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Special Collection:

Land-atmosphere coupling: measurement, modelling and analysis

Key Points:

- We provide a first estimate of the contribution of transpiration from trees and non-tree vegetation to precipitation over major African watersheds
- On average, trees contribute more to continental precipitation (777 mm year⁻¹) compared to non-tree vegetation (342 mm year⁻¹)
- Considering the extent of non-tree vegetation, most watersheds depend mostly on non-tree transpiration for precipitation throughout the year

Supporting Information:

Supporting Information may be found in the online version of this article.

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Critical Importance of Tree and Non-Tree Vegetation for African Precipitation

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Abstract Vegetation is a major contributor of terrestrial evaporation and influences subsequent precipitation over land. Studies suggest that forests are crucial for moisture recycling, although the specific contribution of different vegetation to precipitation remains unclear. Using a moisture recycling approach, we investigate the contribution of transpiration from trees and non-tree vegetation to precipitation over Africa. We use precipitation source regions from simulated atmospheric moisture trajectories, constrained by observation-based evaporation and precipitation products, and fractional vegetation cover data. Our findings show that trees provide a higher flux to precipitation (~777 mm year⁻¹) than non-tree vegetation, precipitation in most watersheds effectively depends more on the latter. Overall, non-tree vegetation appears equally important as trees in terms of volumetric contributions to precipitation, and deserves attention in further research, considering ongoing land use changes that affect the continental water cycle.

Plain Language Summary A large part of rainfall on Earth derives from evaporation from land. This process, referred to as terrestrial moisture recycling, is controlled for a large part by vegetation cover. Different classes of vegetation cover use water differently, but it is unclear how they contribute to moisture recycling (and thus precipitation) over land. In this study, we estimate the contribution of trees and other, non-tree vegetation to precipitation over the African continent. We use major watersheds, and track back the source regions of rainfall. We find that overall, trees contribute relatively more to precipitation compared to non-tree vegetation. However, due to the extensive coverage of other vegetation classes (such as grass- and shrublands), many regions depend on non-tree vegetation for rainfall. Ongoing land use and land cover (LULC) changes may disturb terrestrial moisture recycling patterns. The findings of this study emphasize that the impacts of all LULC changes, including non-tree vegetation, on the water cycle should be considered and further researched.

1. Introduction

Terrestrial moisture recycling is a pivotal Earth system process for redistributing water resources over land. Various studies demonstrate how regions depend on land evaporation for significant shares of their precipitation (Keune & Miralles, 2019; Trenberth, 1999; Van Der Ent et al., 2010). Vegetation cover regulates energy and water exchanges through changes in albedo, aerodynamic conductance, transpiration and rainfall interception (Schlesinger & Jasechko, 2014; Wang-Erlandsson et al., 2014; Wei et al., 2017) and as such, is an important contributor to observed rainfall that originates from the land surface (Keys et al., 2016; Yu et al., 2017). Moisture recycling studies suggest that trees in tropical forests buffer against meteorological drought and rainfall variability by preserving a stable flux of transpiration during dry periods (O'Connor et al., 2021; Pranindita et al., 2021) their rooting system may allow them to access ground water (Syktus & McAlpine, 2016). In tropical regions, transpiration from forests is crucial for maintaining local moisture recycling and forest stability (Staal et al., 2020), while initiating moisture recycling cascades that distribute atmospheric moisture from the coastal regions to the continental interior (Staal et al., 2018, 2020; Zemp et al., 2014). Various studies show how such moisture recycling patterns can be disrupted when tree cover is lost (Bagley et al., 2014; Baudena et al., 2021; Ruiz-Vásquez et al., 2020; Spracklen & Garcia-Carreras, 2015). Considering this hydro-climatic importance of trees, Tuinenburg et al. (2022) suggest that a global forest restoration scenario (Bastin et al., 2019) could increase global evaporation by 0.03 mm day⁻¹, of which almost 70% precipitates over land.



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Overall, forests and trees are ubiquitous in moisture recycling research due to their perceived importance to terrestrial precipitation patterns and water availability. Yet, less attention has been paid to the contribution of moisture from other, non-tree vegetation to precipitation. In fact, the "hydro-climatic functioning"—here defined as the contribution of transpiration to atmospheric moisture and precipitation through atmospheric moisture trajectories—of non-tree vegetated ecosystems (such as grass-, shrub and croplands) remains relatively understudied, in comparison to forests, despite comprising a large extent of the Earth's surface. As strong land-atmosphere interactions exist in semi-arid transition zones outside of densely forested regions, some studies suggest that vegetation in these areas—generally dominated by non-tree vegetation—is of particular importance for moisture feedbacks (Green et al., 2017; Koster et al., 2004; Yu et al., 2017). Furthermore, non-tree vegetation is equally at risk from ongoing land use and land cover (LULC) changes (Herrmann et al., 2020; Winkler et al., 2021), which may affect moisture recycling patterns and regional-to-continental water availability.

Here, we assess the hydro-climatic function of both tree and non-tree vegetation for the African continent, by quantifying the proportion of terrestrial precipitation deriving from transpiration (Precipitation-from-Transpiration, hereafter "P_T") from these two vegetation classes for 25 major African watersheds. We focus on biologically-controlled evaporation (i.e., transpiration) only, while acknowledging that evaporation from interception comprises a significant part of total evaporation (Savenije, 2004; Wang-Erlandsson et al., 2014). We focus on Africa because of its high susceptibility to accelerating LULC changes (Herrmann et al., 2020; Winkler et al., 2021) and climate change-induced water scarcity (Leal Filho et al., 2022). Africa also remains relatively understudied, with most research addressing vegetation-rainfall linkages in Amazonia (e.g., Spracklen & Garcia-Carreras, 2015; Staal et al., 2018; Zemp et al., 2017). To distinguish between tree and non-tree vegetation we use data from MeASURES Vegetation Continuous Fields (VCF) (Friedl and Sulla-Menashe, 2022), based on tall (i.e., tree, >5 m) and short (i.e., non-tree, <5 m) vegetation cover fractions. P_T estimates are derived from the Lagrangian model FLEXPART, driven with ERA-Interim reanalysis data between the years 1981–2019 (Keune et al., 2022). Estimates of terrestrial precipitation (P) are constrained by MSWEP v.2.8 (1981-2019) (Beck et al., 2019), and evaporation (E) and transpiration (T) by GLEAM-Hybrid (1981-2019), a new observationbased model combining sap-flow and eddy-covariance data with satellite observations (Koppa et al., 2022a). GLEAM-Hybrid also provides estimates for short and tall vegetation transpiration using the above-mentioned vegetation cover fraction data from MeASURES. Furthermore, we identify the fraction of transpiration from a prescribed source region that returns as precipitation over the sink region-major African watersheds or the entire African continent, hereafter referred to as transpiration-to-precipitation, or "T_p." Unless defined otherwise, we consider all (global) land surface as source regions to estimate the origin of African precipitation. Both T_P and P_T are estimated monthly over 1981–2019 at 1° spatial resolution, and aggregated to watershed and continental levels. At the continental level, we examine the spatial distribution of $T_{\rm P}$ contributions to identify important precipitation source regions. At the watershed level (Figure S1 in Supporting Information S1), we identify the seasonal dependency of different precipitation sources by examining wet and dry season T_p, to further examine variation of spatial and temporal moisture recycling patterns. We ask to what extent these patterns reveal different hydrological resilience functions of vegetation types, that is, whether trees buffer against drought by providing stable moisture fluxes during dry seasons (O'Connor et al., 2021; Pranindita et al., 2021). We also examine the local difference between tree and non-tree $T_{\rm p}$ ($\Delta T_{\rm p}$), across climatic conditions, to use as a proxy indicator for the areas where an increase in tree cover over non-tree vegetation, may increase precipitation over the continent.

2. Methods

2.1. Moisture Trajectories Over African Watersheds

We applied the Lagrangian model FLEXPART to identify atmospheric moisture trajectories over African watersheds. The model is driven with ERA-Interim reanalysis data over 1981–2019. The moisture tracking framework from Keune et al. (2022) is applied to estimate the spatially explicit (1°) daily source regions contributing to precipitation over each watershed (Te Wierik et al., 2022). FLEXPART based simulations have been used in various studies (see Te Wierik et al., 2022) and facilitate moisture flux identification with a reasonable accuracy (Keune et al., 2022). The resulting spatially explicit source–sink relationships are biascorrected using evaporation from the hybrid version of the Global Land Evaporation Amsterdam Model (GLEAM-Hybrid) (Koppa et al., 2022a) and precipitation from the multi-source weighted ensemble precipitation (MSWEP v2.8, Beck et al., 2019) and aggregated to monthly values. Further, the framework disaggregates source region contributions into fluxes of evaporation, transpiration from tall vegetation (i.e., trees), and transpiration from short vegetation (i.e., non-tree vegetation). This hybrid model deploys a deep-learning algorithm to estimate a transpiration stress parameter underlying estimations of E and T, yielding better performance based on validation with flux towers and sap-flow data compared to the process-based model of GLEAM (Koppa et al., 2022a). The latter differentiation between tall and short vegetation is based on vegetation fractions from MeASURES Vegetation Continuous Fields (VCF). We only use transpiration fluxes, which we aggregate to mean annual and seasonal (i.e., dry- and wet-season) contribution to precipitation (%) over all watersheds. Dry and wet seasons were differentiated for individual watersheds, based on the method described in Te Wierik et al. (2022). The extent of the wet and dry seasons are defined based on the particular month being wetter or dryer compared to mean monthly P.

2.2. Estimating Tree and Non-Tree Contributions

Source regions of P were linked to global fractional vegetation cover data from MeASURES VCF. We use mean fractions of tall vegetation (>5 m) and short vegetation (<5 m) cover over 1981–2019 as a proxy for trees (i.e., tall) and non-tree vegetation (i.e., short). The fractions are aggregated from their original resolution (0.05°) to 1° spatial resolution to match the moisture source-sink data. We derive the following metrics to understand absolute and relative contributions of trees to precipitation for each watershed and at the continental level. First, to understand the absolute rainfall dependency on trees and non-tree vegetation (km²) from tree and non-tree vegetation (i.e., km³ year⁻¹). Second, we compute the mean T_P flux from tree and non-tree vegetation (mm year⁻¹), normalized over the extent of tree and non-tree vegetation (km²) from MeASURES VCF fractions for each grid cell of the contributing source region (i.e., defined by all grid cells where the mean annual T_P contribution is higher than the threshold T_{min} = 0.1, 0.5, 1.0, and 5.0 mm year⁻¹), see Figure S2 and Table S1 in Supporting Information S1. At last, we identify the fraction of mean annual, wet and dry season share of T-sourced P over total P (%) in the sink regions. Furthermore, we evaluate local difference in mean annual T_P (Δ T_P) at the grid cell level (1°) across local climate conditions, for which we use mean annual P (mm year⁻¹) from MSWEP.

3. Results

3.1. Transpiration Contribution to Precipitation Over the Continent

In line with previous studies on the contribution of trees to moisture recycling (Pranindita et al., 2021; Staal et al., 2018), we find that tree transpiration is an important contributor to precipitation across the African continent. On average, our results confirm that T_p from trees (777, $\sigma = 110$ mm year⁻¹) is higher than from nontree vegetation (342, $\sigma = 103$ mm year⁻¹) (Figure 1a). Our estimate for tree T_P is within the range of previous estimates on the contribution of forests to precipitation. For example, Tuinenburg et al. (2022) estimated that tropical forest evaporation (including transpiration and interception loss) contributes 1-3 mm day⁻¹ (corresponding to 365-1,095 mm year⁻¹) to precipitation over land This estimate was derived from estimates of current evaporation for different land use classes, based on PCRaster GLOBal Water Balance Model (PCR-GLOBWB, v.2) and reference evaporation using Penman-Monteith equation. Evaporation change associated with land cover change is based on the (potential) evaporation difference between the four identified land use classes in a given location. Subsequently, the sink of evaporation differences was tracked with the atmospheric moisture tracking model UTrack. However, considering the smaller extent of tree cover in the contributing source region (5.4 Mkm²) (Figure 1b) in comparison to non-tree cover (16.8 Mkm²), the total precipitation supplied through non-tree vegetation ($T_P \sim 5.7 \cdot 10^3 \text{ km}^3 \text{ year}^{-1}$) well-exceeds the contribution of trees ($T_P \sim 4.2 \cdot 10^3 \text{ km}^3 \text{ year}^{-1}$) (Figure 1c). Note that the contributing source region estimate is based on the (global) source region where mean $T_P > 0.5$ mm year⁻¹. We apply this threshold (T_{min}) to reduce noise from marginally contributing areas. Around 68% and 77% of the contributing source region for non-tree and tree vegetation, respectively, is located in Africa, but the majority of T_P (km³ year⁻¹) derives from the continent itself (98% of all P_T from non-trees, and 99% of tree T_p). Figures 1d–1g show important regions for tree (d and f) and non-tree (e and g) transpiration contributions to African precipitation. Figures 1d and 1e show the regions where trees and non-tree vegetation, respectively, provide high volumetric amounts of T_p (km³ year⁻¹) to continental P; Figures 1f and 1g represent the corresponding flux rates (mm year⁻¹) of T_p from tree- and non-tree cover in each grid cell of the global source region. In other words, these figures identify regions where vegetation is particularly important to supply moisture for precipitation over the African continent. For trees, the Congo rainforest, the Ethiopian highlands, and the coastal region of West Africa provide significant amounts of volumetric T_P (local contributions reach up to 15 km³ year⁻¹



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Figure 1. Mean annual contribution of global tree and non-tree transpiration (here visually constrained to the African extent) to precipitation over the African continent. (a) The mean flux of transpiration-to-precipitation (mm year⁻¹) from trees and non-tree vegetation; (b) The total coverage of both vegetation classes in the contributing source region (km²). Note that the (global) contributing source region is determined using a local (mean) threshold for transpiration-to-precipitation (T_{min} , >0.5 mm year⁻¹), see Figure S2 in Supporting Information S1; (c) The mean flow of transpiration-to-precipitation (km³ year⁻¹) from trees and non-tree vegetation; (d) Spatial distribution of mean annual transpiration-to-precipitation flow from trees (km³ year⁻¹) and non-trees (e); (f) Spatial distribution of mean annual transpiration-to-precipitation flux from trees (mm year⁻¹) and non-trees (g). Flux estimates are based on the fractional tree or non-tree vegetation cover in each grid cell.

at grid cell level, Figure 1d). The volumetric T_P from non-tree vegetation appears more spread out over the continent but are equally important around the equator and in the Ethiopian highlands, and the area surrounding Lake Victoria (local contributions sum up to 10 km³ year⁻¹, Figure 1e). Figures 1f and 1g show how flux contributions (mm year⁻¹) are similarly spread out over the continent. In contrast to the volumetric contributions, these fluxes are less dependent on the land cover extent, and therefore are relevant to consider in terms of its dependency for regions with less volumetric water availability. Solely looking at volumetric contributions, would only highlight regions with high total water availability, and would ignore the relative dependencies of watersheds on the crucial contributions of moisture.

These figures highlight regions that may be important to consider in ecosystem conservation and land management to protect water availability across the continent. Overall, 33% of precipitation over the African continent (varying $\sim 4\% - 40\%$ across watersheds) derives from transpiration: $\sim 14\%$ ($\sim 1\% - 25\%$) from trees and $\sim 19\%$

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Figure 2. The contribution of tree and non-tree vegetation transpiration to precipitation over individual African watersheds. (a) Distribution of the proportion of mean annual precipitation (%) deriving from tree (green) and non-tree (yellow) transpiration (individual watersheds are represented by dots); (b) Dry and wet season differentiation of the proportion of precipitation deriving from tree and non-tree vegetation transpiration (%) over all watersheds.

(~4%–32%) from non-tree vegetation. Note that in some regions along the equator, the estimated contributions of T_p are higher than local precipitation, suggesting either that T_p estimations are overestimated, or P is underestimated (Figure S3 in Supporting Information S1).

3.2. Contribution to Precipitation Over Major African Watersheds

Following the approach of Te Wierik et al., 2022 (see Section 2), we explored T_P fluxes over individual watersheds, and find that, despite a higher mean T_P flux (mm year⁻¹) from trees, most watersheds depend substantially and persistently on non-tree vegetation transpiration for their precipitation supply (Figure 2). This can be explained by its larger spatial extent compared to trees (see Figure S4 in Supporting Information S1 for the flux-based contributions for each watershed). Figure 2a represents the mean annual contribution of tree transpiration (green bar) and non-tree vegetation transpiration (yellow bar) to annual precipitation for all watersheds. The Congo watershed (nr. 4 in Figure S2 in Supporting Information S1) is a clear exception, where more than 25% of the precipitation within the watershed derives from tree transpiration (green dot outlier in Figure 2a), compared to 15% from non-tree vegetation. Figure 2b further differentiates between contributions of dry season (light shades) and wet season (dark shades) precipitation and confirms a persistent high dependency on non-tree sourced precipitation throughout the year in most watersheds, although in none of the watersheds, the actual contribution of vegetation is higher in the dry season compared to the wet season (Figure S4 in Supporting Information S1).

Observation-based sap flow and soil moisture availability in the Amazon rainforest show that, during the dry season when soil moisture availability in the upper soil is limited, there are variable responses of tree water use, suggesting that—at least some—trees preserve sap flows (and hence precipitation over land) even in the dry period. This is due to their ability to tap into water in deeper layers of the soil through their rooting network (Spanner et al., 2022). Sap flow measurements provide suitable proxies for quantifying temporal dynamics of transpiration and subsequent precipitation over land (Poyatos et al., 2021). This implies that trees could play a crucial role for the water cycle and precipitation patterns when soil moisture availability is limited. The findings presented here do not show a consistent increase in the relative contribution to precipitation from trees in the dry season in most watersheds. Yet, some watersheds (i.e., Orange, Zambezi, Limpopo, nr. 19, 14, 16 respectively, in



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Figure 3. Local difference between transpiration-to-precipitation from trees and non-tree vegetation. (a) Frequency distribution of local (grid-cell based) differences between transpiration-to-precipitation from trees and non-trees (ΔT_p). The tenth percentile outliers were removed from the distribution for improved visualization of the data and scaling of the *x*-axis. (b) Local difference between tree and non-tree vegetation T_p . (a, b) Are geographically constrained by the African continent (i.e., exclude all other regions). Blue colors indicate locations where local transpiration-to-precipitation from trees is higher compared to non-tree vegetation; red colors indicate locations where local transpiration-to-precipitation is higher compared to trees. (c) Spatial distribution of local transpiration-to-precipitation differences (ΔT_p) between trees and non-tree vegetation.

Figure S2 in Supporting Information S1) do show a strong drop in the non-tree contribution to P_T in the dry season, while the relative contribution of trees remains stable throughout the years. This suggests that at least in some regions, P_T from trees ensures water availability during the dry season, whereas the contribution from non-tree vegetation drops. The Congo basin, however, shows a relative increase of tree transpiration-sourced precipitation during the dry season (almost 30% of total dry season P derives from tree T), aligning with other studies that consider the importance of dry season forest T (Worden et al., 2021). Also, Lake Chad (a watershed with marginal tree coverage) shows an increase in the relevance of tree-derived P in the dry season, while this seasonal difference does not emerge as strongly for the non-tree vegetation, which suggests precipitation in the dry season is particularly dependent on transpiration from trees outside the watershed. In short, despite these local differentiations and overall higher flux of trees, water availability in most watersheds depends largely on non-tree vegetation throughout the year.

3.3. Local Differentiation Between Trees and Non-Tree Vegetation

Further examining *local* differences between trees and non-trees contribution to continental precipitation (ΔT_P , mm year⁻¹), Figure 3 shows how these are distributed over space (Figure 3c) and across precipitation gradients (Figure 3b) over the African continent. Blue colors indicate locations where mean annual T_P from trees is larger than from non-tree vegetation; in red, where T_P from trees is smaller than from non-tree vegetation. Overall, regions with lower precipitation rates (<1,500 mm year⁻¹) have relatively larger non-tree vegetation contributions (Figure 3b). This is also illustrated by the clear transitional region developing around the Sahel, most likely because of rainfall being a limiting factor for tree growth. Interestingly, we find similar patterns in some coastal regions and land surrounding the African Great Lakes. Relatively high T_P contributions from trees are for example, found in the Ethiopian Highlands, suggesting that (amongst others) topography plays and important role explaining high T_P rates.

4. Discussion

This study has explored patterns of moisture recycling dependencies associated with different types of vegetation, and is a first attempt to quantify their contributions to rainfall patterns. This is important for research on vegetation functions in the hydrological cycle, and further inform policy regarding protection of ecosystems for water availability. Yet, it is also limited by data availability in three major ways. First, although VCF data is widely used in modeling studies, the differentiation of trees (>5 m) and non-trees (<5 m) is not equally well represented across regions. For example, Adzhar et al. (2022) report that tree cover in woody savanna regions (which are significantly covering the African continent) is strongly underrepresented (up to 32% of tree cover). This implies, that particularly in those regions, the importance of non-tree vegetation presented here is likely to be overestimated. Second, although the performance of GLEAM-Hybrid is more accurate compared to remote-sensing only estimates of T, we exclude interception, while it a major vegetation-regulated water flux (Wang-Erlandsson et al., 2014), particularly in regions with dense canopies. At last, major uncertainties remain with limited opportunities of "ground truthing" of moisture recycling studies. Here, we also find erroneous estimates of P or T estimates in some regions, that may over- or underestimate the importance of vegetation for rainfall in some regions (Figure S3 in Supporting Information S1). Furthermore, we have included a threshold-based mask to exclude grid cells with marginal contributions. The threshold value here $(T_{min} > 0.5 \text{ mm year}^{-1})$ is chosen based on the exclusion of regions that are known to contribute close to no T_P (such as the Sahara). However, it affects the presented mean flux and contributing area estimates here. In Table S1 in Supporting Information S1, the various key metrics are presented with a range of T_{min} values.

5. Conclusion

Most moisture tracking studies that address vegetation-induced rainfall focus on trees and forests (Hoek van Dijke et al., 2022; Pranindita et al., 2021). Such studies also suggest that forest cover loss can reduce rainfall by up to 20% through moisture recycling (Zemp et al., 2017). However, using an observation-based moisture tracking model, we find that non-tree vegetation (i.e., grass-, shrub-, and croplands) transpiration is a critical source of P throughout the African continent too. Although trees contribute a larger flux of water to terrestrial precipitation, we estimate that the large extent of non-tree vegetation in the contributing source region contributes just as much moisture for precipitation on average, around 14% of the annual precipitation over Africa is estimated to originate from tree transpiration, while around 19% is estimated to originate from non-tree vegetation. Our results show that most watersheds strongly depend on non-tree vegetation for their supply of precipitation and, hence, regional water availability, throughout the year. The Congo and Guinea water basins (nr. 4 and 23, Figure S2 in Supporting Information S1) are the only basins where trees are a more important source of P during both the dry and wet season. However, underrepresentation of tree cover in savanna regions may overestimate the importance of nontree vegetation in some areas. This indicates the need to further investigate hydro-climatic dynamics of all vegetation classes and their importance in the water cycle, particularly in the context of ongoing LULC changes, that also affect non-forest ecosystems. In light of increasing water scarcity and climate change, understanding how vegetation can and should be managed to increase water availability within and across watersheds becomes critical.

Data Availability Statement

Code and data used for this study is openly available via te Wierik et al. (2024).

The HAMSTER framework for analysis of FLEXPART data is available via Keune et al. (2022).

Other data sources used in this study are available via:

- MEaSUREs vegetation continuous fields (VCF), Yearly, Global, 0.05° is available via https://lpdaac.usgs.gov/products/mcd12q1v061/.
- HydroSHEDS data is available via Lehner et al. (2008).
- ERA-Interim data is available via https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land? tab=overview.
- GLEAM-Hybrid data can be accessed via Koppa et al. (2022b).



- Free access to MSWEP is restricted to non-commercial use but can be requested via http://www.gloh2o.org/ mswep/ (see "APPLY HERE" button in the data license section).
- OAFlux data is available from https://oaflux.whoi.edu/data-access/.

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