked soil samples and the known volume of the soil cores. Subsamples of soil were tested for total carbon and nitrogen. The subsamples were homogenized by pulverizing in a shatterbox (Spex Inc., Edison, NJ) and analyzed by dry combustion on a Flash EA1112 elemental analyzer (ThermQuest, Rodano, Italy).

Sand, silt, and clay fractions of the sampled soils were determined gravimetrically by the pipette method [*Gee and Or*, 2002]. Replicate samples allowed quantification of the error at approximately 2%.

2.1.9. Biomass and Litter Measurements

[17] The litter removed from each site prior to the infiltration measurements was bagged and dried at 70°C for 48 h before being weighed. Aboveground biomass estimates in the forests were conducted by measuring the diameter at breast height (*dbh*) of all trees with *dbh* > 1 cm located within a 3 m radius of the infiltration site. Allometric equations (*Naidu et al.* [1998] for pines and *Clark et al.* [1986] for hardwoods) were used to estimate the mass of these trees, allowing an estimate of the standing biomass within a 3 m radius of the infiltration site and thus an estimate of local aboveground biomass density. Within the grass sites, live and dead grasses were trimmed together and a single estimate of biomass made.

2.1.10. Data Analysis

[18] Within each vegetation type multiple stepwise regression was used to obtain the best fit between covariates and infiltration rates measured. Infiltration rates were log transformed prior to this analysis. When considering goodness of fit, we report the unbiased coefficient of determination (i.e., "adjusted r^2" value), which allows meaningful comparisons between models with 1 or 2 predictive variables (unlike a raw r^2, this parameter may adopt negative values). The adjusted r^2 is computed using the residual degrees of freedom ($v = n - m$), where n is the number of data points and m is the number of total fitted coefficients. The adjusted r^2 is then computed as $1 - r^2 \times (n - 1)/(v)$ where r^2 is the standard coefficient of determination. The adjusted r^2 only increases if additional parameters increase the predictive capacity of a model relative to a single parameter model, and as such compensates against spurious overparameterization [*Wooldridge*, 2009].

[19] Between sites, a nonparametric analysis of variance (one way Kruskal-Wallis test [*Gibbons*, 1985; *Hollander and Wolfe*, 1999]) was used to determine whether significant differences in infiltration and other explanatory covariates were in place.

2.2. Meta-Analysis

[20] The meta-analysis consisted of data gathering, standardization and analysis.

2.2.1. Data Gathering

[21] A literature survey was conducted to assemble a database of colocated measurements of infiltration capacity and biomass. Studies were chosen to meet the following criteria:

[22] 1. Studies reported direct measurements of biomass, or sufficient information to allow biomass estimates to be made (e.g., through allometry of the dominant species).

[23] 2. Studies reported sufficient information to derive a robust estimate of infiltration capacity or saturated hydraulic conductivity. Studies that reported cumulative infiltration, sorptivity or a runoff coefficient, rather than steady state runoff or infiltration rates, were excluded.

[24] 3. Studies where the effect of vegetation could not be separated from disturbance were excluded. The majority of infiltration studies in mesic climates have been undertaken in the context of agricultural and tillage research, and con-

sequently were excluded from the meta-analysis. Due to the paucity of data in mesic sites, we included data from three tropical agroforestry sites.

[25] After these criteria were applied, 21 studies were retained for analysis. Combined, these studies yielded 261 infiltration and biomass measurements. These data are summarized in Data Set S2 (available as auxiliary material), which also details the specific references used to arrive at biomass estimates, and where applicable (see below) the sources used to obtain climatic and soil properties, if these were not explicitly reported in the original studies.[1]

2.2.2. Data Standardization

[26] Unsurprisingly, there was considerable variety in data gathering methods, the nature of the data reported and the format of reporting across the 21 studies reviewed. Data were standardized with the aim of obtaining an estimate of infiltration capacity (or equivalently the saturated hydraulic conductivity of the undisturbed soil surface) in mm/h; an estimate of aboveground biomass in g/m^2; average annual precipitation and pan evaporation; and soil textural properties in terms of the sand, silt and clay fractions. Infiltration and biomass estimates were of primary importance, and some studies with incomplete soil or meteorological data were retained for analysis.

2.2.3. Biomass Estimates

[27] Standing biomass was the most problematic parameter to standardize, as it is not widely reported. Biomass estimates were available directly for 13 of the 21 studies [*Branson et al.*, 1962; *Johnston*, 1962; *Rhoades et al.*, 1964; *Kelly and Walker*, 1976; *Blackburn et al.*, 1992; *Hulugalle and Ndi*, 1993; *Nicolau et al.*, 1996; *Spaeth et al.*, 1996; *Hester et al.*, 1997; *Mwendera and Saleem*, 1997; *Chirwa et al.*, 2003; *Boone Kauffman et al.*, 2004; *Bowen et al.*, 2005]. Aboveground biomass was computed allometrically for the Duke Forest sites as reported in section 2.1.9. For the remaining studies, biomass was estimated as follows:

[28] 1. Biomass was estimated by regression between a subset of site biomass estimates reported in the study and the reported percentage vegetation cover (for example, in shrubland in Burkina Faso [*Rietkerk et al.*, 2000] and woodland in Australia [*Loch*, 2000]).

[29] 2. Biomass was estimated by estimates of biomass density in similar vegetation types at the same or similar locations (for example, the estimates of forest biomass in Ecuador, the Southern Appalachians and Puerto Rico [*Harden and Scruggs*, 2003]).

[30] 3. Biomass was estimated by application of allometric equations to site specific parameters such as tree density, age and height (for example, in a teak plantation in Sri Lanka [*Mapa*, 1995], and the Khalenberg forest in Germany [*Buczko et al.*, 2006]).

[31] 4. Biomass was estimated by application of allometric equations to dominant species, combined with site-specific measures such as percentage canopy cover, vegetation volume or height (for example, in the North American deserts allometry for *Larrea tridentata*, *Prosopis glandulosa* and *Bouteloua eriopoda* was used to estimate biomass based on percentage cover and other measures of the geometry of the vegetation distribution [*Castellano and Valone*, 2007;

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[1]Auxiliary materials are available at ftp://ftp.agu.org/apend/jg/2009jg001134.

Bedford and Small, 2008], and in the degraded sites in the Andes, biomass density estimates for *Cynodon dactylon, Holcus latanus, Vulpia myuros, Trifolium* sp. and *Pennisetum clandestinum* were made based on available literature, averaged to obtain an estimate of biomass density for fully vegetated sites, and then the percentage vegetation cover at individual sites was used to estimate biomass as a proportion of the estimated biomass density [*Molina et al.*, 2007]).

2.2.4. Infiltration Capacity Estimates

[32] There are many different methods to measure infiltration capacity, which agree with each other to differing extents. Unfortunately, there is no consensus position in the literature for normalizing these different measurement techniques. This is not surprising considering that tension infiltrometers, for example, have been found to underestimate infiltration by comparison to ring or rainfall simulators [*Reynolds et al.*, 2000], to overestimate infiltration compared to ring infiltrometers while being comparable to rainfall simulators [*Gomez et al.*, 2001], to provide a better estimate of infiltration capacity than (underestimating) ring or rainfall simulators [*Pott and De Maria*, 2003], or to provide comparable estimates [*Bagarello et al.*, 2000]. Site-specific details are often the determinants of which method is most applicable [*Smettem and Smith*, 2002]. Given this uncertainty, no correction to measured infiltration rates has been applied on the basis of methodology. Where multiple estimates of the infiltration rate were made at a site, we report those estimates made by ring infiltrometers or rainfall simulators. This choice simply reflects that the preponderance of available data was gathered using these methods and is an attempt to limit variability in the data set arising from infiltrometer type.

2.2.5. Soil Texture Estimates

[33] When no specific soil textural data were available, the average sand, silt and clay fractions were estimated based on reported site soil type or soil series. For four sites, soil data were not available.

2.2.6. Climatic Data

[34] Annual rainfall estimates were reported for almost all of the study sites. Pan evaporation, and where necessary, annual rainfall, were taken from the nearest weather station providing pan evaporation rates. In some cases, particularly for African, Asian and South American sites, estimates of pan evaporation were made on the basis of other studies at nearby sites. For two studies, pan evaporation data was not available. In one study, excellent biomass and infiltration data were available, but site locations were reported only to the level of the state (within the United States) in which the sites were located. For this study, meteorological data are omitted. These sites, located in U.S. rangelands, were grouped with the dry sites.

2.2.7. Data Analysis

[35] Prior to analysis, the data were divided into mesic-hydric sites and arid sites, based on the ratio of annual evaporative demand (estimated as pan evaporation) to annual precipitation: E_p/P. The formulation E_p/P is comparable to the dryness index used in the Budyko Curve [*Budyko*, 1974], and other climatic classification schemes. Because of the somewhat arbitrary nature of the classification, we did not correct the pan evaporation estimates to estimates of potential evapotranspiration (PET). Sites where $E_p/P > 1$ were treated as arid, and were analyzed separately from mesic-hydric sites where $E_p/P < 1$.

[36] We used linear regression to assess the following relationships within and between sites: log biomass and log infiltration, log biomass and soil texture, and log infiltration and soil texture. For several sites, only a single estimate of biomass or of soil texture fraction was available for multiple infiltration rates. To account for this, we took the geometric mean of the measured infiltration capacities to obtain a single representative data point for a given biomass or soil texture estimate, prior to log transformation.

[37] We reevaluated the biomass-infiltration relationship after controlling for the effect of soil type. Two different controls were adopted: a statistical control in which the effect of soil type was accounted for via linear regression; and a mechanistic control in which the effect of soil type was accounted for by normalization against empirical hydraulic conductivity properties documented by *Clapp and Hornberger* [1978].

[38] Within-site variability was assessed using all data points to determine statistical agreement between log biomass and log infiltration capacity within a given site. Finally, the strength of the within-site biomass infiltration relationship, as quantified by the slope of the log-log regression, was assessed for those sites where: (1) there were at least three data points available (to avoid spurious regressions between two points), (2) regression relationships were significant at an 80% confidence level (this relatively low threshold for assessing significance was chosen to reflect the large degree of variability associated with most of the data analyzed), and (3) there was an estimate of E_p/P (i.e., reliable climatic data).

[39] Variation in the slope of the biomass-infiltration regression was examined as a function of E_p/P as a surrogate for climate type.

3. Results

[40] This section will again present results separately for the field and meta-analytical components of this work. The links between the results and the three driving questions that motivated this study are addressed in section 4.

3.1. Field Study

[41] The data gathered from the Duke Forest field study and subsequent laboratory analyses are presented in Data Set S1.

3.1.1. Infiltration Rates Between Sites

[42] Mean infiltration capacity (f) was ≈20% greater in the hardwood forest, where the mean infiltration rate was 14.4(15.15) mm/h, standard deviation is shown in brackets; than in the grass field (11.77(11.6) mm/h). The pine plantation had substantially lower infiltration rates of 5.3(4.9) mm/h. These differences were not significant at the 95% confidence level as assessed by nonparametric Kruskal-Wallis analysis of variance (see Figure 1).

[43] The low infiltration rates observed in the pine plantation were attributed to hydrophobicity in the soil there. Drop penetration tests conducted on samples of surface soils from the pine plantation found that 7 of 10 sampled soils had a drop penetration time exceeding 1 s and three of the samples had drop penetration times exceeding 1 min. In one
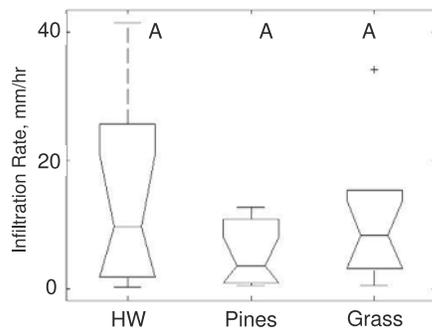
Figure 1. Biomass-infiltration relationships within (solid lines) and between (dashed line) mesic-hydric sites (the slopes shown are those from a multiple regression between percent sand, biomass, and infiltration). Site names, slope values, correlation coefficients, and p values are shown in Table 3.

sample, drop penetration time repeatedly exceeded 5 min. Field drop penetration tests indicated that the degree of hydrophobicity varied at the centimeter scale. Hydrophobicity is known to confound interpretation of tension infiltrometer readings [*Clothier*, 2001], so the pine infiltration data were excluded from the meta-analysis. No hydrophobicity was identified in the hardwood or grass sites. Hydrophobicity of soils is widely reported for evergreen species including pines. Water repellency in the soil is associated with the presence of hydrophobic organic compounds such as cuticular waxes in pine needles[*Doerr et al.*, 2000]. The accumulation of these compounds in the soil is associated with relatively low rates of decomposition, leading to deep litter layers as observed in the Duke Forest pines, and with low-intensity fires, leading to the accumulation of hydrophobicity in the organic and mineral surface soils, respectively. Although an ecological role for hydrophobicity as analogous to allelopathy has been proposed [*Ens et al.*, 2009], it remains unclear whether hydrophobicity should be considered primarily as a byproduct of plant-soil-environment interactions, or whether it confers competitive advantage and may as such be considered to be a plant strategy. These complex interactions are beyond the scope of this study and will not be further addressed.

3.1.2. Infiltration Capacity Within Sites

[44] Infiltration trends in the hardwood site were explained by significant (p = 0.04) negative correlations to the soil clay content and the coarse root mass (CRM), which determined 60% of the variance in log transformed infiltration rates. The relevant regression equation was:

$$Log(f) = -47.5(\%clay) - 1.46(CRM) + 8.03 \qquad (4)$$

[45] No significant relationships to the measured covariates were identified in the pine plantation, presumably due to the hydrophobicity. An infiltration-soil relationship was identified for the grass site, although it was weaker than the relationship for the hardwood site and not significant (r^2 = 0.21, p = 0.18):

$$Log(f) = -43.4(\%clay) + 7.77. \qquad (5)$$

3.1.3. Factors Varying Between Sites

[46] With the exception of the total root mass and the soil nitrogen content, significant differences were found between all covariates at all sites (Table 2). The pine site differed from the grass and hardwood sites in having higher carbon and sand content, more litter mass, and lower bulk densities. Lower macropore fluxes arose on the pine site than in the other vegetation types. The total macropore flux was similar between the grass and hardwood sites, but macropore flow represented a greater proportion of the total flux on the grass site than in the hardwoods. As expected, the grass and hardwood sites differed significantly in terms of biomass and root properties, with significantly more root biomass occurring in the form of coarse roots in the hardwood site than the grass site. The soil properties varied significantly between all sites, but all soils could be classified as loams.

3.2. Meta-Analysis

3.2.1. Soil Type–Biomass Relationship

[47] The various soil fractions (% sand, silt and clay) were regressed against the log transformed biomass values. In the mesic-hydric sites (where $E_p/P < 1$), none of the soil fractions were related to biomass (for each fraction, adjusted $r^2 < 0$, p > 0.05). In the arid sites, there were no significant relationships between biomass and soil type (p > 0.05 for all fractions).

3.2.2. Soil Type–Infiltration Relationship

[48] Regression analysis was performed between the sand/silt/clay fractions and the log transformed infiltration values. In the hydric sites, a relationship was found between the clay fraction and the log of infiltration (adjusted r^2 = 0.63 and p < 0.05, respectively), but there were no significant relationships with the sand and silt fractions (adjusted r^2 = 0.12, 0.02, respectively, and p > 0.05). In the xeric sites, no significant relationship could be discerned between soil type and infiltration measurements (p > 0.05 for all soil fractions).
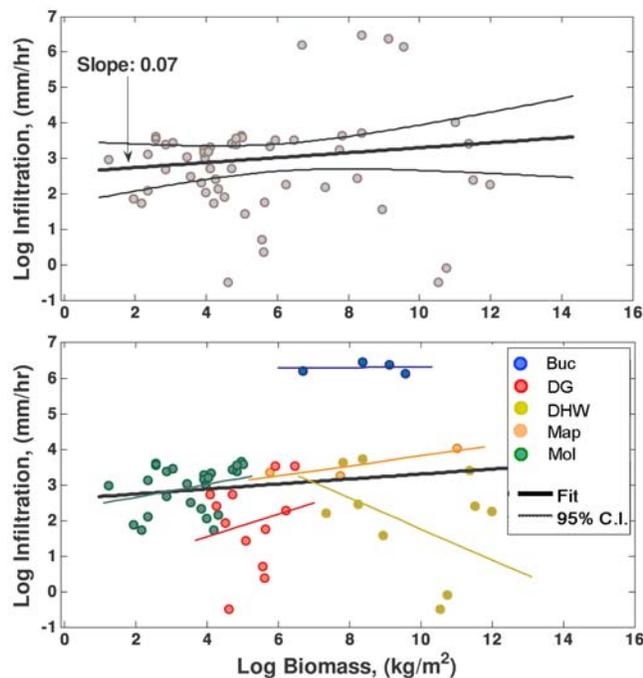
3.2.3. Biomass-Infiltration Relationship

3.2.3.1. Mesic-Hydric Sites: Between Site Variation

[49] Biomass was not related to infiltration capacity on hydric sites (adjusted $r^2 < 0$ for the log biomass–log infiltration regression). Nor did biomass explain the variance in infiltration capacity after controlling for soil type via a multiple regression. This result was verified using the empirical values of K_{sat} published by *Clapp and Hornberger* [1978, hereafter CH] to "normalize" the measured values of Ksat

Table 2. Average Value of Covariates Between Sites[a]

Factor	Hardwood Mean	Pines Mean	Grass Mean
Biomass	56.8025 (a)	17.0808 (a)	0.2425
Litter	0.2330 (a)	0.4636	0.2416 (a)
Bulk density	0.7997 (a)	0.6217	0.7548 (a)
Surface nitrogen	0.21% (a)	0.19% (a)	0.18% (a)
Surface carbon	3.24%	4.88%	2.49%
Macropore flux (% K_{sat})	10% (a)	15% (a, b)	15% (b)
Fine roots	0.8694 (a)	0.8137 (a)	1.8134
Coarse roots	0.6188 (a)	0.4364 (a)	0.0185
Total roots	1.4882 (a)	1.2501 (a)	1.8319 (a)
Percent sand	0.4500 (a)	0.5356	0.4840 (a)
Percent silt	0.4318	0.3356 (a)	0.3800 (a)
Percent clay	0.1182 (a)	0.1300 (a, b)	0.1360 (b)

[a]Letters in parentheses indicate that there is no significant difference between measures.

Figure 2. Biomass-infiltration relationships (top) between and (bottom) within mesic-hydric sites (the slopes shown are those from a multiple regression between percent sand, biomass, and infiltration). Site names, slope values, correlation coefficients, and p values are shown in Table 3.

based on soil type. Log biomass did not explain the variance in the transformed variable $\log[K_{sat}(\text{measured})/K_{sat}(\text{CH})]$.

3.2.3.2. Mesic-Hydric Sites: Within Site Variation

[50] With the exception of a single agroforestry study in Sri Lanka ("Map," see Figure 2), the within-site biomass-infiltration dependence was also weak. Controlling for the effects of soil improved the relationship between biomass and infiltration in some sites (Duke Forest sites and Kahlenberg Forest, Germany), but worsened it in others (Andes highland sites and the Sri Lankan agroforestry site). No clear trends in infiltration capacity with respect to variation in biomass could be ascertained within or between the mesic-hydric sites (see Figure 2 and Table 3).

3.2.3.3. Xeric Sites: Between Site Variation

[51] Biomass was significantly related to infiltration capacity without controlling for soil on arid sites with $r^2 = 0.35$ and $p \approx 0.00$ (see Figure 3 and Table 3). Including soil type caused a large increase in r^2, which appeared to be largely due to the averaging procedure, whereby single, averaged biomass and infiltration values were used for each soil type measurement. Other averaging procedures (including all biomass-infiltration measurements, or averaging on a site, rather than soil-type basis) while controlling for soil type resulted in r^2 values of ≈ 0.3. Controlling for soil type via the CH values resulted in an r^2 of ≈ 0.3 for the transformed variable $\log[K_{sat}(\text{measured})/K_{sat}(\text{CH})]$.

3.2.3.4. Xeric Sites: Within Site Variation

[52] Within individual arid sites, the relationship between biomass and infiltration varied from strong (e.g., in the Australian woodland site measured by Loch, $r^2 = 0.86$, $p < 0.01$, ponderosa pine stands measured by Hester, $r^2 = 0.88$, $p < 0.1$, and Arizona desert plots measured by Bowen $r^2 =$

0.81, $p < 0.1$); to moderate (e.g., in Burkina Faso shrublands measured by Rietkerk, $r^2 = 0.2$, $p < 0.05$ in Spanish badlands measured by Nicolau $r^2 = 0.34$, $p < 0.05$), or very weak (see Figure 3 and Table 3). Several studies reporting only 1 or 2 data points were included in the overall between-site regressions but are not of value for understanding relationships within sites.

3.2.4. Trends With Climate

[53] There were six sites within which the regression relationship:

$$\log(f) = a\log(B) + b, \qquad (6)$$

was significant at an 80% confidence level. Amongst these sites, there was an increasing trend in the slope a (i.e., the exponent of the power law with E_p/P). When a linear regression was taken between E_p/P and a, climate explained some 58% of the variance in the values, with the slope of the $E_p/P - a$ relationship being 0.15. Because the significance criterion resulted in relatively few sites being included in this analysis, we broadened the analysis to include all sites where the regression explained more than 5% of the variance in the data set. This lead to eight sites being included, an r^2 value of 0.65, and again a slope of 0.15 (see Figure 4).

4. Discussion

[54] Three goals motivated this study: to examine whether the known trends in vegetation biomass and infiltration extended outside of arid climates; to determine a mathematical relationship between infiltration and biomass; and to evaluate the climatic sensitivity of that relationship and the processes contributing to it.

Table 3. Regression Parameters for All Sites With >1 Data Point[a]

Site	Label	Slope	r^2	p Value
Within Xeric Sites				
BS	Bedford and Small	−0.4753	0.0072	0.8730
Bla	Blackburn	0.2988	1 (only two sites)	NA
Bow	Bowen	1.3782	0.8180	0.0956
BK	Boone Kauffman	−3.5011	1 (only two sites)	NA
Bra	Branson	1.0094	1 (only two sites)	NA
Cas	Castellano	−0.0780	0.0125	0.8328
Chi	Chirwa	0.0054	0	0.9780
Hes	Hester	0.1156	0.8836	0.0600
KW	Kelly and Walker	−0.2551	0.0318	0.6463
Loc	Loch	0.5440	0.8697	0.0001
Mwe	Mwendera	−5.8608	1 (only two sites)	NA
Nic	Nicolau	0.5045	0.3467	0.0164
Rk	Rietkerk	0.1773	0.2017	0.0213
Spa	Spaeth	0.0712	0.0098	0.6526
Between xeric sites		0.4293	0.3552	0.00
Within Mesic-Hydric Sites				
Buc	Buczko	0.0099	0.0067	0.9179
DG	Duke Grass	0.2271	0.0249	0.6633
DHW	Duke Hardwood	−0.2530	0.0905	0.3982
Map	Mapa	0.1417	0.77	0.3176
Mol	Molina	0.1826	0.09	0.1418
Between mesic-hydric sites[b]		0.1315	0.65	0.0282

[a]Regression is for log (infiltration) against log biomass, excluding soil type.
[b]Multiple regression values.
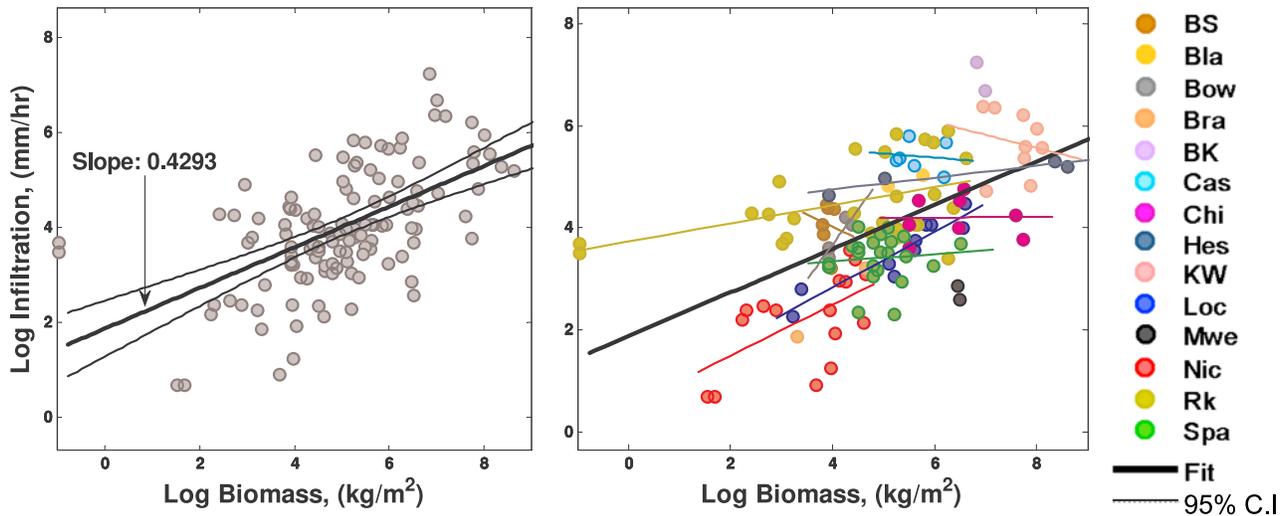
Figure 3. Biomass-infiltration relationships (left) between and (right) within xeric sites (the slopes shown are those from a regression between biomass and infiltration). Site names, slope values, and correlation coefficients are given in Table 3.

4.1. Biomass-Infiltration Trends in Mesic-Hydric Climates

[55] Biomass-infiltration trends did not appear to occur within sites in mesic-hydric climates, in contrast to the existence of strong and significant within-site trends in arid climates (see Table 3). Nor did biomass values correlate to infiltration rates between sites. Instead, soil type was the dominant factor in determining infiltration rates in mesic-
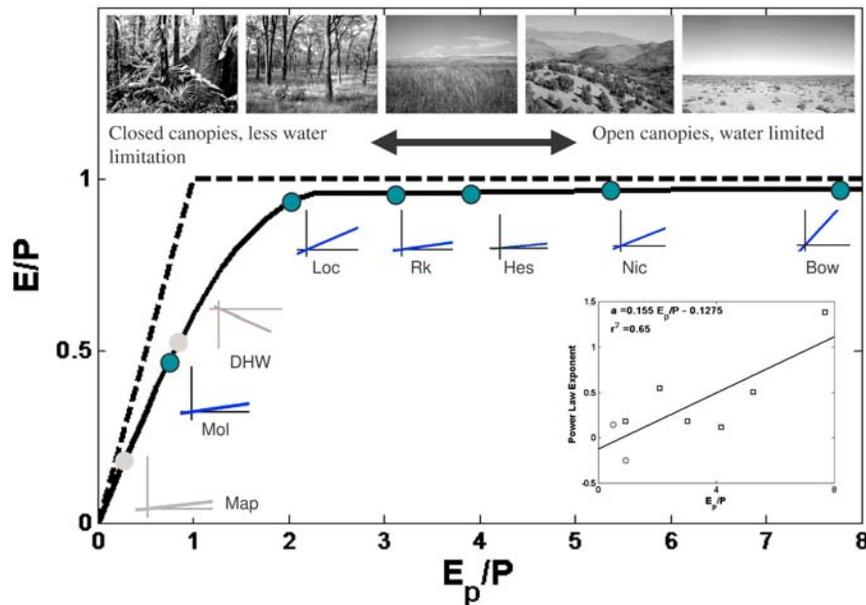
Figure 4. Hypothesized relationships between the power law exponent characterizing the biomass-infiltration relationship, and the dryness index. The relationship is suggestive of ordering on the Budyko Curve. The linear fit between the dryness index and the power law exponent for all sites is shown as an inset (within site biomass-infiltration relationship adjusted $r^2 > 0.05$; sites where $p > 0.2$ are shown in gray). Site name abbreviations are defined in Table 3. Images sourced from T. Schoch (Australia 2005, available at http://www.retas.de/thomas/travel/australia2005/index.html, 2005), B. Kell (Oglala national grassland, available at http://commons.wikimedia.org/wiki/file:oglala_national_grassland.jpg, 2005), H. Hillewaert (Cathedral mopane forest, available at http://commons.wikimedia.org/wiki/file:cathedral_mopane_forest_south_luangwa_valley.jpg, 2005), Temsabuita (Simpson Desert Australia, available at http://commons.wikimedia.org/wiki/file:desert_de_simpson.jpg, 2007), and Bureau of Land Management (Cedar mountain wilderness, available at http://www.blm.gov/ut/st/en/fo/salt_lake/blm_special_areas/cedar_mountains_wilderness/photo_gallery.html, 2008).
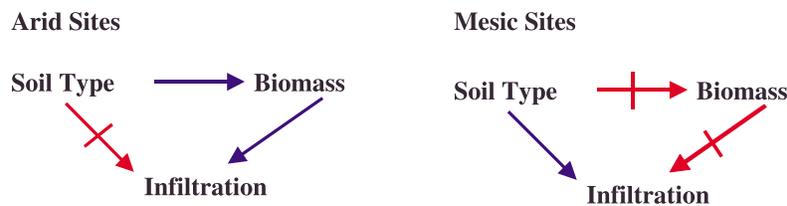
Figure 5. Hypothesized causal relationships between soil, biomass, and infiltration in arid and mesic sites. The former is consistent with the effect of surface processes decoupling infiltration rates (to a large extent) from the underlying soil type. The latter is consistent with soil type being the primary determinant of infiltration capacity.

hydric sites. Thus, we conclude that the infiltration-biomass relationship does not generally persist in wetter climates. The processes contributing to the biomass-infiltration feedback are presumed to either saturate under humid conditions or the driver for plants to develop features that enhance infiltration rates is too weak to allow for the feedback to be observed. In well watered sites it is likely that light and nutrient limitation are colimiting with water and are thus additional drivers of allocation. Consequently, large shifts in the allocation ratio above and below ground may be observed depending on relative nutrient status [*Oren et al.*, 2001]. The use of the aboveground biomass as an independent variable in humid sites may be problematic if these allocation ratios are highly variable. Further measurements to relate infiltration capacity to root distributions and density in mesic-wet climates would provide insight not only into the relative effects of changing root biomass and distribution on infiltration properties, but also on how these links feed back to water or nutrient limitation and plant allocation strategy.

4.2. Nature and Strength of Biomass-Infiltration Trends

[56] The observed statistical relationships amongst soil, biomass and infiltration in this study support the interpretation that biomass constitutes a primary influence on infiltration capacity in water limited ecosystems. The data contradict a plausible hypothesis that improved soil texture increases infiltration capacity which leads to higher aboveground biomass.Instead, in mesic-hydric climates, biomass was decoupled from the trend in infiltration behavior, and in xeric sites infiltration and soil type were uncorrelated (see Figure 5). Note that the potential links between belowground biomass and infiltration capacity, however, cannot be assessed with the available data, and remain as an area where additional future work is required. In water limited climates power law relationships were relatively successful in describing the biomass-infiltration relationship (see Figures 2 and 3). Power law biomass-infiltration relationships between sites described approximately 35% of the variance in the infiltration values across an aridity gradient. Infiltration capacity is not under the direct physiological control of plants, and therefore the coupling between vegetation and infiltration is unlikely to be "first order" in nature. Thus, finding that biomass explained such a large proportion of variance in infiltration rate over such a broad range of sites is somewhat surprising. Throughout the study the use of aboveground biomass has been motivated in part

by an expected order-of-magnitude relationship between aboveground biomass and root extent. While this may be suitable for discerning between-site variability, there is considerable scope for variation in the shoot:root ratio within individual species or sites [*Pallida et al.*, 2005; *Martre et al.*, 2002; *Gerard et al.*, 1982]. Consequently, belowground biomass might be expected to exert important controls on infiltration behavior, and further data are needed to constrain such relationships.

4.3. Climatic Sensitivity of Biomass-Infiltration Relationship

[57] Two broad trends were observed with changes in climate as measured by the dryness index. The first was that the slope of the log biomass–log infiltration regression declined as climates became wetter. A linear trend emerged in the power exponent of individual sites where biomass-infiltration relationships existed (see Figure 4). The second trend was the influence of soil type on infiltration. Soil type increased in importance from being weakly related to infiltration in arid sites, to explaining some 60% of the variance in infiltration in wet sites. Furthermore, in examining the factors influencing infiltration in one particular location, where the climate and soil type were the same (e.g., the Duke Forest sites), it was evident that soil texture and coarse root mass, but not aboveground biomass, were correlated with infiltration capacity.

5. Conclusions and Future Work

[58] The influence of vegetation on soil properties and soil formation (i.e., pedogenesis) has been studied since the late 1800s when V. D. Dokuchaev introduced the concept of dynamic soils that evolve under the influence of climate and vegetation. Exploring biomass-infiltration trends extends this conceptual framework to emergent properties of the soil-climate-vegetation system. Future work is needed to discriminate the generality of processes that result in the large-scale biomass-infiltration relationships identified in this study. In particular, it remains to be determined whether the trend observed in arid sites is a passive response to increased soil cover, or whether it is strongly influenced by adaptive features and dynamics of vegetation. The strongest "within site" biomass-infiltration trends occurred on sites with patchy vegetation cover, suggestive of a binary presence/absence relationship between infiltration and vegetation cover. Certainly physical and biological processes including the prevention of physical crusts or seals and the

"resource island" effect which concentrates ecological processes near vegetation [*Schlesinger et al.*, 1996] are consistent with such a binary relationship. However, spatially explicit studies of infiltration in the proximity of Australian mulga (*Acacia aneura*) found that infiltration capacity increased with proximity to the mulga trunk, and declined smoothly with distance from the trunk over distances of up to 10 m. The absence of a discontinuity in infiltration capacity at the canopy edge (2–3 m from the trunk) suggests that the modification of infiltration capacity is associated with root properties and not simply surface cover [*Dunkerley*, 2002a, 2002b]. Consequently, further research to elucidate the links between belowground biomass characteristics and infiltration response is needed. Similarly, a study by *Spaeth et al.* [1996] concluded that plant species effects significantly improved prediction of infiltration capacity compared to purely physically based predictions. These observations are suggestive of a complex suite of processes affecting infiltration into the rooting zone. Manipulative experiments that can discriminate between presence/absence effects induced by natural or artificial soil protection, as well as further studies of infiltration processes at a species specific level are needed to resolve this question.

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