4-1-2012

Fertilization Effects on the Ecohydrology of a Southern California Annual Grassland

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[1] Nitrogen limits leaf gas exchange, canopy development, and evapotranspiration in many ecosystems. In dryland ecosystems, it is unclear whether increased anthropogenic nitrogen inputs alter the widely recognized dominance of water and energy constraints on ecohydrology. We use observations from a factorial irrigation and fertilization experiment in a nitrogen-limited southern California annual grassland to explore this hypothesis. Our analysis shows growing season soil moisture and canopy-scale water vapor conductance are equivalent in control and fertilized plots. This consistency arises as fertilization-induced increases in leaf area index (LAI) are offset by reduced leaf area-based stomatal conductance, g_s. We interpret this as evidence of a hydraulic feedback between LAI, plant water status, and g_s, not commonly implemented in evapotranspiration models. These results support the notion that canopy physiology and structure are coordinated in water-limited ecosystems to maintain a transpiration flux tightly controlled by hydraulic constraints in the soil-vegetation-atmosphere pathway. **Citation:** Parolari, A. J., M. L. Goulden, and R. L. Bras (2012), Fertilization effects on the ecohydrology of a southern California annual grassland, *Geophys. Res. Lett.*, *39*, L08405, doi:10.1029/2012GL051411.

1. Introduction

[2] Plant physiological activity links the carbon and nitrogen cycles with the surface water and energy balances [*Schimel et al.*, 1997]. Ecophysiological traits that control evapotranspiration (ET) and photosynthesis vary with the relative supplies of soil water and nitrogen. Therefore, increased exogenous nitrogen supply from either fertilization or deposition may alter interaction between plants and the water balance.

[3] Fertilization induces changes in leaf area index (LAI), stomatal conductance, and the conductivity of leaf, stem, and root tissues. In fertilized *Pinus taeda* stands, increased LAI was compensated by decreased tissue and stomatal

conductances, such that ET and leaf water potential were relatively unchanged [*Ewers et al.*, 2000]. These responses were not observed in irrigated stands, indicating drought exposure as an important determinant of hydraulic capacity. In another study, fertilized savanna trees did not fully adjust hydraulic capacity, resulting in increased ET and decreased leaf water potential [*Bucci et al.*, 2006]. These results demonstrate the ET response to fertilization is mediated by plant hydraulic characteristics that respond to both soil moisture and nitrogen availability, although it is unclear which is the dominant factor.

[4] Dryland ecosystems present a compelling forum in which to study the relative effects of soil moisture and nitrogen on ecohydrology. These systems are characterized by strong interactions between vegetation and hydrology, experience frequent periods of water stress [*Rodriguez-Iturbe et al.*, 2001], and are often co-limited by water and nitrogen [*Hooper and Johnson*, 1999]. We use an ecohydrological framework to explore fertilization effects on interactions between canopy characteristics, ET, and the growing season water balance in a southern California annual grassland. Inferences are made from data collected in a factorial irrigation and nitrogen fertilization experiment, where biomass production responds to the addition of either resource.

2. Background

2.1. Canopy Structure, Physiology, and Transpiration

[5] Ecohydrological dynamics in drylands are the result of strong interaction between transpiration, controlled by vegetation canopies, and soil moisture. This interaction can be understood through a mechanistically simple transpiration model [*Laio et al.*, 2001], similar to that commonly implemented in land surface models (LSMs). The transpiration rate T [mm s^{-1}] is defined as the product of a climate- and vegetation-specific potential transpiration rate T_p [mm s^{-1}] and a linear scaling factor β that accounts for soil water deficit,

$$T(\theta) = T_p \cdot \beta = T_p \cdot \begin{cases} 0 & \theta \leq \theta_w \\ \dfrac{\theta - \theta_w}{\theta^* - \theta_w} & \theta_w < \theta \leq \theta^* \\ 1 & \theta > \theta^* \end{cases} \quad (1)$$

where θ [-] is the volumetric water content averaged over the root zone, θ_w [-] is the permanent wilting point, below which transpiration ceases, and θ^* [-] is the incipient stress point, above which transpiration occurs at the potential rate.

[6] This formulation captures the two most general aspects of plant-water interactions. First, when soil moisture is plentiful, vegetation transpires at a potential rate that is determined by soil hydraulic properties, the hydraulic conductance of the

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root-stem-leaf system, canopy structure, and atmospheric variables governing the demand for water (e.g., wind speed, air temperature, humidity). Second, when subject to hydraulic limitations associated with soil water deficit (i.e., $\theta < \theta^*$), plants reduce stomatal opening (and subsequently T) to maintain leaf water potential and avoid damage due to water stress.

[7] $T(\theta)$ in equation (1) can be expressed in terms of observable canopy characteristics. Net carbon assimilation, transpiration, and stomatal conductance vary with depth in the canopy as light is extinguished by upper canopy layers. We assume the energy available for photosynthesis decreases exponentially with cumulative leaf area index (LAI, L [m^2 leaf m^{-2} ground]) [Monsi and Saeki, 2005] and stomatal conductance is proportional to the local irradiance through the carbon assimilation rate [Oleson et al., 2010]. The total canopy water vapor conductance G_c [mol H$_2$O m^{-2} ground s^{-1}] is then,

$$G_c = \int_0^L g_s^{max} \beta \exp(-kl) dl = g_s^{max} \beta k^{-1}[1 - \exp(-kL)] \quad (2)$$

where g_s^{max} [mol H$_2$O m^{-2} leaf s^{-1}] is the light-saturated leaf-specific stomatal conductance measured at the top-of-canopy and k [m^2 ground m^{-2} leaf] is the canopy light extinction coefficient. Under the diffusion analogy,

$$T = G_c D = g_s k^{-1}[1 - \exp(-kL)]D \quad (3)$$

where D [-] is the vapor pressure deficit and g_s represents the actual stomatal conductance under water-stressed conditions (i.e., the product $g_s^{max} \beta$).

[8] An alternative model also constrains T by the capacity of the soil, roots, and xylem to deliver water to the leaf surface for evaporation,

$$T = g_{srp}[\psi_s(\theta) - \psi_l] = g_s k^{-1}[1 - \exp(-kL)]D \quad (4)$$

where g_{srp} [mol MPa^{-1} s^{-1}] is the soil-root-plant conductance and $\psi_s(\theta)$ and ψ_l [MPa] are the soil and leaf water potentials, respectively. g_{srp} is reduced at low ψ_s and ψ_l [Daly et al., 2004]. Equations (3) and (4) are now used to generate hypotheses of the hydrologic response to fertilization.

2.2. Nitrogen Modulated Vegetation-Water Feedbacks

[9] Plant hydraulic characteristics constrain the supply of water from the soil to the leaf where evaporation occurs. Their cumulative effect is ultimately expressed in the leaf-specific transpiration rate. Thus, the sensitivity of transpiration to nitrogen supply can be described through changes in g_s and LAI.

[10] When the soil water supply is not limiting (i.e., $\beta = 1$), g_s^{max} varies directly with leaf nitrogen content, N_{leaf} [g N m^{-2} leaf]. The majority of N_{leaf} is utilized in the photosynthetic apparatus, such that N_{leaf} controls the photosynthesis rate, which is strongly correlated with g_s^{max} [Lambers et al., 2008]. Therefore, it is anticipated that increased nitrogen availability will lead to increased g_s^{max}, a common assumption in LSMs [Oleson et al., 2010]. An increase in LAI is also anticipated with increased nitrogen availability as a consequence of increased photosynthesis, above-ground primary productivity, and reduced root investment for nitrogen uptake.

[11] From equation (3), it is clear that an increase in either g_s or LAI will increase T for a given D and θ, regardless of whether the plant hydraulic capacity can support this rate.

This implies more rapid soil moisture depletion and earlier arrival of water stress, stomatal closure, and drought-induced tissue loss. We refer to this scenario as the "soil moisture" plant-water feedback mechanism below and anticipate nitrogen fertilization to decrease θ with a corresponding decrease in g_s (i.e., through β).

[12] Equation (4) implies that the plant-water feedback mechanism and T are mediated by the hydraulic capacity of the plant tissues, g_{srp}. If the soil-root-plant pathway is limiting, an increase in either g_s or LAI cannot increase T, generating a so-called "hydraulic" feedback. In this case, we predict T is constrained such that the θ and T dynamics are relatively insensitive to changes in LAI. As a consequence, the predicted decrease in g_s is associated with increased LAI and not decreased θ.

3. Loma Ridge Observations

[13] The Loma Ridge experimental site is located in the Santa Ana foothills in central Orange County, California (33.742°N, 117.704°W). The climate is Mediterranean with cool, wet winters and dry, hot summers. Annual rainfall follows a lognormal distribution with median 281 mm yr^{-1}, of which approximately 90% falls between November and April. The grassland is composed primarily of invasive annual grasses and forbs, whose composition varies with precipitation. In a typical year, this mixture includes *Bromus diandrus*, *Lolium multiflorium*, and *Avena spp.* at approximately 15–20% relative cover each. Forbs and remnants of the historically dominant perennial grass *Nassella pulchra* (<5%) are also present. The local soil is homogeneous and characterized as sandy loam.

[14] Factorial plot experiments at Loma Ridge were established in 2007 to study ecosystem responses to changing climate and increased nitrogen deposition. Twenty-four plots (approx. 6.1 × 8.5 m) are divided into eight replicates of three water input treatments: ambient, ambient minus 40% (dry), and ambient plus 40% (wet). All plots were burned in the October 2007 Santiago wildfire. Rainfall is excluded from dry plots with retractable polyethylene roofs that were closed during approximately half of the rain events (closed <5% of the days during a year). Water draining from the roofs was collected in polyethylene tanks for subsequent application to the wet plots using pressure compensated drip tubing. Excluded events and irrigation rates are chosen to simulate observed patterns in storm frequency and intensity. Each plot is split lengthwise and half of the ground area is fertilized and half remains unfertilized (control). Plots are fertilized with 2 g N m^{-2} immediate-release calcium nitrate (15.5-0-0+ 19% Ca) prior to the growing season and 4 g N m^{-2} 100-day release calcium nitrate during the growing season. Additional details regarding the experimental design and site history are described by *Potts et al.* [2012].

[15] Fertilization effects on the Loma Ridge water balance are investigated through estimates of the variables in equation (3), g_s and L. The data presented were collected during the 2008 growing season (13, 17, and 25 March) and shortly following (10 April) peak LAI. Ambient water input in 2008 was 223 mm, 80% of the median year, and the dry and wet treatments received 133 and 305 mm, respectively. Late season vegetation cover was 100%, composed of 97% annual grasses and forbs. Observations are averaged across the replicates in each treatment (n = 8).
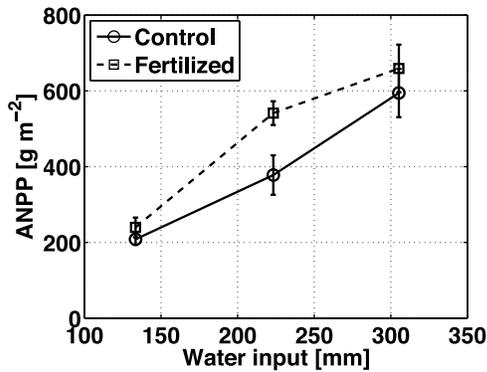
Figure 1. Above-ground net primary productivity as a function of water input and fertilization treatment ($\mu \pm$ SE, n = 8).

[16] Nitrogen limitation in Loma Ridge grassland is dependent on water input (Figure 1). Above-ground net primary productivity (ANPP) was estimated by harvesting two 14×50 cm strips from each plot on 23–25 April 2008. In general, ANPP responded positively to fertilization with the strongest effect in ambient water input plots. At low water input, ANPP was strongly limited by water availability. Estimates of below-ground biomass are not available. However, a study in a similar site nearby indicated no fertilization effect [*Harpole et al.*, 2007].

3.1. Soil Water Content

[17] Volumetric water content was recorded at 2–4 week intervals by time domain reflectometry using 15 cm waveguides (MiniTrase, ICT International). Probes were installed vertically at the soil surface, providing an estimate of average water content over the upper 15 cm of soil, $\overline{\theta}_{15}$ [$m^3 m^{-3}$].

3.2. Leaf Area Index

[18] Subcanopy photosynthetically active radiation (PAR) [μmol m^{-2} s^{-1}] was measured in each plot with the SunScan Canopy Analysis System (Dynamax). To compute a plot-scale value, a single measurement was taken at the top of the canopy and 5 evenly spaced measurements were taken below the canopy. PAR is related to LAI assuming exponential light attenuation within the canopy,

$$f_{PAR} = \exp(-kL) \tag{5}$$

where $f_{PAR} = PAR_{below}/PAR_{above}$ [-] is the fraction of PAR transmitted through the canopy and $k = 0.5$ for grassland [*Monsi and Saeki*, 2005].

3.3. Leaf Gas Exchange
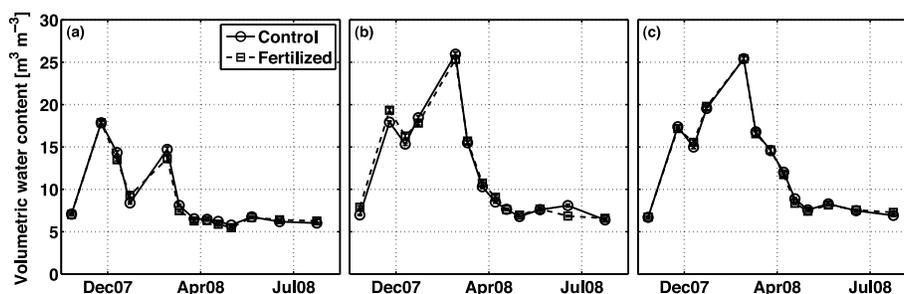
[19] Light-saturated leaf-specific stomatal conductance to water vapor g_s [mol H$_2$O m^{-2} leaf s^{-1}] was measured by open gas exchange analysis (LI-6400, LI-COR). Measurements were taken between 10 am and 2 pm at high irradiance (PAR = 1500 μmol m^{-2} s^{-1}), 380 ppm CO$_2$, and ambient temperature and soil moisture conditions. Under these conditions, we assume g_s reflects the effects of water stress and atmospheric demand (i.e., β and D). Measurements for *B. diandrus* are assumed to be valid for various annual forb species that were not measured.

4. Results

[20] The surface soil water describes the cumulative behavior of the terrestrial water balance. Each of the surface water fluxes (evaporation, transpiration, runoff, and leakage) are dependent on this quantity through the soil hydraulic properties. Measurements of $\overline{\theta}_{15}$ indicate no significant influence of fertilization in all water input treatments (Figure 2). Equivalent $\overline{\theta}_{15}$ suggests at least the sums of the water fluxes are equivalent among ambient and fertilized plots. The scale of these observations is likely smaller than the rooting depth of the grass species at this site [*Holmes and Rice*, 1996], so it is not an exact representation of the root zone water content as defined in equation (1). However, 30-cm TDR data collected in the 2009 and 2010 growing seasons show similar results (data not shown).

[21] We decompose G_c into contributions of the canopy characteristics that control the transpiration flux, L and g_s (Figure 3). Two distinct regimes are evident in the data. When water is strongly limiting, canopies exhibit low LAI and g_s in both control and fertilized plots. This occurs in the dry plots (circles) and late in the season (10 April, closed symbols). When water is less limiting, LAI increases (a), but g_s decreases (b) in fertilized plots. These canopy changes offset one another, leading to a similar G_c (c). Therefore, under conditions of low water stress, the unfertilized and fertilized grasses achieve the same G_c via unique L-g_s pairs. Unfertilized plots are characterized by low L, high g_s canopies; whereas fertilized plots are high L and low g_s.

5. Discussion

5.1. Ecosystem Interactions With Multiple Resources

[22] The fertilization experiments analyzed here illuminate the interactive roles of water and nitrogen in canopy function. Plants adjust g_s^{max} to balance CO$_2$ supply for photosynthesis with the inevitable consequence of water loss via transpiration. In the absence of water stress, increased
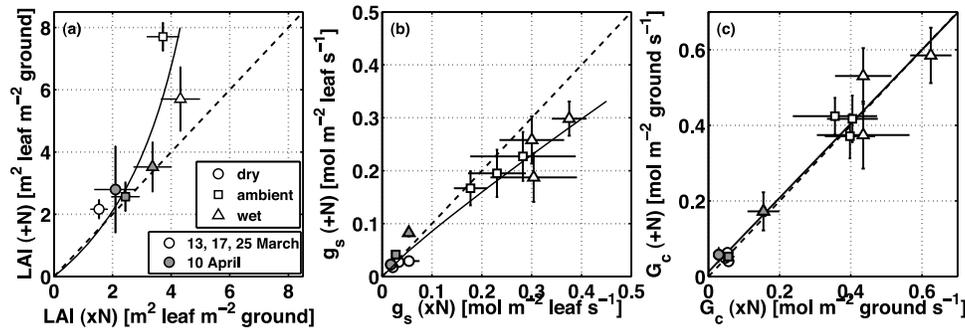

Figure 2. Growing season 15-cm averaged volumetric water content in (a) dry, (b) ambient, and (c) wet plots ($\mu \pm$ SE, n = 8).

Figure 3. Comparison of canopy attributes in control (xN) and fertilized (+N) plots: (a) LAI, (b) light-saturated top-of-canopy stomatal conductance, and (c) canopy-scale conductance ($\mu \pm$ SE, n = 8). The black dashed line indicates $y = x$ and the black solid lines represent interpreted relationships between the variables.

nitrogen availability and photosynthetic capacity will increase g_s^{max}. On the other hand, water deficit induces stomatal closure as plants limit transpiration to avoid desiccation and tissue loss. Given the same water supply, fertilization did not increase g_s, which demonstrates the water stress response dominates stomatal function and ET in this ecosystem.

[23] Despite the principal role of water supply at Loma Ridge, nitrogen availability did affect the canopy characteristics expressed in executing this strategy. Fertilization decreased g_s and increased LAI such that total canopy water use remained the same. Therefore, water supply exerts the primary control on transpiration, whereas nitrogen supply coordinates variation in canopy characteristics. This is consistent with the notion that, in water-limited ecosystems, canopy physiology and structure work in an integrated fashion to maintain a transpiration flux tightly controlled by soil and climate properties [*Eagleson*, 1978; *Rodriguez-Iturbe et al.*, 2001].

5.2. Implications for Modeling Dynamic Vegetation and Evapotranspiration

[24] The observed relationship between canopy characteristics, canopy conductance, and soil moisture is not consistent with existing LSM parameterizations that represent water stress through the soil moisture feedback alone (i.e., $\beta(\theta)$). Fertilization decreased g_s in this ecosystem, while soil moisture was not affected, suggesting that the soil moisture feedback is not sufficient to explain the stomatal response to increased nitrogen supply.

[25] Models that represent the hydraulic feedback may better predict dynamic vegetation and ET responses to fertilization. The relative control of hydraulic supply (LHS of equation (4)) and canopy conductance (RHS) on ET depends on the root and leaf allocation strategy. We hypothesize that root water supply was not adjusted to match the observed increase in leaf development in the fertilized plots. The resulting imbalance in leaf water supply and demand was then alleviated by stomatal adjustment, likely mediated by changes in plant water potential [*Sperry et al.*, 1998]. In this case, above-ground carbon investment proceeds despite increased drought vulnerability associated with decreased root-leaf area ratio [*Sperry et al.*, 1998]. This suggests Loma Ridge grasses may adjust resource allocation to compete for the most limiting resource [*Shipley and Meziane*, 2002], which shifts from below-ground (nitrogen) to above-ground (light) in the fertilized plots.

[26] Our results are consistent with other studies that demonstrate the importance of hydraulic constraints in modeling stomatal behavior and canopy gas exchange. Leaf hydraulic status is a well-established physical mechanism underlying stomatal movement [*Buckley*, 2005]. In addition, models that represent the hydraulic feedback successfully predict soil moisture and evapotranspiration dynamics [*Fisher et al.*, 2007]; and global patterns of vegetation and hydrologic fluxes at least as well as the soil moisture feedback [*Hickler et al.*, 2006; *Alton et al.*, 2009]. The data presented here argues that the explicit modeling of hydraulic constraints and their dependence on allocation is also important to accurately capture hydrologic sensitivity to variable nitrogen inputs.

5.3. Further Development of the Water Balance

[27] In this study, we use observations in an annual grassland to study transpiration during the growing season. However, factors controlling transpiration vary over seasonal, inter-annual, and ecological time-scales and this variability depends on the nitrogen supply rate. For example, this analysis does not capture seasonality of vegetation activity or the relative contributions of evaporation and transpiration. Further, fertilization causes changes in community composition [*Suding et al.*, 2005] that may alter the water balance.

[28] Finally, it is important to emphasize that these results were observed for an exogenous increase in nitrogen availability; that is, the increase is independent of soil water availability. The strong coupling between soil moisture and nitrogen mineralization in natural systems [*Brady and Weil*, 2001] may dampen the variability observed here and preserve G_c-LAI correlations. It is quite possible that vegetation responds this way only when the system is shifted from an equilibrium where vegetation, hydrology, and biogeochemistry are balanced [*Schimel et al.*, 1997]. However, soil water and biogeochemical cycles in natural systems may be decoupled by short-term perturbations in the atmospheric forcing, such as drought, that propagate via much longer time-scales in the biogeochemical dynamics [*D'Odorico et al.*, 2003].

6. Conclusions

[29] In this annual grassland, a first-order characterization of canopy controls on transpiration reveals the dominant role of hydraulic constraints along the soil-vegetation-atmosphere pathway. Changes in the availability of a second important plant resource, nitrogen, did not affect surface moisture

storage or canopy-scale water vapor conductances. Equivalent conductance was achieved by offsetting a fertilization-induced increase in leaf area with a complementary reduction in the leaf-specific water vapor conductance. This result contrasts with existing assumptions in the LSMs, which require soil moisture depletion to induce stomatal closure. Explicit representation of soil-plant hydrodynamics in LSMs would improve predictions of vegetation surface properties and water-energy fluxes, particularly under conditions of increasing nitrogen supply.

[31] The Editor and authors thank two anonymous reviewers for assisting with the evaluation of this paper.

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