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Root functioning modifies seasonal climate

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Hydraulic redistribution (HR), the nocturnal vertical transfer of soil water from moister to drier regions in the soil profile by roots, has now been observed in Amazonian trees. We have incorporated HR into an atmospheric general circulation model (the National Center for Atmospheric Research Community Atmospheric Model Version 2) to estimate its impact on climate over the Amazon and other parts of the globe where plants displaying HR occur. Model results show that photosynthesis and evapotranspiration increase significantly in the Amazon during the dry season when plants are allowed to redistribute soil water. Plants draw water up and deposit it into the surface layers, and this water subsidy sustains transpiration at rates that deep roots alone cannot accomplish. The water used for dry season transpiration is from the deep storage layers in the soil, recharged during the previous wet season. We estimate that HR increases dry season (July to November) transpiration by ≈40% over the Amazon. Our model also indicates that such an increase in transpiration over the Amazon and other drought-stressed regions affects the seasonal cycles of temperature through changes in latent heat, thereby establishing a direct link between plant root functioning and climate.

Amazon | evapotranspiration | hydraulic redistribution

In nearly all ecosystems, 90–95% of roots are found within 2 m of the soil surface (1), where most of the nutrients reside (2). This common root distribution is known to maximize nutrient uptake (2). In contrast, deep roots comprise only a small fraction of the root system, yet the deepest 5% of roots may supply enough water to sustain transpiration and, therefore, ecosystem-level water loss in some environments (1, 3). Deep roots also have water transport conduits with much greater diameters and, therefore, higher hydraulic conductivity compared with shallow roots or stems (4–6). This structure allows for much higher water transport per cross-section of root.

Deep roots also are known to increase whole-plant water transport efficiency by redistributing deep soil water into shallow layers when leaf stomata are closed, mostly during the night but also on cloudy days (7, 8). This water helps maintain a shallow soil-water reservoir that then is used during the day by the "lifter" and/or the neighboring vegetation (9). This phenomenon is termed hydraulic lift (HL) (7, 8) or upward hydraulic redistribution (HR) (10). HR is the general term for upward or downward soil water transport by roots after Burgess *et al.* (10), who had not only observed HL but also the downward movement of water from shallow to deep soil layers following rainfall, after extended periods of drought. These processes allow recharge of soil water reservoirs to occur much more quickly than by percolation or capillary forces alone (8). HR also can serve to maintain functional roots year-round in all parts of the soil profile. Based on a review of existing studies that had documented HR, Caldwell *et al.* (8) speculated that the quantity of deep roots commonly seen in most plants would be too small to increase overall transpiration unless HR could occur. Thus, HR enhances the efficiency of deep roots; otherwise, plants should invest more carbon to roots to increase the availability of deep-soil water.

Although mean annual precipitation is close to 2,000 mm, about two-thirds of the Amazon forests experience a marked dry season from July to November [the timing and duration could be different depending on the year and the location (3, 11)]. Despite the lack of precipitation, Amazon forests maintain a very high level of canopy greenness (3, 12) as well as high photosynthetic rates (13–16) during the dry season. Additionally, da Rocha *et al.* (17) observed that tower-based measurements of evapotranspiration (ET) in dry season remained as high as during the wet season. Deep roots, and especially those related to HL, are thought to be responsible for supplying the water needed to sustain these unexpectedly high photosynthetic and transpiration rates during the dry season (3, 17). This conclusion is supported by data showing diel fluctuations in soil water content (17), which are always associated with HL. More importantly, however, both upward and downward HR have recently been documented in Amazonian trees (ref. 18 and Fig. 1), setting a precedent to now incorporate this important plant behavior into models.

Global climate and ecosystem models have difficulties simulating the seasonal cycle of temperature and photosynthesis in the Amazon. For example, ecosystem models commonly show a large decrease in photosynthesis during the 5-month dry season in the Amazon (19), yet some eddy flux measurements do not detect such a pattern (13). Also, atmospheric general circulation models (AGCMs) overestimate temperature over the Amazon during the dry season (11, 20) and predict a large decrease of ET at the same time. An underlying reason for this contradiction could be uncertainties in the parameterization of plant functioning in these models. Indeed, earlier work showed that artificially increasing rooting depth in an AGCM to maximize net primary production resulted in increasing plant-dominated ET and decreasing temperature up to 8°C during the dry season (11). However, observations indicate that the actual amount of deep roots may not be enough to account for such a change (1, 3).

Based on new observations at the ecosystem (13, 17) and whole-tree (18) scales, we hypothesize that HR is a major reason for the increase of the efficiency of deep roots with regards to water transport. This hypothesis finds support from the work of Dawson (9) who estimated that the increase in transpiration associated with HR could range between 19% and 40% for temperate forests (see also ref. 5). Moreover, when HL is modeled at the local scale (see refs. 21 and 22), Ryel *et al.* (21) in particular showed that transpiration increased up to 20.5% by adding HL. These estimates did not include the effect of storage during the wet season by reverse HR, meaning that the effect could be much greater if this storage in fact occurs as recently shown for Amazonian trees (ref. 18 and Fig. 1). These observations and model results led us to test further our hypothesis with an AGCM.

Methods

Measurements. We used the heat-ratio method (HRM) (10) to make continuous measurements of sap flow in roots and stems
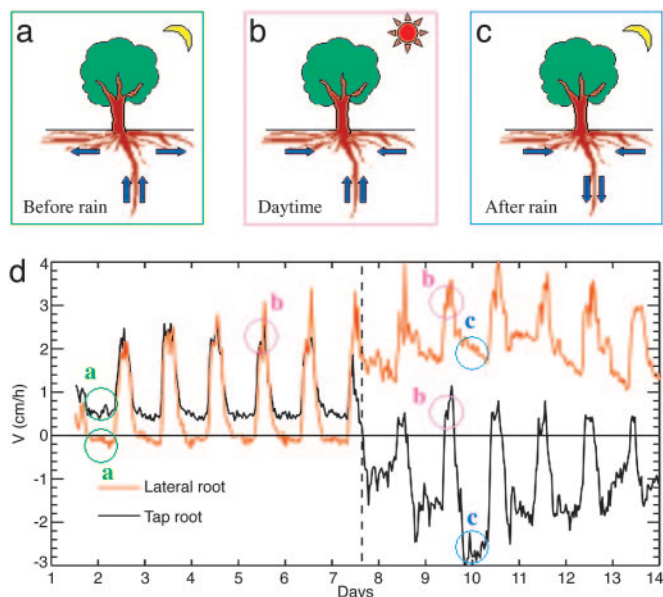

Fig. 1. Sap velocity in the taproot and lateral root of *P. robustum* during the transition from the dry to wet season in the Floresta Nacional do Tapajós. (*a–c*) Schematics for water movement at nighttime before the rain (*a*), daytime before and after the rain (*b*), and nighttime after the rain (*c*). Arrows shown the dominant flow direction determined by sapflow. (*d*) Graph showing sap velocity. Positive values mean that water flows to the plant, and negative values means away from the plant into the surrounding soil. The dashed line represents a rain event (36 mm). See the text for a complete explanation.

of our study species. The principle of the HRM is to measure the increase in temperature after a heat pulse at two points, above and below a heater inserted 6 mm into the active sapwood. We elected to use this technique because it allows bidirectional measurements of sap flow and also measures very slow flow rates.

Model. To assess the impact of HR on global climate, we carried out two simulations using the National Center for Atmospheric Research Community Atmospheric Model Version 2 (CAM2) (23) coupled with the Community Land Model (CLM) (24). In the CLM, stomatal conductance of plant leaves is determined as a function of top-of-canopy air temperature, CO_2 concentration, sunlight, and soil moisture. The corresponding photosynthesis (CO_2 uptake) and plant transpiration (H_2O loss) are in turn determined as a diffusive flux across the stomatal opening, and are proportional to the gas (CO_2 and H_2O) pressure gradient between the stomata and the surrounding atmosphere. The carbon dioxide and water fluxes are integrated over the multiple layers of leaves by using an assumed function of light attenuation through the canopy. Soil water is moved from the soil to the atmosphere in proportion to the prescribed root density within each soil layer (24).

In the AGCM, soil water transport is modeled by using Darcy's law (24). Hydraulic conductivity for soil water infiltration is parameterized as a function of soil texture and soil water content. For the HR run, we include in addition the rate of hydraulically redistributed water as

$$q = -C\Delta\psi, \qquad [1]$$

where q is the amount of water flux (m^3/s), C is the hydraulic conductance of HR, and $\Delta\psi$ is defined as the difference in soil water potential between the uptake and release layers in the soil profile. Following refs. 21 and 25, we formulate C as

$$C = C_{sat}\left(1 + \frac{\psi}{\psi_{50}}\right)^n r, \text{ and } C_{sat} = A \cdot LAI. \qquad [2]$$

Here, C_{sat} is the hydraulic conductance for water uptake from the uptake layer when soil water is saturated, ψ is the water potential of the uptake layer, ψ_{50} is the water potential when soil hydraulic conductance (in Darcy's law) is reduced by 50%, r is the root fraction in the uptake layer, LAI is the leaf area index and is used here as a proxy for transpirational demand, and A is an empirical coefficient. We set $n = 2$, and $A = 0.5 \times 10^{-3}$ $kg/s \cdot Pa^{-1}$. Eq. **2** essentially allows water transport between two layers when there is a large transpiration demand and difference in water potential. All plants are allowed to redistribute water through their roots, with the amount of HR proportional to the leaf area index, so that if plants maintain canopy greenness while water stress exists, more water will be lifted by upward HR. For more details, see *Supporting Text* and Fig. 6, which are published as supporting information on the PNAS web site. Many researchers have shown that leaf area index is a good measure of the whole-tree hydraulic conductance when soil water is saturated (25, 26). HR is now recognized as a widespread phenomenon, with many plants showing the ability to transport water and redistribute it within their rhizosphere, when a water potential gradient exists in the soil. To date, there are only three tree species [*Quercus margaretta* (27), *Acer rubrum*, and *Castanea dentata* (T.E.D., unpublished data)] and one grass species [*Schizachyrium scoparium* (27)] that we know of where HR has been explicitly sought but not found. In contrast, >60 species, across xeric, semiarid, temperate, and tropical biome types, have been observed to possess the ability to redistribute soil water during the night (8). Moreover, recent evidence on the ultra-structure of root and other plant cell membranes indicates that channels, often called aquaporin channels, may be more widespread than originally thought (28) and serve as the pathway for water movement into and out of roots during HR events.

We carried out two 10-year integrations, one control and one with HR. In both runs, climatological sea-surface temperature and sea ice distributions were specified. The soil depth was extended from 3 to 10 m by adding two layers at the bottom of the standard model, based on the field data showing that water uptake by Amazonian forest plants can occur down to a depth of 12 m during the dry season (3). This extension of soil layer would be too deep in some places where bedrock appears below a certain depth. However, the amount of deep roots in those regions would be very small because we followed the observed root distribution so that this effect would be minimal. For the HR run, we assumed that upward HR during the dry season brings water to only within 4 cm of the surface, because many superficially shallow (0–5 cm deep) roots die in very dry soils (29, 30). Water drawn up by upward HR is therefore not available for soil evaporation in the HR run; however, soil water coming directly from rain will be continuously evaporated. Furthermore, root fraction r (Eq. **2**) in the HR run is modified to have linearly increasing hydraulic conductivity with depth so that roots at 10-m depth have 20 times higher hydraulic conductivity than those near the surface, consistent with published data (4–6). A sensitivity experiment included increased conductance of deep roots but not HR to highlight the role of HR (see Fig. 3).

The resolution of the model is T42 ($\approx$2.8° latitude $\times$ 2.8° longitude) with 12 layers in the soil and 26 layers in the atmosphere. We initialized soil water with 0.3 m^3/m^3 everywhere for both runs. For all of the runs, we modified the runoff parameters by changing the portion of low water table area in a grid box from 0.3 to 0 so that more water could infiltrate the soil. The models were integrated for 10 years, and results from year 3 to 10 were averaged and are analyzed below.
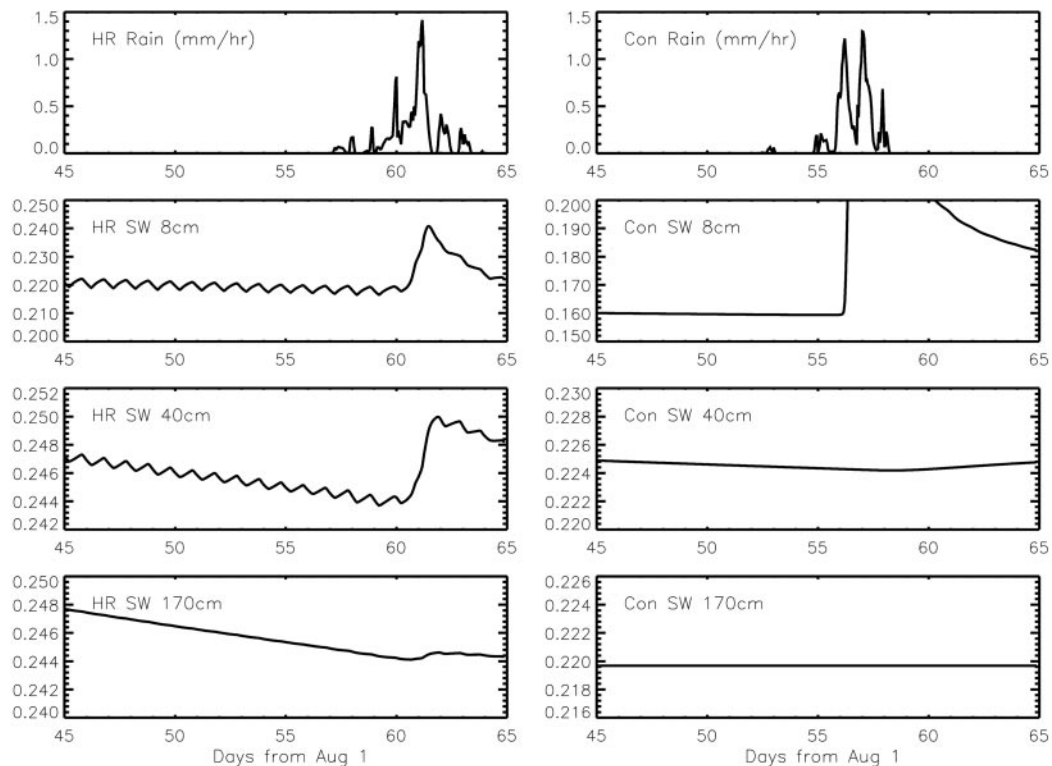
Fig. 2. Rainfall (mm/day) and soil water content (m³/m³) at 8, 40, and 170 cm below the surface for the HR (*Left*) and control runs (*Right*) at the grid point near the observation site from ref. 17 (3.01°S, 54.58°W).

Results and Discussion

Our field studies confirmed the occurrence of HR in Amazonian trees (18). The data in Fig. 1 show nighttime reversals in sap flow in the lateral roots (acropetal flow; from the roots away from the stem) and positive sap flow (basipetal; toward the stem) in the tap root of *Protium robustum* in the dry season (see sap flow traces on Fig. 1 before the dashed line). Other species, *Cousarea racemosa* and *Manilkara huberi*, common trees in the Floresta Nacional do Tapajós, Amazonia, also exhibit HR (18). With the onset of heavy, wet season rainfall, we observe basipetal nocturnal sap flow (water uptake) in the shallow lateral roots and continuous nighttime reversals in sap flow in the tap root of this species, indicating nighttime water movement from wet top soil into lateral roots and then downward toward deeper soils via the deep tap root. This finding means that HR helps store (or restore) water into the deep soil layer after significant rainfall events.

One of the most remarkable phenomena related to HR is the daily fluctuation of soil water content (7, 17) (Fig. 2) that is brought about by roots actively replenishing soil water reservoirs each day. The difference in plant water use between AGCM runs can be seen in the fluctuations of the soil moisture profile, especially during the dry season and after a heavy rainfall (Fig. 2). Consistent with direct observations (7, 17), our model with HR simulates the nighttime increase and daytime decrease of shallow soil water during the dry period as well as after the rain. After the rain event, deep-soil water increased for the HR but not the control run. Because of this enhanced vertical transfer of soil water by roots, runoff decreased from 11% of total precipitation in the control run to 1% in the HR run (data not shown), which is comparable with the observations (31). We estimated deep-soil water recharge based on the increase of soil water content measured in deep soil layers (5–11 m) between March and April 2002 (18). We found out that 64.8 mm of water was

transferred as a result of 567.7 mm of rain over 26 days. Therefore, the amount of transferred water was ≈11% of precipitation for this period, and this amount is comparable with our estimation of 10% decrease of runoff by HR. With HR, more water is transported to the deep soil layers during the wet season, available for use during the dry season (as shown in ref. 18), resulting in greater seasonal fluctuation of deep-soil water in the HR than the control run (data not shown), which is also the pattern commonly observed when HR is present (5, 7–10). The lack of soil-water transport to the deep soil layer in the control run could be because of the lack of macropores (old root channels or large cracks in the soil profile) in the model; however, observations (10, 18) certainly show the existence of downward HR after rain, and we believe that this factor enhances wet season storage of soil water.

With HR by roots, there is greater storage of soil water at depth during the wet season, available for subsequent withdrawal from and redistribution into shallow layers during the dry season. This additional water allows photosynthesis to increase during the dry season, as compared with the control run (Fig. 3). When there is a greater deep-root contribution to water uptake, but no HR, photosynthesis is almost identical to the control run during the dry season. Fig. 3 confirms that HR is largely responsible for the photosynthesis increase as well as for the enhanced ET. During the wet season, photosynthesis shows a depression for plants with more deep-root contribution (green dash-dot line in Fig. 3). During the wet season in the control run, transpiration is supplied by shallow water. The increase in deep-root fraction is accompanied by a decrease in shallow-root fraction. As a result, the deep roots enable more efficient extraction of the small amount of deep-soil water, and there is less shallow water transpired. Furthermore, the downward infiltration rate of water remains the same between the control and deep-root cases. As a result of the faster uptake by the deep roots, there is a
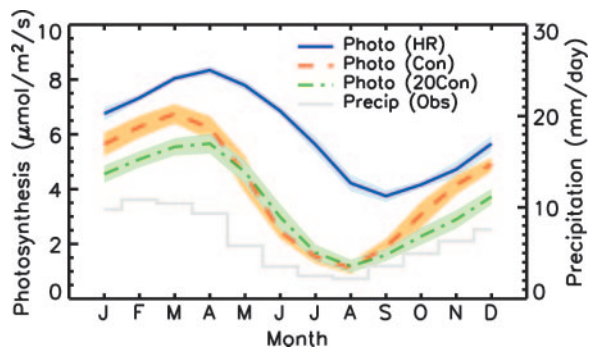
Fig. 3. Seasonal evolution of photosynthesis (μmol/m² per s) for the Amazon basin (10°S–equator, 70°W–50°W) from the HR (blue solid line), control (red dashed line), and control run with increase deep-root conductance (green dash-dot line) runs. Shaded area represents one standard deviation from 8 years of the simulation. Gray line represents observed mean monthly precipitation for the region.

progressive drying of deep soils, and water becomes limiting for photosynthesis.

The influence of HR on climate is evident in the reduced seasonality of ET over the Amazon compared with the control run (Fig. 4a): substantial ET is sustained at the end of rainy season in April and continuing into the dry season in September. There is also a 40% higher rate of transpiration during the July to November dry season in the HR case because the access to deep-water stores permits continued daytime water use. An important finding from our model results is the reduction of dry season surface-air temperature associated with HR (Fig. 4b), because of enhanced latent cooling associated with the increased plant transpiration (Fig. 4b). Thus, the HR run captures, and thus helps explain, the observed temperature decrease in June and July when the solar zenith angle is at its lowest. In the HR run, surface-air temperature has a seasonal pattern that is closer to the observations than in the control case, especially in the latter part of the dry season (from August to October) when upward HR is known to occur (18). Remaining differences in surface-air temperature could be because of a $\approx$30% underestimation of precipitation in the model (for example, due to errors in remote forcing or local cloud and convective parameterizations) and consequently of soil water contents in the wet season (31) and transpiration during the dry season.

In the HR run, all plant types possess the capability for HR, resulting in an increase in transpiration over the entire water-stressed regions of the Earth (Fig. 5a) (South America including

Amazon, eastern and western U.S., the Mediterranean region, southern Africa, southeastern Asia, and southeastern Australia). Temperatures in these regions decrease significantly, by as much as 2°C during the dry season, with the incorporation of root hydraulic water redistribution (Fig. 5b). What is important to note is that all of these regions are actually regions that contain plants for which HR has been previously documented (refs. 7–10, 17, 18, 21, 29, 30, 32, and 33 and P. Becker, personal communication), lending empirical support for the broad nature of our model findings and a perspective on the global impact of plant-root functioning on global climate. Because of the marked temperature decrease and simultaneous moisture input increase in the water-stressed regions, the tropical convective climate is significantly affected (34). A change in this vast and important climate driver is therefore propagated to the higher latitudes.

Conclusions

We have incorporated HR into the National Center for Atmospheric Research AGCM and shown that the redistribution of soil water via plant roots is the main reason that rates of photosynthesis in Amazonian forests are sustained during the dry season. HR represents an increase in the overall water transport efficiency of deep roots, transferring wet season "recharge rainfall" downward for storage and transferring the stored water upward to meet the demand by plants during the dry season. As a result, transpiration is enhanced, and temperature decreases during the dry season. In our modeling experiments, we assumed that most of the plants have the capability to redistribute water, and the amount of the soil-water transport is proportional to the leaf area index. This parameterization is shown to yield soil-water profiles and fluxes consistent with available observations and also to enhance transpiration where HR is observed.

Our modeling and observations have implications for how plant-level cycling of water and carbon impacts the global climate system. As shown, the capability of wet season "banking" of water and its subsequent dry season withdrawal by the root system is crucial in the determination of the seasonal cycle of ET and temperature over the Amazon and over the globe (Fig. 5 c and d). The functioning of plant roots will feedback on the carbon balance over the Amazon and other regions because both plant photosynthesis (carbon uptake) and respiration (loss) are very sensitive to temperature and moisture regimes. For example, if wet season precipitation is not enough to recharge the deep reservoir after severe drought, photosynthesis will be diminished in the following "normal" dry season. A recent report of productivity decreases in subcanopy species (35) lends support to this notion and illustrates that declines might be due
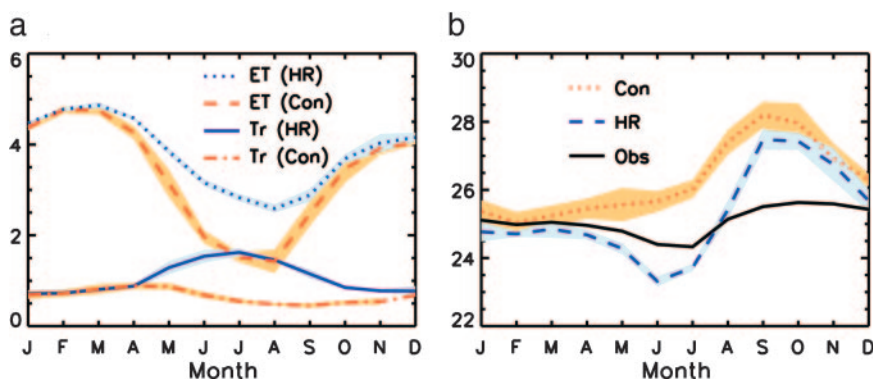
Fig. 4. Seasonal evolution of AGCM results for the Amazon basin (10°S–equator, 70°W–50°W) from the HR and control runs. (a) Mean monthly transpiration (mm/day) with (blue solid line) and without (red dash-dot line) water redistribution; total ET (mm/day) with (blue dotted line) and without (red dashed line) water redistribution. (b) Surface temperature (°C) with (blue dashed line) and without (red dotted line) water redistribution, and observed (black solid line). Shaded area represents one standard deviation from 8 years of the simulation.
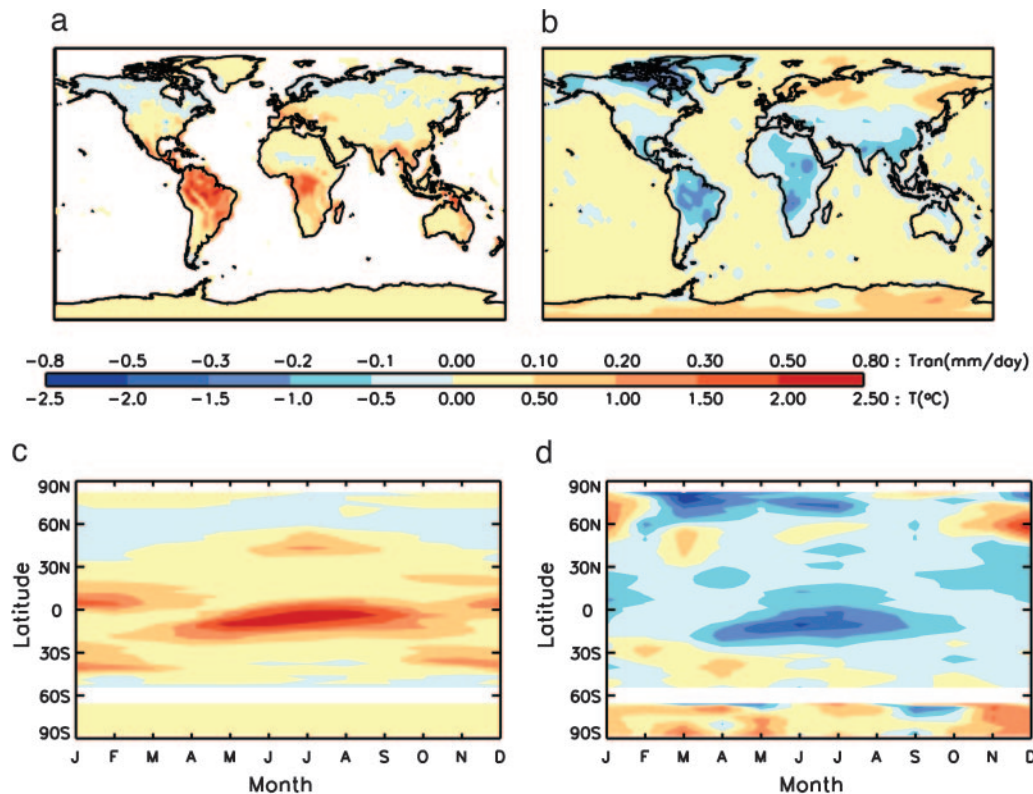
Fig. 5. The effect of HR on global transpiration and temperature. Global distribution of the departures of mean annual transpiration (mm/day) (*a*) and mean annual temperature (°C) (*b*) in the HR run from those in the control run. Latitudinal and seasonal distribution of the zonally averaged departure of transpiration (*c*) and land temperature (*d*) in the HR run relative to that in the control run, showing moistening and cooling of the boundary layer during the dry season.

to the prolonged decrease of precipitation during the unusually strong El Niño events that occurred at the end of the last century. Some subcanopy species might depend on deep-rooted open-canopy species for their dry season water supply (as described in ref. 9), and this supply via HR can, in fact, be limited during drier years (29). If that is the case, the impact of deforestation in the Amazon on climate might be greater than we had previously thought. Finally, because the global water and carbon cycles are so intimately coupled, our work also enhances our confidence in accurately predicting how land use and climate changes will impact global biogeochemical cycles.

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