

Impact of the hydraulic capacity of plants on water and carbon fluxes in tropical South America

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[1] Angiosperms (flowering plants) have higher transpirational capacities than any other plants. Here we use climate model simulation to test the hypothesis that the high transpirational capacity of angiosperms plays a unique role in the maintenance of tropical rainforest. Their elevated transpiration rates are shown to increase recycling of precipitation up to ~300 mm/yr (~20% of total precipitation) averaged over the whole of tropical South America and to increase the wet season duration over the Amazon basin. Transpiration triggers convection by increasing moisture in the boundary layer and thereby decreasing atmospheric stability. If the moisture content of the boundary layer is sufficient, a double Intertropical Convergence Zone (ITCZ) is generated in October around 60°W–50°W, as observed in present-day climate, and the eastern part of the Amazon basin becomes wet (~200 mm/month of precipitation). This double ITCZ is lost, however, and the region becomes dry (<50 mm/month of precipitation) in the absence of full angiosperm transpiration. Although higher water use efficiency is usually associated with plants with lower transpiration rates, water use efficiency actually increases with higher hydraulic capacity in our simulations as a result of the higher humidity and, thus, lower vapor pressure gradient between the intercellular air space within the leaf and the external atmosphere. We speculate that the high transpirational capacity of angiosperms played a significant role in the expansion of tropical rain forest.

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1. Introduction

[2] Water is a major ingredient in the chemical reactions of photosynthetic carbon fixation by land plants, but this water represents no more than a few percent of the total water used during photosynthesis. Most of the water is transpired out; when plants open stomata to take up CO₂, water diffuses out along the water vapor pressure gradient. The water use efficiency of this stomatal gas exchange, the ratio of CO₂ assimilative uptake to H₂O transpirational loss [Field *et al.*, 1983], varies depending on species and climate. Water loss is an unavoidable part of carbon uptake, and the rates of photosynthesis and transpiration are highly correlated [Rosenzweig, 1968; Brodrigg *et al.*, 2007].

[3] Plant transpiration is a significant component of energy and water flux and the water exchange between land surface and atmosphere has been studied as an important determinant of precipitation [e.g., Koster, 2004; Dirmeyer, 2000]. Using Illinois soil moisture data, Findell and Eltahir [1997] show that summer precipitation is highly correlated with late spring/early summer soil moisture. Other observational and modeling studies [e.g., Stidd, 1975; Taylor *et al.*, 1997;

D'Odorico and Porporato, 2004] also demonstrate the importance of soil moisture for precipitation. Most studies focus on soil moisture status during the growing season, implying the central role of plants. Focusing on this role, modeling studies of deforestation have demonstrated the importance of the flux of evapotranspiration (ET) to the atmosphere in determining precipitation [e.g., Shukla and Mintz, 1982; Oyama and Nobre, 2004]. Models have also shown the climatic importance of access to deep soil moisture over the Amazon basin [Kleidon and Heimann, 2000], and plant activity within the soil can play a direct role in modifying temperatures and the hydrological cycle through the redistribution of soil water by roots [Oliveira *et al.*, 2005; Lee *et al.*, 2005].

[4] Transpiration rate is driven by atmospheric demand when stomata are open, but stomata shut, preventing photosynthetic gas exchange, when the local transpiration rate of leaf tissues exceeds the rate at which water can be supplied from the substrate through the roots and shoot vasculature. Therefore, plant hydraulic architecture has an important influence on water loss from leaves in addition to soil moisture availability [Jackson *et al.*, 2000; Brodrigg, 2009]. Leaves alone average 30% and can be greater than ~80% of total plant resistance and leaf resistance scales with total plant resistance [Sack and Holbrook, 2006]. Most hydraulic transport within plants is through xylem cells that are dead and devoid of cell contents at maturity and are, thus, spe-

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cialized as water conduits. Much of the concentration of high resistance within the leaf results from the passage of water out of the leaf veins en route to the stomata through the living cells of the mesophyll tissue that is specialized for photosynthesis, not water transport. Thus, vein positioning limits transpiration, and leaves with a higher density of leaf veins will have a shorter transit through the high-resistance mesophyll and a higher hydraulic conductance overall [Brodribb *et al.*, 2007]. Leaf hydraulic conductance varies between species by more than a factor of 65 [Sack and Holbrook, 2006] due in no small part to a large variation in leaf vein density [Boyce *et al.*, 2009].

[5] The variation in leaf vein density is not evenly distributed across the evolutionary lineages of land plants. Angiosperms (flowering plants) have much higher vein densities than any other plant types over the more than 400 million years of history of terrestrial life, and hence, angiosperms have uniquely high leaf hydraulic conductances [Boyce *et al.*, 2009]. Angiosperms dominate present-day midlatitude and low-latitude landscapes except at high altitude and comprise 85%–99% of the regional species diversity globally [Mutke and Barthlott, 2005]. Because of their overwhelming abundance, angiosperm physiology has served as the natural basis of climate model formulations of photosynthesis [e.g., Collatz *et al.*, 1991]. However, an important open question is the extent to which the unique physiological characteristics of angiosperms lead to an evolutionarily unique role in the climate system. The increased hydraulic capacity of angiosperms is expected to allow increased transpirational recycling relative to other types of plants, which would result in precipitation increases from the tropics to midlatitude with the largest changes occurring in the tropics, particularly of South America [Boyce and Lee, 2010]. Here, this work is focused on water and carbon fluxes, regional differences, and atmospheric conditions in tropical South America.

2. Model

[6] The National Center for Atmospheric Research (NCAR) Community Atmospheric Model 3.0 [Collins *et al.*, 2006] was coupled with the Community Land Model 3.5 [CLM 3.5; Oleson *et al.*, 2008]. Results are averaged over the last 10 years of 13-year runs. The resolution of the model is T42, each grid size is $\sim 2.8^\circ$ latitude and $\sim 2.8^\circ$ longitude, with 10 layers in the soil and 26 layers in the atmosphere. The model is forced with climatologically fixed sea surface temperature observations of today.

[7] The land component of the model simulates CO_2 , water, momentum, and energy exchanges between land surface and atmosphere. CO_2 uptake (photosynthesis) and water loss (transpiration) by plants are determined as a diffusive flux between the stomata and the surrounding atmosphere. Soil water moves from the soil to the atmosphere following the prescribed root density in each soil layer. CLM3.5 has much better soil hydrology compared with previous versions of NCAR CLMs, and its simulated ET more closely resembles observations. In particular, simulated ET stays relatively constant over the Amazon basin [Oleson *et al.*, 2008], which is consistent with observation [da Rocha *et al.*, 2004].

[8] To assess the potential dependence of tropical environments on the evolution of angiosperm hydraulics, we performed climate model simulations while varying physio-

logical capacities. Photosynthetic and transpirational capacities are both highly correlated with leaf vein density [Brodribb *et al.*, 2007; Boyce *et al.*, 2009]. The differences in mean vein density between angiosperms and all other plants correspond to roughly 4 times higher transpiration rates [Boyce *et al.*, 2009]. The NCAR CLM does not resolve water-transporting processes from soil to leaf separately from photosynthetic capacity, but transpiration could be altered along with by modifying photosynthetic capacity because of their close correlation.

[9] The maximum rate of carboxylation V_{\max} relates photosynthesis and transpiration to soil moisture availability. As a first step toward understanding the impact of angiosperms on climate, nonangiosperm physiology was substituted for that of angiosperms while maintaining modern vegetative biomass [cf. Bonan, 2008], including root profile, leaf, and stem area, by decreasing V_{\max} globally by a factor of 2, 4, or 8 ($0.5 \times \text{HYD}$, $0.25 \times \text{HYD}$, and $0.125 \times \text{HYD}$, respectively). Additional simulations of present-day conditions ($1 \times \text{HYD}$) complete coverage of the full range of physiological capacities likely over vascular plant evolution. Since our focus is on estimation of the effect that the high hydraulic capacity of angiosperms has on climate, the results are presented as the difference of present-day values from those involving vegetation with lower hydraulic capacity (for example, $1 \times \text{HYD}$ – $0.25 \times \text{HYD}$; e.g., Figures 1b, 1c, and 1d).

[10] The goal here is not to model the evolution of angiosperms but to explore the importance of their current existence to modern climate in the tropics. Our modeling does not capture the continental configurations, temperatures, or atmospheric composition of the Late Cretaceous/Early Cenozoic when the current ecological dominance of angiosperms began. Because each of those parameters changed substantially even during just the Cretaceous initial diversification of angiosperms, modeling of angiosperm evolution will be extremely difficult. Furthermore, it is still widely debated when the ecological dominance of angiosperms was first achieved in different regions and environments [Upchurch and Wolfe, 1987; Morley, 2002; Burnham and Johnson, 2004; Davis *et al.*, 2005; Wing *et al.*, 2009], so no single set of parameter values would be sufficient. Modeling the potential climate effects of Cretaceous angiosperm evolution is an important future goal for our work, but the crucial first step undertaken here is to isolate the contribution of angiosperms from other factors within the well-constrained conditions of the modern world.

[11] Allowing dynamic vegetation would be an important future refinement of this research, but vegetation, here, was fixed at modern values in order to isolate the effect of lowering transpiration rates. In a real world that lacked angiosperms, a partial compensation for the loss of high transpiration capacities per unit leaf area perhaps could be achieved by an increase in total leaf area. However, high leaf area plants are typically found in exposed, high-light environments, and it is highly unlikely that the higher capacities per unit leaf area of angiosperms could be offset by quadrupling the leaf area in the already dense vegetation of tropical rainforests. Furthermore, many nonangiospermous plants actually have lower leaf area than angiosperms, and the lineage with the highest leaf areas, *Pinaceae conifers*, has never been important in the low-altitude tropics [Boyce *et al.*, 2009]. Thus, the one quarter modern transpiration run, for

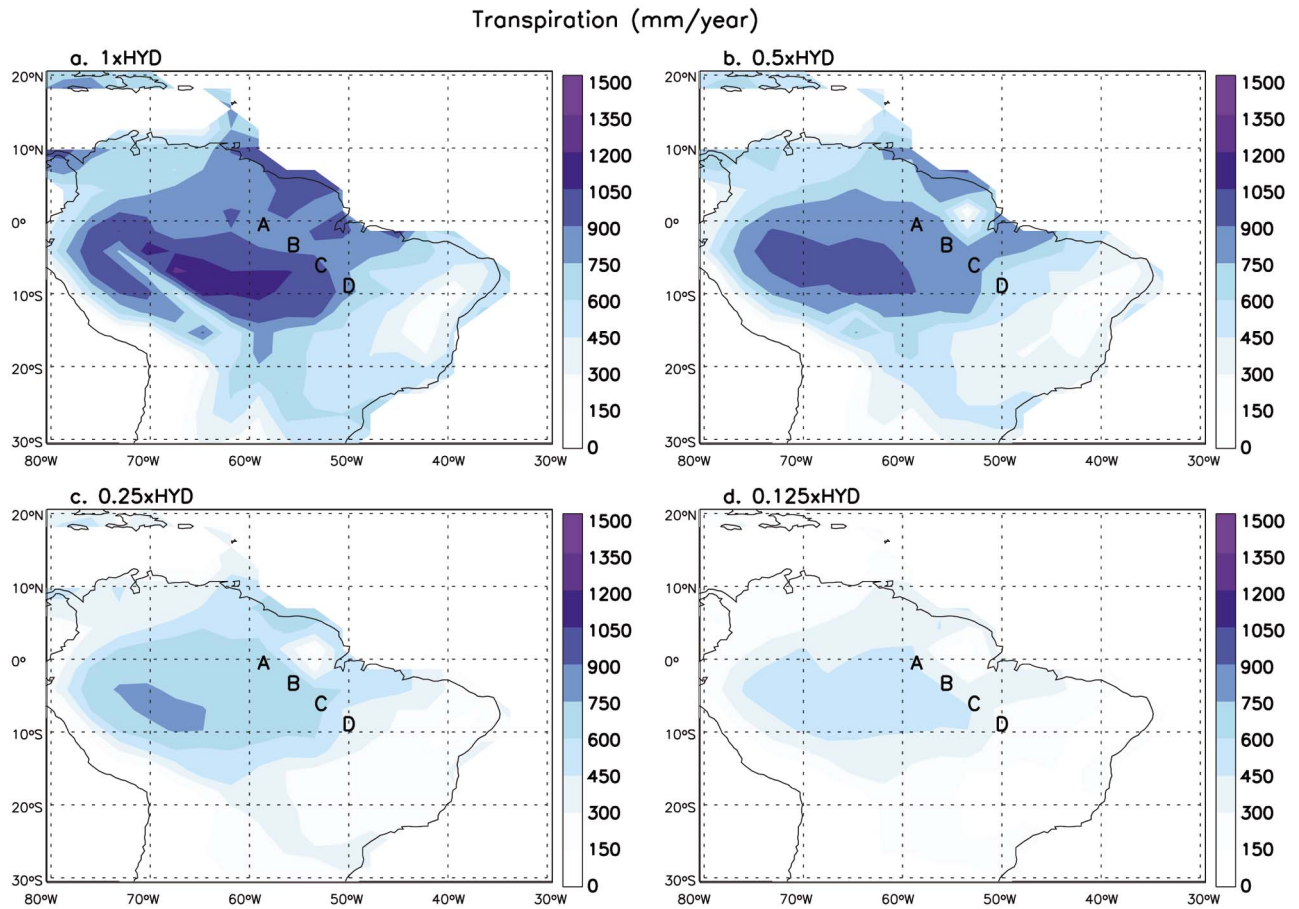


Figure 1. Mean annual transpiration (mm/yr) for (a) $1 \times \text{HYD}$, (b) $0.5 \times \text{HYD}$, (c) $0.25 \times \text{HYD}$, and (d) $0.125 \times \text{HYD}$ runs. Letters A–D represent the locations used in Figures 3 and 6–9.

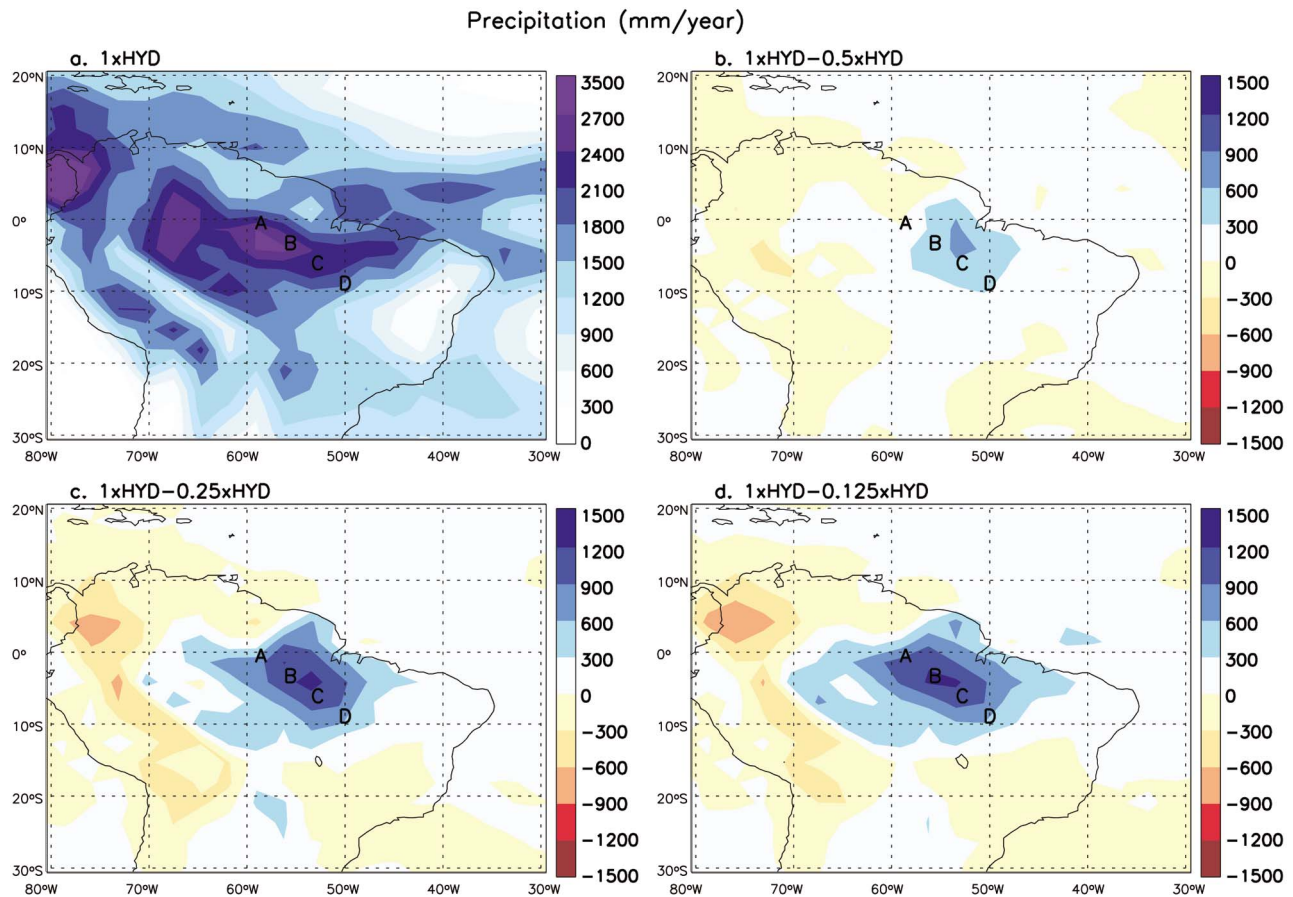


Figure 2. Mean annual precipitation (mm/yr) for the (a) $1 \times \text{HYD}$ run and the difference from $1 \times \text{HYD}$ to (b) $0.5 \times \text{HYD}$, (c) $0.25 \times \text{HYD}$, and (d) $0.125 \times \text{HYD}$. Letters A–D represent the locations used in Figures 3 and 6–9.

which the transpiration drop per leaf area implied by changes in vein density is taken at face value, is considered as a conservative estimate of actual transpiration differences between a preangiosperm and angiosperm world, and one eighth transpiration may be a closer estimate. In any case, the V_{\max} range of the four simulations performed indicate climate sensitivity to all levels of transpiration reduction.

3. Results and Discussion

[12] The increased transpirational capacity of angiosperms relative to other plants is responsible for a large increase in transpiration and photosynthesis over tropical South America (Figure 1). The moistening of the atmospheric boundary layer with higher transpiration can trigger atmospheric convection in otherwise nonconvecting areas, thus increasing precipitation by decreasing atmospheric stability [Fu *et al.*, 1999; Li and Fu, 2004]. The pattern of precipitation increase does not exactly correspond to that of the transpiration increase because water vapor is moved around by prevailing winds and precipitation is governed by large-scale circulation and local atmospheric profiles [Findell and Eltahir, 2003]. The precipitation increases resulting from transpirational recycling (Figure 2) allow further increases in transpiration and photosynthesis as soil moisture limitations are relieved. This feedback between transpiration and spatially variable pre-

cipitation also explains why transpiration itself is not spatially uniform (Figure 2).

[13] With decreasing hydraulic capacity, the magnitude of precipitation differences is larger, but the overall patterns are similar. Without the elevated transpiration levels of angiosperms, the largest precipitation decrease occurs in the eastern part of the Amazon basin (Figure 2), where precipitation is known to be sensitive to ET [Fu and Li, 2004; Lintner and Neelin, 2009]. This overall annual pattern is largely due to precipitation changes during the transition periods between wet and dry seasons (Figure 3), a response that is found over a range of distances from the equator, and of overall precipitation abundance (Figure 3, showing mean monthly precipitation for areas A through D, labeled on Figures 1 and 2). For both the beginning and end of the wet season (October and April, respectively), elevated transpiration results in a large increase in moisture convergence (Figures 4 and 5), decreasing atmospheric stability and potentially initiating convection. Areas that are currently everwet become drier without angiosperms because changes of transpiration and water vapor convergence ensure delayed onset of the wet season and decreased precipitation during the wet season (Figures 3a and 3b). In contrast, areas that already possess a longer dry season also experience substantial changes in precipitation level during the transition season when

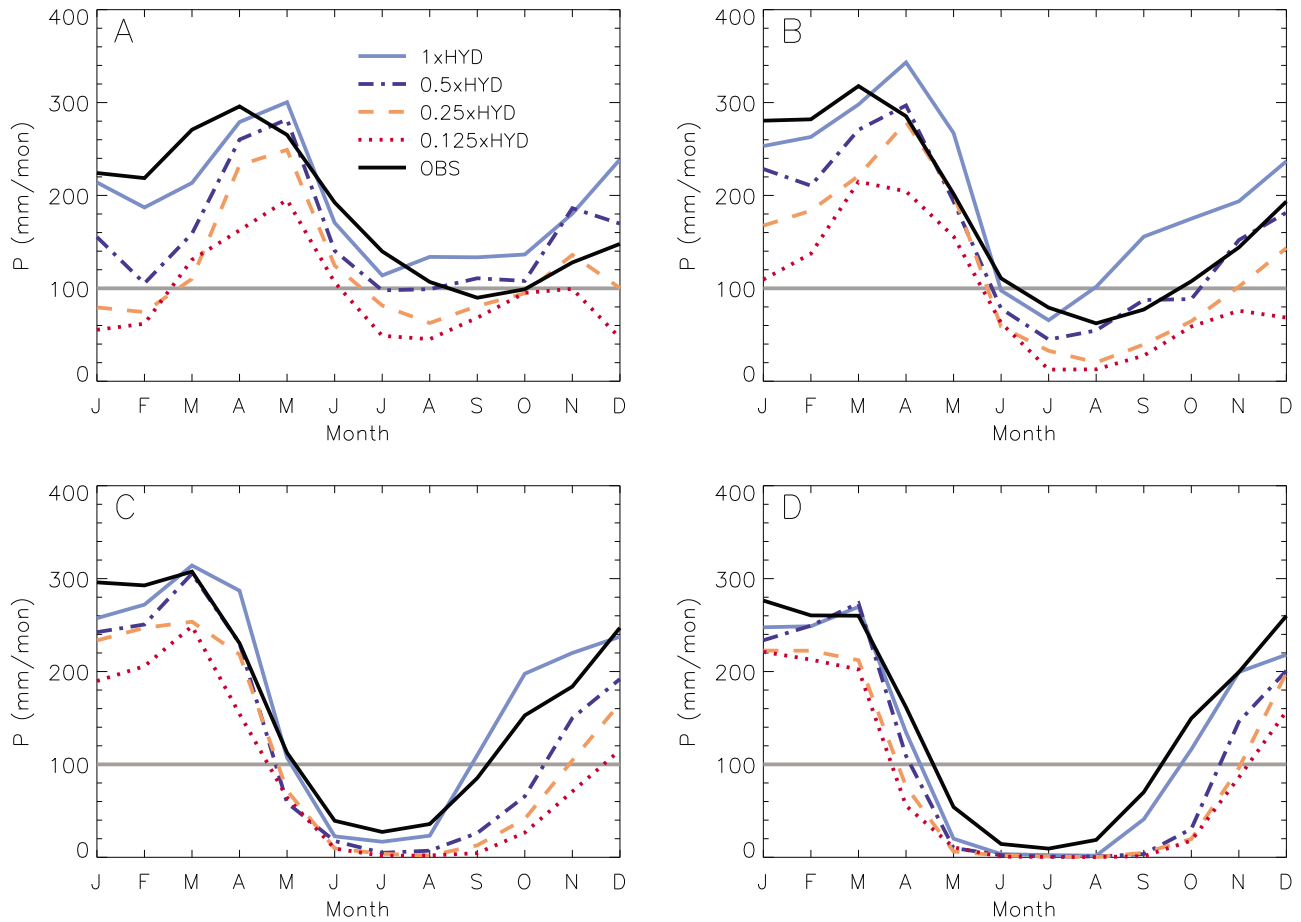


Figure 3. Monthly mean precipitation (mm/month) for 1xHYD (light blue solid line), $0.5 \times$ HYD (blue dash-dotted line), $0.25 \times$ HYD (orange dashed line), and $0.125 \times$ HYD (red dotted line) runs in the grid A (upper left), B (upper right), C (lower left), and D (lower right) from Figure 2.

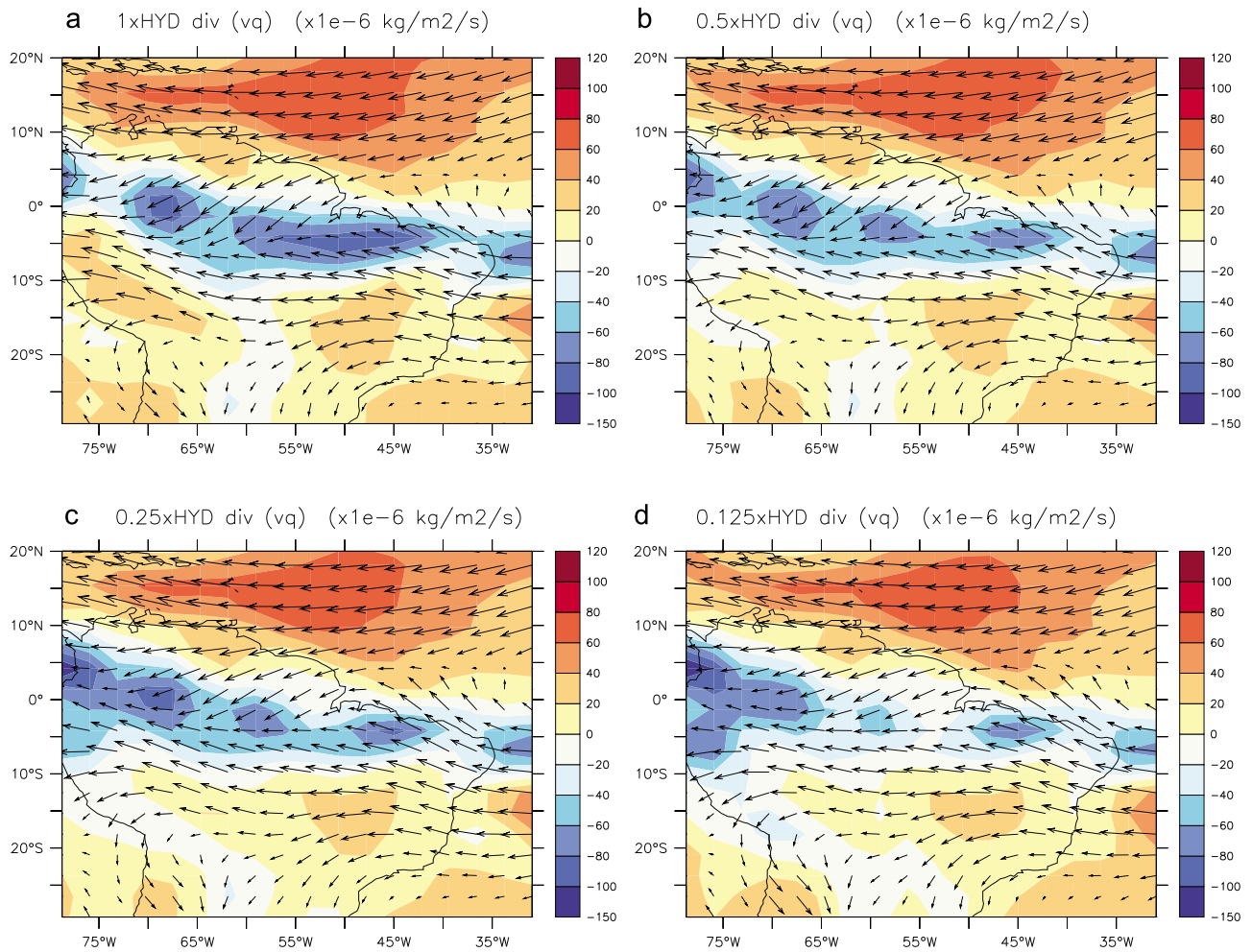


Figure 4. Column-integrated moisture divergence (contours; kg/m²/s) and column-integrated \overline{uq} and \overline{vq} (vectors) for (a) $1 \times \text{HYD}$, (b) $0.5 \times \text{HYD}$, (c) $0.25 \times \text{HYD}$, and (d) $0.125 \times \text{HYD}$ runs in April.

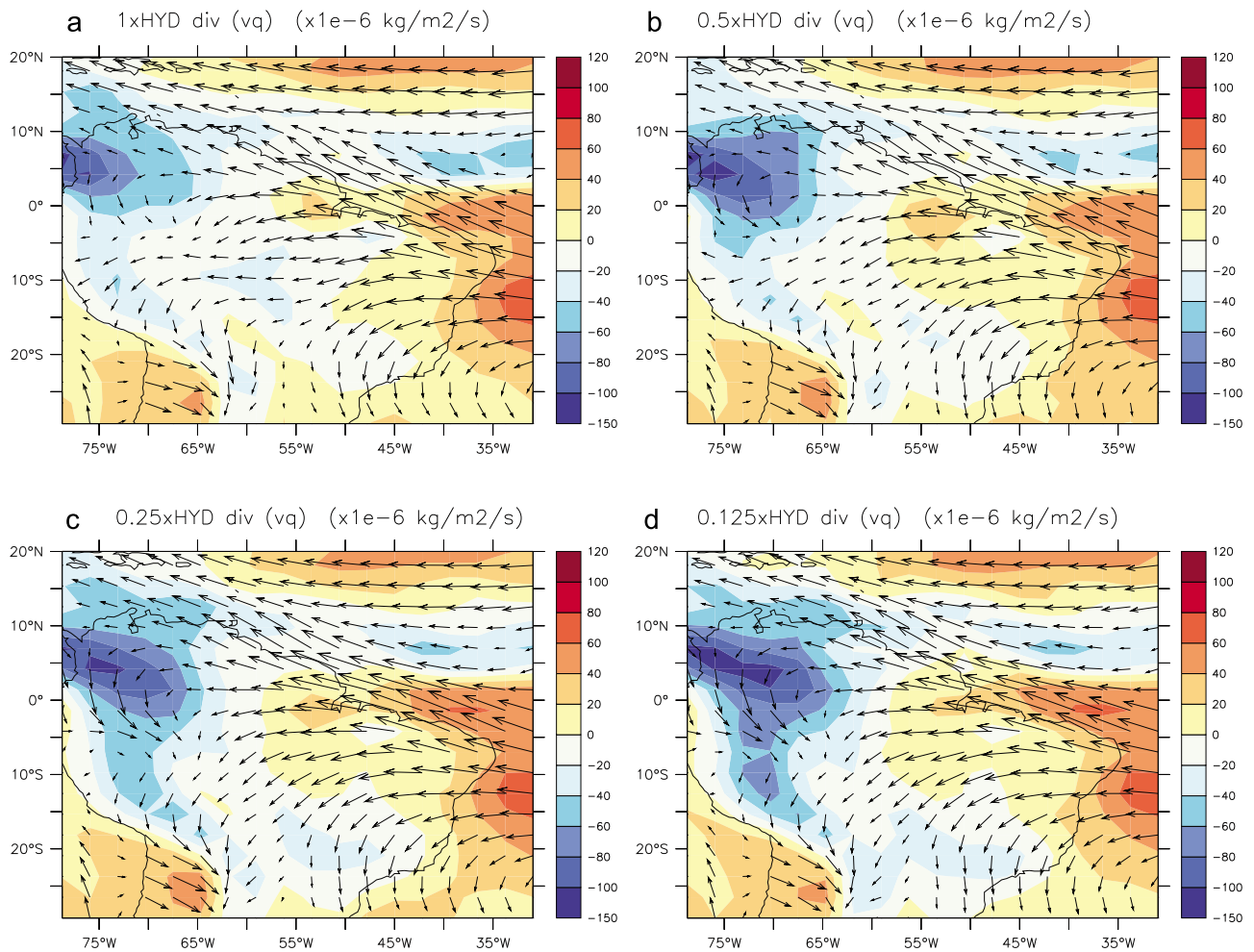


Figure 5. Column-integrated moisture divergence (contours; $\text{kg/m}^2/\text{s}$), and column-integrated \overline{uq} and \overline{vq} (vectors) for (a) $1 \times \text{HYD}$, (b) $0.5 \times \text{HYD}$, (c) $0.25 \times \text{HYD}$, and (d) $0.125 \times \text{HYD}$ runs in October.

angiosperms are replaced but experience small changes during the wettest and driest months (Figures 3c and 3d).

[14] Moist static energy is often used to represent the total energy of an air parcel, reflecting both its temperature and the potential of latent heat release if its water vapor content were to condense. It is defined as $C_p T + Lq + gz$, where C_p is specific heat at constant pressure ($\text{J}^\circ\text{C}/\text{kg}$), T is temperature (K), L is latent heat of vaporization (J/kg), q is specific humidity (kg of water vapor/kg of dry air), g is gravitational acceleration (m/s^2), and z is height in the air column (m), and is a good indicator for the first-order precipitation pattern [Privé and Plumb, 2007; Bordoni and Schneider, 2008]. For both April and October, the greater transpiration of angiosperms is simulated to produce a large increase in moisture over land (south of 10°N) and an accompanying decrease in temperatures with the transfer of energy to latent heat during evaporation (Figures 6a, 6b, 7a, and 7b). The resulting increase in moist static energy (Figures 6c and 7c) produces a wider precipitation band and a higher peak precipitation that is consistent with observations, although with some offset (Figure 6d). During the April transition season, widespread delays in the local onset of the dry season are caused by this widening of the precipitation band when angiosperms are present (Figure 3).

[15] In October, moist static energy and precipitation maxima occur simultaneously in both hemispheres when angiosperm transpiration is present, but only a single maximum is present in the simulations with decreased hydraulic capacity (Figure 7c). The resulting double precipitation maxima seen with full angiosperm transpirational capacity match observations (Figure 7d). The more southerly maximum disappears in all three simulations of reduced transpirational capacity. This region, between 15°S and the equator, is over the eastern part of the Amazon basin where the largest precipitation changes are seen in the response to modifying transpirational capacity (Figure 2). This region becomes dry, even with only a 17% drop in evapotranspiration ($0.5 \times \text{HYD}$ case compared to $1 \times \text{HYD}$), and appears to have two equilibrium states depending on the moisture content in the lower atmosphere. A large moisture gradient between hemispheres, as is the case in decreased hydraulic capacity runs, favors a single Intertropical Convergence Zone (ITCZ) in the Northern Hemisphere (P. Xian and R. L. Miller, Multiple equilibria in an axisymmetric model of the tropical circulation with prognostic BL moisture, submitted to *Journal of Climate*, 2008), but two convergence zones can be formed if the Southern Hemisphere becomes wetter [cf., Chao and Chen, 2001]. In October, the hemispheric water vapor gradient is small for the full transpi-

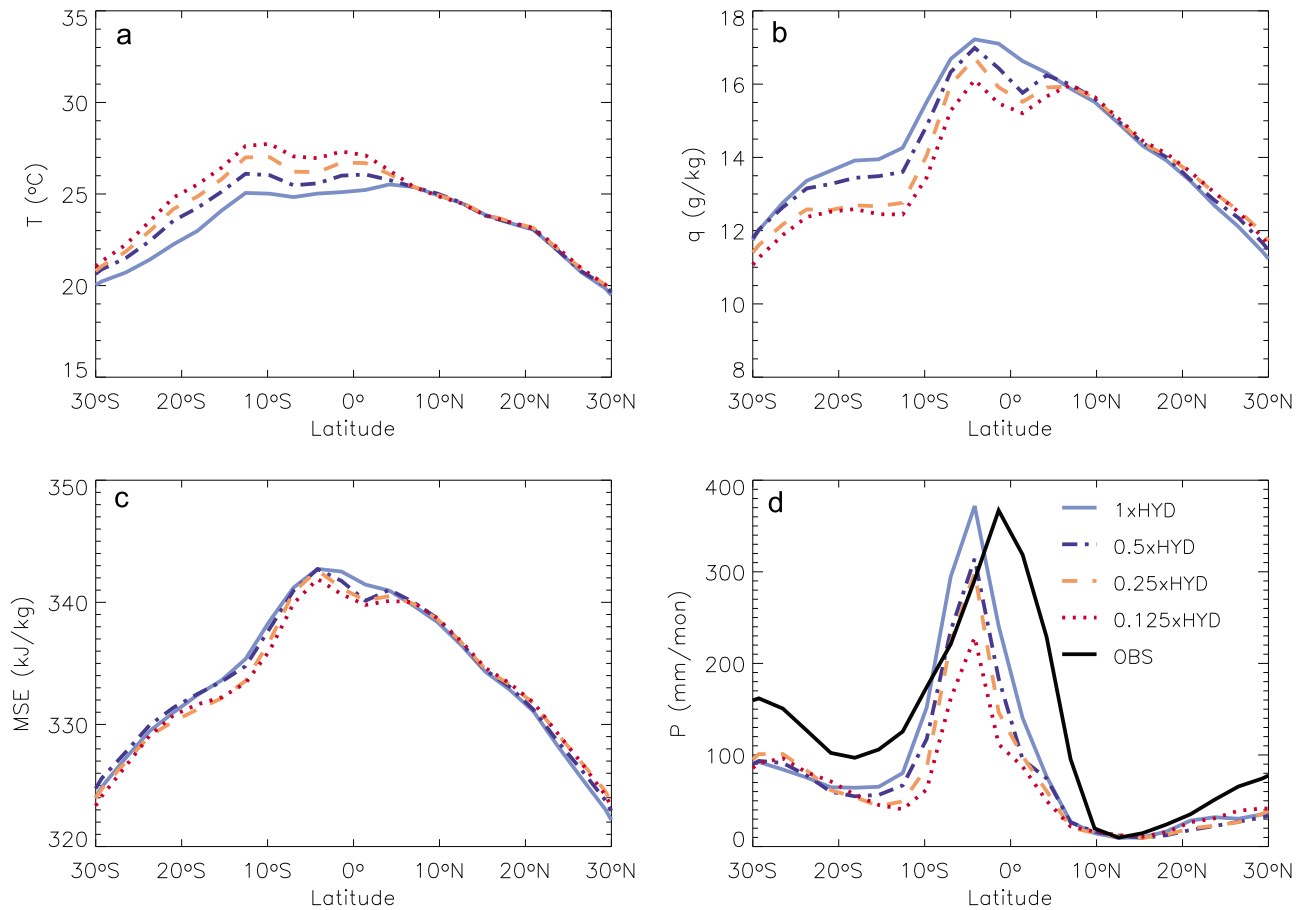


Figure 6. Latitudinal distribution of zonal mean (60°W – 50°W) (a) surface air temperature, (b) surface air humidity, (c) moist static energy, and (d) precipitation for $1 \times \text{HYD}$ (light blue solid line), $0.5 \times \text{HYD}$ (blue dash-dotted line), $0.25 \times \text{HYD}$ (orange dashed line), and $0.125 \times \text{HYD}$ (red dotted line) runs in April. Temperature change is larger over the Southern Hemisphere because the ocean is covered at this longitude in the Northern Hemisphere, and surface air temperature over the ocean is modulated by the sea surface temperature, which is fixed in all simulations.

rational capacity case, and double ITCZ are formed (Figure 7), but the gradient becomes much larger without angiosperm transpiration and only a northern hemispheric ITCZ is present as a result. The largest precipitation increases in the presence of angiosperm transpirational capacity over the course of a year come from the earlier onset of the wet season (around October) accompanying the double ITCZ.

[16] Although there is spatial offset between the distributions of transpiration (or ET) and precipitation, the total precipitation increase over tropical South America (20°S – 10°N , 80°W – 30°W) is similar to the total increase in ET (Table 1). For example, the ET and precipitation increases with full angiosperm transpiration relative to transpiration reduced by a factor of 8 are 317 and 284 mm/yr, respectively. These changes are large in comparison to the differences in moisture convergence (Figures 4 and 5), equal to precipitation minus evaporation (P–E), which are no more than 30 mm/yr. Thus, the transpired moisture itself, rather than the changes in moisture convergence from the ocean, provides the dominant contribution to simulated precipitation increases.

[17] The mean monthly carbon assimilation by photosynthesis, or gross primary production (GPP), increases with higher photosynthetic/hydraulic capacity. With full angio-

sperm transpiration levels, changes in photosynthesis in area A (Figure 8a) and B (not shown) are free to track the incoming solar energy (compare with Figure 1 in *Myneni et al.* [2007]), with minimum photosynthesis in June when the solar zenith angle is the lowest, because high year-round precipitation (Figures 3a and b) ensures little soil moisture stress. Observations show a similar dependence of productivity on incoming solar energy in the absence of moisture stress for tropical forest [*Myneni et al.*, 2007]. Photosynthesis during austral spring (SON) is larger than austral fall (MAM) because there are fewer cloudy days.

[18] For regions that have a distinct dry season even with full angiosperm hydraulic capacity, such as 3 months in region C and 5 months in region D, GPP decreases during the end of the dry season due to the deficit of soil moisture (Figure 9a). Over these regions, GPP does not track the incoming solar energy in simulations because soil moisture uptake becomes more limiting than solar energy. This decrease in GPP is delayed in runs with lower hydraulic capacity because biomass is fixed for all runs and the effect of soil dryness, thus, appears later with the slower depletion of deep soil moisture with lower transpirational capacity [cf. *Jipp et al.*, 1998].

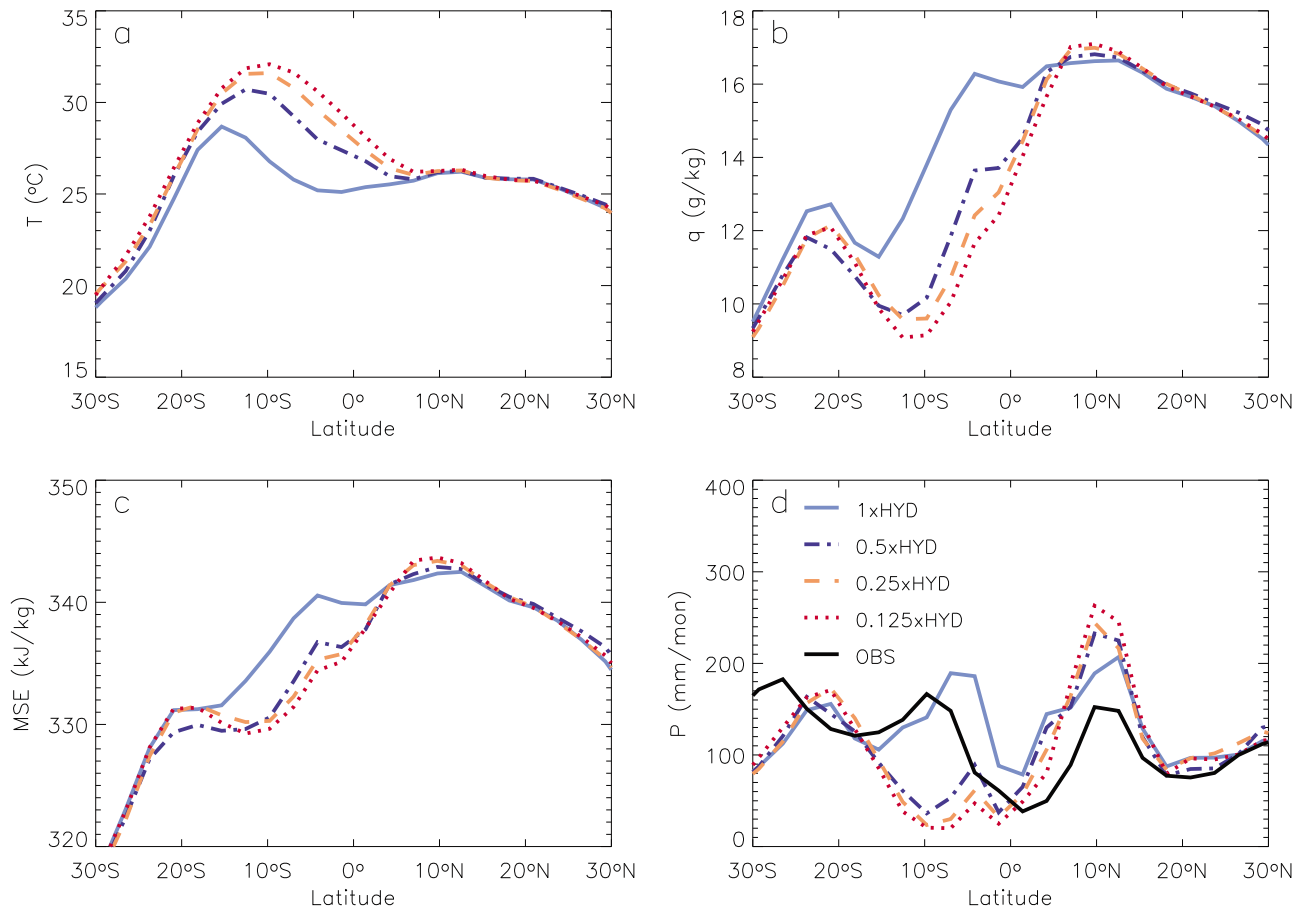


Figure 7. Latitudinal distribution of zonal mean (60°W – 50°W) (a) surface air temperature, (b) surface air humidity, (c) moist static energy, and (d) precipitation for 1xHYD (light blue solid line), $0.5 \times$ HYD (blue dash-dotted line), $0.25 \times$ HYD (orange dashed line), and $0.125 \times$ HYD (red dotted line) runs in October. Temperature change is larger over the Southern Hemisphere because the ocean is covered at this longitude in the Northern Hemisphere, and surface air temperature over the ocean is modulated by the sea surface temperature, which is fixed in all simulations.

[19] Transpiration and assimilation are calculated using the same conductances (while accounting for differences in diffusivity and molecular weight), but water vapor and CO_2 have different pressure gradients between the intercellular air spaces and the ambient air surrounding the leaf. Transpiration E_v can be formulated as

$$E_v = \rho g_w (q_{s,T_L} - q_a),$$

Table 1. Water Balance for Each Run in Tropical South America (20°S – 10°N ; 80°W – 30°W)^a

	1 × HYD	0.5 × HYD	0.25 × HYD	0.125 × HYD
Transpiration	735	618	460	298
Canopy evaporation	266	249	237	222
Soil evaporation	262	305	366	428
Total evapotranspiration	1264	1172	1062	947
Precipitation	1612	1489	1408	1325
P-E (mm/yr)	348	317	346	378
Subsurface drainage	278	257	282	304
Surface runoff	71	64	67	69

^aAll are mean annual values, and units are given in mm/yr.

where ρ is the density of the air, g_w is the conductance for water transport, q_{s,T_L} is the specific humidity at saturation within the leaf (intercellular air spaces are saturated at leaf temperature), and q_a is the specific humidity for the ambient air surrounding the leaf. Because of the different concentration gradients of CO_2 and water vapor, seasonal variations in transpiration (Figures 8b and 9b) are not the same as those for photosynthesis [cf. *Katul et al.*, 2010]. The water vapor pressure gradient becomes larger with increasing leaf temperature and with decreasing ambient humidity. With full angiosperm transpiration capacity, transpiration in regions A and B is largest in austral spring when there is enough soil

Table 2. Water and Carbon Flux and Water Use Efficiency for Each Run in Tropical South America (20°S – 10°N ; 80°W – 30°W)^a

	1 × HYD	0.5 × HYD	0.25 × HYD	0.125 × HYD
GPP ($\mu\text{mol}/\text{m}^2/\text{s}$)	9.5	6.5	4.2	2.3
Transpiration ($\mu\text{mol}/\text{m}^2/\text{s}$)	1296	1088	809	525
Water use efficiency (% mol/mol)	0.73	0.60	0.52	0.44

^aAll are mean annual values.

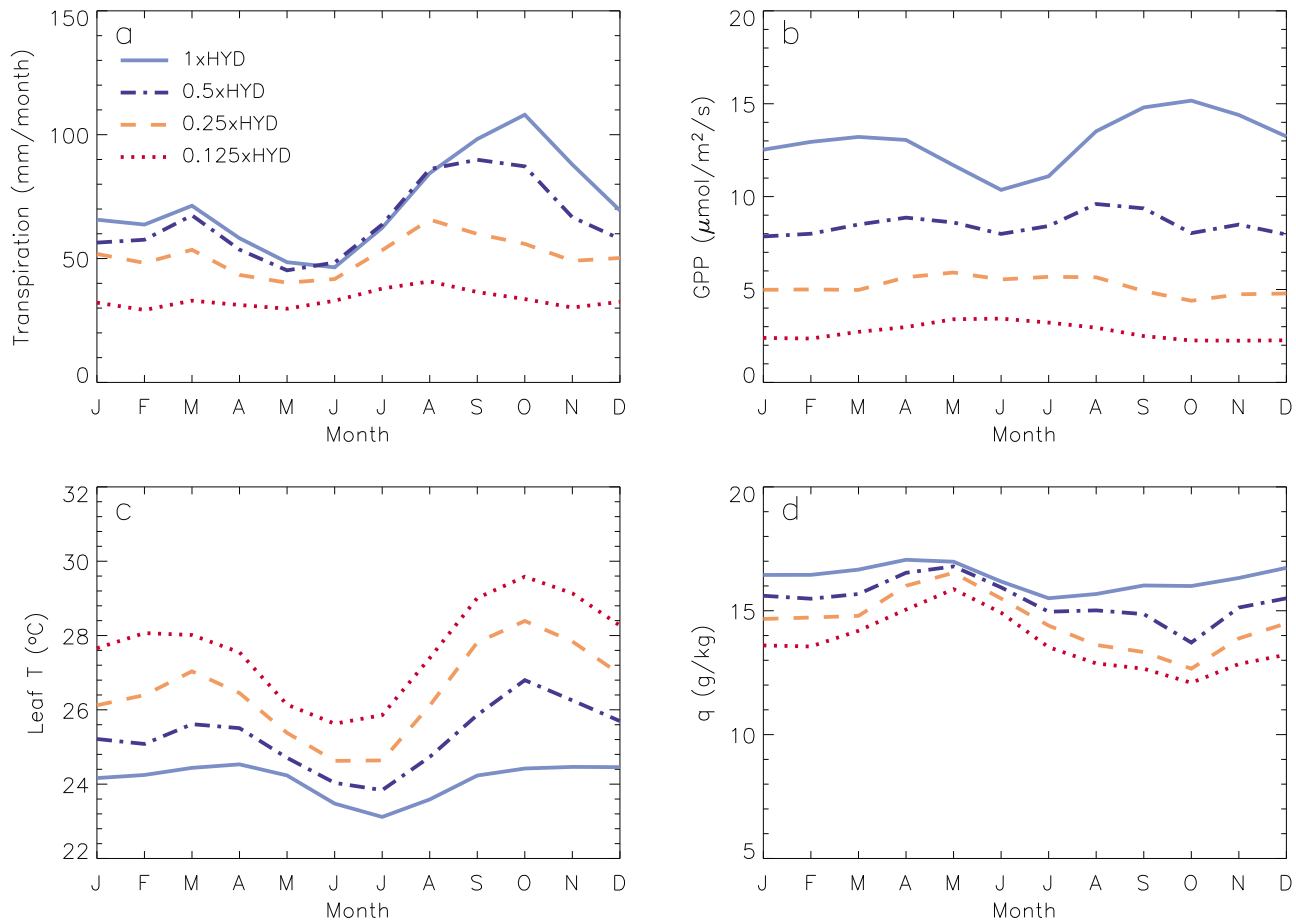


Figure 8. Monthly mean (a) GPP ($\mu\text{mol}/\text{m}^2/\text{s}$), (b) transpiration (mm/month), (c) leaf temperature ($^{\circ}\text{C}$), and (d) specific humidity (g/kg) for $1 \times \text{HYD}$ (light blue solid line), $0.5 \times \text{HYD}$ (blue dash-dotted line), $0.25 \times \text{HYD}$ (orange dashed line), and $0.125 \times \text{HYD}$ (red dotted line) runs at the point A in Figure 1.

moisture and the water vapor pressure gradient is large. This transpiration increase is larger than the corresponding increase in photosynthesis. When transpiration capacity is cut in half, GPP is much smaller, but actual transpiration does not decrease much (except during the austral spring when precipitation amounts, and thus soil moisture contents, are different) because there is a larger water vapor pressure gradient (and biomass is fixed). Leaf temperature in the wet tropics largely depends on the amount of ET, which cools the leaf. Leaf temperature (Figures 8c and 9c) decreases, and ambient air specific humidity (Figures 8d and 9d) increases with increasing ET and decreasing dryness. As a result, the vapor pressure gradient decreases with increasing hydraulic capacity. Thus, although greater water use efficiency is typically thought of as a characteristic of plants that transpire less, our simulation produce a counterintuitive increase in water use efficiency when plants have a greater transpirational capacity (Table 1).

[20] ET consists of evaporation from the soil, evaporation of precipitation intercepted by the canopy, and transpiration from plants. Even if there is less photosynthesis and transpiration in the runs with decreased hydraulic capacity, evaporation from the soil and of precipitation intercepted by the canopy still exist and are larger during the wet season because of the higher temperatures. As a result, ET differ-

ences between runs are smaller during the wettest month (not shown). ET differences also are smaller over the driest site (D) during the driest month because there is little available soil moisture in all cases as a result of low precipitation. The largest impact on climate is seen when the differences in ET are largest (austral spring).

4. Implications and Conclusion

[21] Plant transpiration is limited by the supply of soil moisture to the leaves, which in turn depends on the both the availability of soil moisture and the hydraulic architecture of the plant. The transport system of angiosperms allows them to transpire more water than any other types of plants and thereby enhances their photosynthetic capacities. This increase of transpiration can trigger precipitation when the additional atmospheric moisture initiates convection, mostly during the transitions between wet and dry seasons. During the austral spring (dry-to-wet transition), the eastern part of the Amazon basin can have climate regimes with two equilibria depending on the moisture content in the boundary layer. If this moisture content is sufficient, a double ITCZ is generated in the simulation during October, which matches observations of the present-day climate. This region becomes dry in the simulations without full angiosperm transpiration.

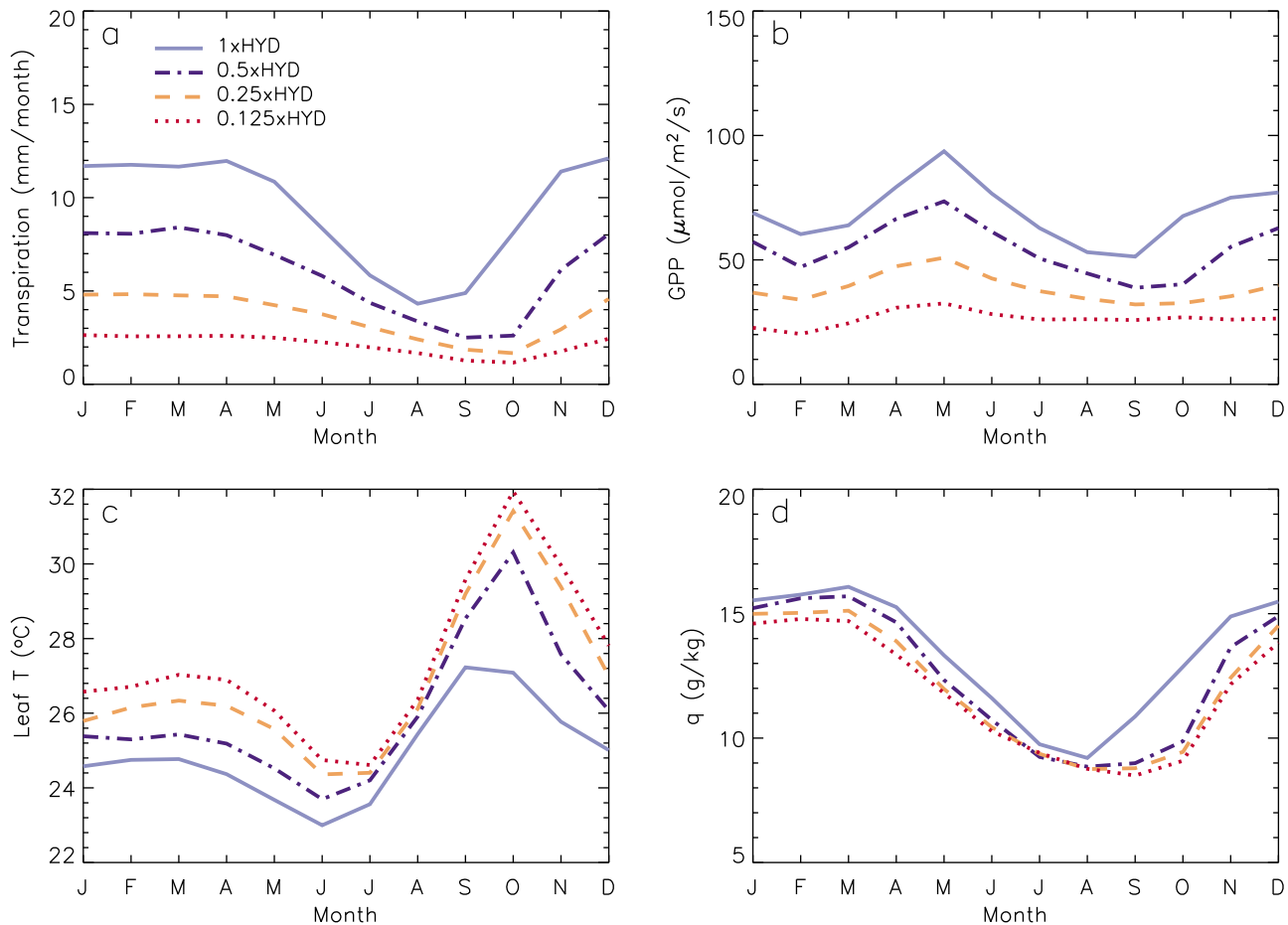


Figure 9. Monthly mean (a) GPP ($\mu\text{mol}/\text{m}^2/\text{s}$), (b) transpiration (mm/month), (c) leaf temperature ($^{\circ}\text{C}$), and (d) specific humidity (g/kg) for $1 \times \text{HYD}$ (light blue solid line), $0.5 \times \text{HYD}$ (blue dash-dotted line), $0.25 \times \text{HYD}$ (orange dashed line), and $0.125 \times \text{HYD}$ (red dotted line) runs at the point D in Figure 1.

[22] Depending on the scenario, the total increase of ET and rainfall averaged over tropical South America is about 100–300 mm, although with local differences as high as 1000 mm/yr. Over the study area, the ET increase ranges from 8% to 33% increase and the precipitation increase ranges from 8% to 22% (although proportionally smaller, absolute precipitation changes are similar to absolute changes in ET; Table 1). Because the continental-scale changes in convergence are small in comparison, the changes in moisture recycling with the higher hydraulic capacity of angiosperms are the dominant factors. Although large-scale atmospheric dynamics prevent a uniform effect, the overall result is an increase in the length of the rainy season and annual number of rainy days over the Amazon basin (Figure 10). Extension of the rainy season by angiosperm transpiration greatly increases the area of everwet rainforest, which corresponds to a minimum monthly precipitation of 100 mm [Morley, 2002] and at least 240 rainy days per year in our model. Both rainforest area and the number of the rainy days are important correlates of plant diversity [Leigh *et al.*, 1993; Krefl and Jetz, 2007]. Wetter climates also indirectly result in greater animal diversity due to the higher GPP and production of vegetative biomass, as well as the greater plant diversity allowing more specialist herbivores [Novotny *et al.*, 2006; Kay *et al.*, 1997; compare with Table 1].

[23] Angiosperms rose to ecological dominance during the Late Cretaceous and Early Cenozoic [Wing and Boucher, 1998], and we speculate that the high transpirational capacity of angiosperms was an important driver for the contemporaneous expansion of tropical rainforest. Changing land-ocean configuration and CO_2 concentrations [Ziegler *et al.*, 2003; Berner and Kothavala, 2001] may have both also contributed to the appearance and spread of tropical rainforest and are not addressed by the modeling performed here involving modern boundary conditions. However, we hypothesize that evolution of angiosperm physiology may have been an important biotic contribution in addition to those abiotic factors. Consideration of the Late Cretaceous/Paleogene and quantification of the effect of physiological evolution relative to other contributing factors will be an important next step.

[24] Intergovernmental Panel on Climate Change (IPCC) models predict hotter and drier tropical terrestrial climates with future increases in atmospheric CO_2 concentration [IPCC, 2007]. Deforestation [e.g., Asner *et al.*, 2006] will further contribute to decreasing precipitation through decreasing ET. Our work suggests that these climate changes will decrease tropical net ecosystem production not only by decreasing the soil moisture availability to plants and increasing soil respiration [King *et al.*, 1997; Cramer *et al.*,

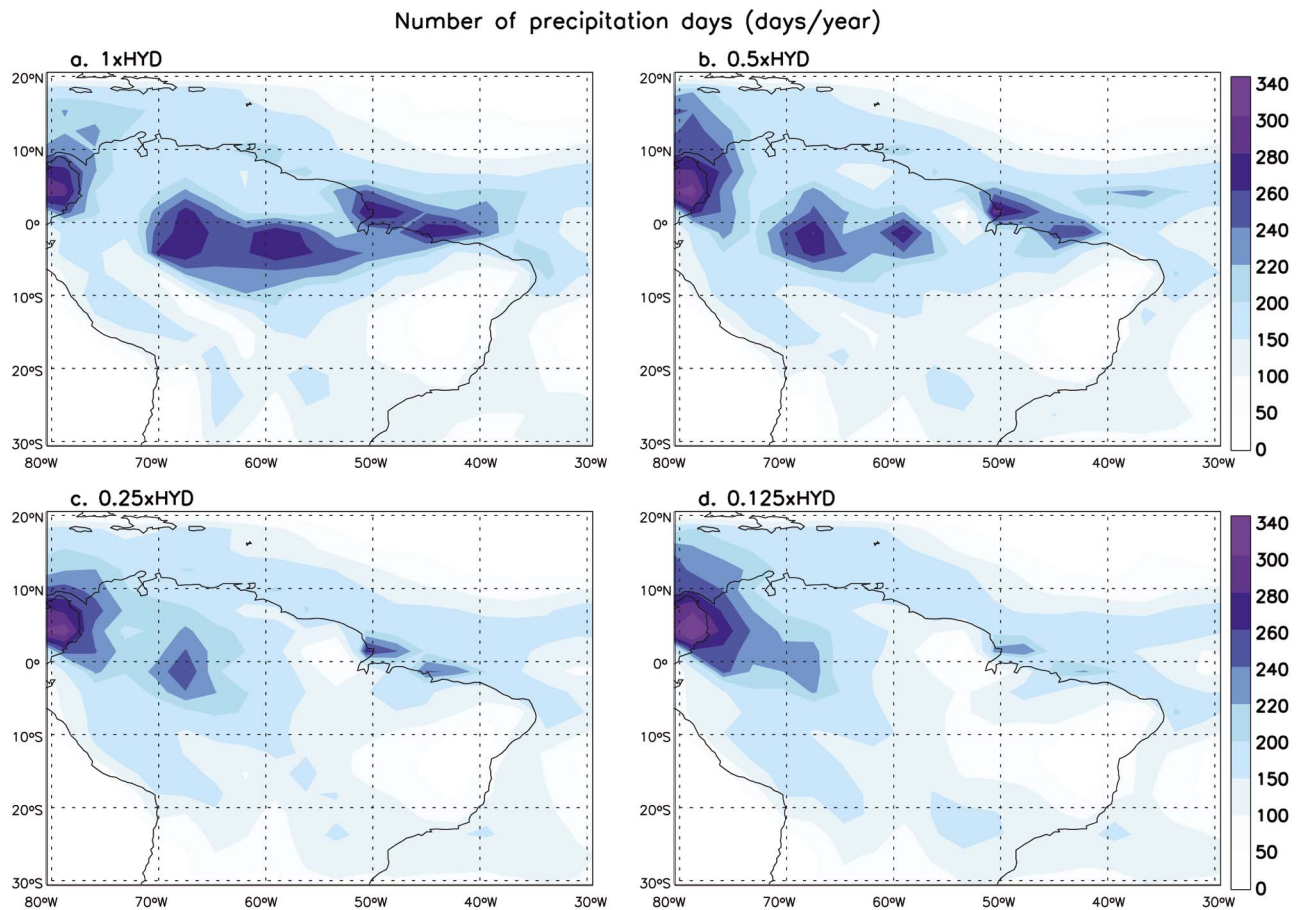


Figure 10. Number of precipitation days for (a) $1 \times \text{HYD}$, (b) $0.5 \times \text{HYD}$, (c) $0.25 \times \text{HYD}$, and (d) $0.125 \times \text{HYD}$. Precipitation days are defined as days when precipitation exceeds 3 mm/d. Using an alternative cutoff would change the number of rainy days but not the pattern. Area in which rainy day exceeds 240 days roughly corresponds to everwet tropics.

2001] but also by the increased water vapor pressure gradient between leaf and atmosphere resulting in decreased water use efficiency.

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