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## **Anthropogenic forcing increases the water use efficiency of African trees**

Tommy H. G. Wils,<sup>1</sup> Iain Robertson,<sup>2\*</sup> Stephan Woodborne,<sup>3,4</sup> Grant Hall,<sup>4</sup> Marcin Koprowski,<sup>5</sup> Zewdu Eshetu<sup>6</sup>

### **Affiliations:**

<sup>1</sup> Department of Geography, Rotterdam University, Museumpark 40, 3015 CX Rotterdam, The Netherlands.

<sup>2</sup> Department of Geography, Swansea University, Singleton Park, Swansea SA2 8PP, UK.

<sup>3</sup> iThemba LABS, Private Bag 11, Wits 2050, South Africa.

<sup>4</sup> Mammal Research Institute, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa.

<sup>5</sup> Institute of Ecology and Environment Protection, Nicolaus Copernicus University, Gagarina 9, 87-100 Toruń, Poland.

<sup>6</sup> College of Natural Sciences, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia.

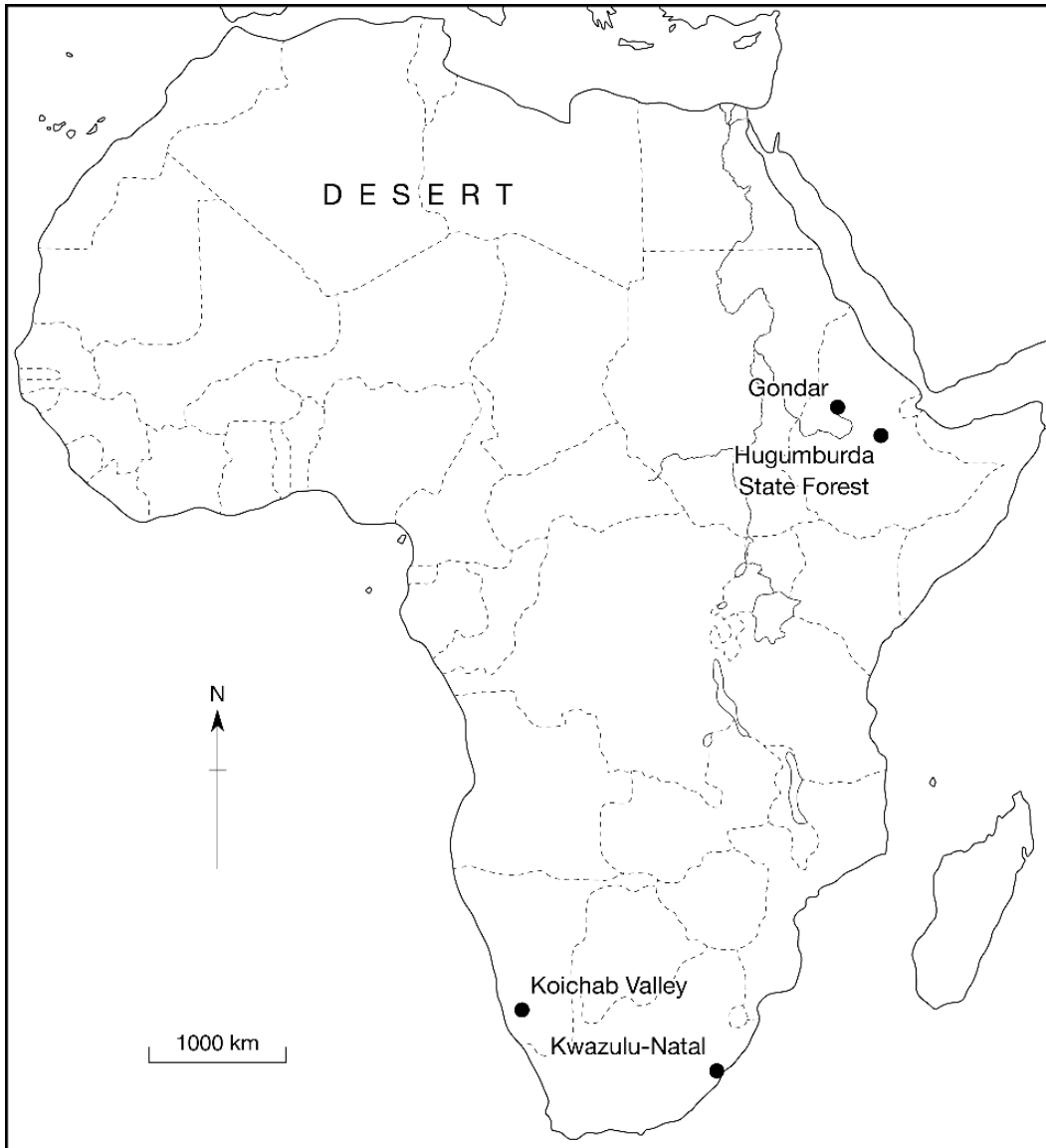
\*To whom correspondence should be addressed. E-mail: i.robertson@swansea.ac.uk

**Abstract:** Rising atmospheric CO<sub>2</sub> concentrations affect climate directly through radiative effects and indirectly by changing plant water-use efficiency. Under global warming scenarios these widely reported changes will have a substantial impact on future bush encroachment, crop yields, river flow and climate feedbacks. Tree-ring intrinsic water use efficiency (iWUE) records for Africa show a 24.6% increase over the twentieth century. As high iWUE can partly counterbalance projected decreases in regional precipitation, this research has important implications for those involved in water resource management and highlights the need for climate models to take physiological forcing into account.

**Keywords:** carbon dioxide (CO<sub>2</sub>), physiological forcing, Africa, intrinsic water use efficiency (iWUE), water resource management

**Introduction:** Most C<sub>3</sub> plants have responded to anthropogenic increases in the concentration of atmospheric CO<sub>2</sub> with enhanced assimilation and/or decreased stomatal conductance resulting in an increase in water use efficiency (van der Sleen *et al.*, 2015; Saurer *et al.*, 2014; Waterhouse *et al.*, 2004). Although leaf gas exchange measurements provide a measure of the instantaneous water use efficiency of a plant (*inst*WUE: ratio of assimilation to transpiration), the intrinsic water use efficiency (iWUE: ratio of assimilation to stomatal conductance), inferred from  $\delta^{13}\text{C}$  values, integrates temporal changes in ecophysiological processes and represents the most appropriate long-term measure. During the latter Anthropocene (post-AD 1850), iWUE has been shown to increase for trees growing under a wide range of environments (Andreu-Hayles *et al.*, 2011; Brienen *et al.*, 2010; Frank *et al.*, 2015; Saurer *et al.*, 2004, 2014). Until now evidence of long-term changes in iWUE has been limited for trees growing on the African continent (van der Sleen *et al.*, 2015; Swanborough *et al.*, 2003). This is remarkable, as increases in iWUE have been modelled to partly mitigate the effects of increased temperature, declining precipitation and increasing drought frequency in semi-arid and sub-humid environments, effectively offsetting losses in crop yield (Long *et al.*, 2006). Physiological forcing of the hydrological cycle may also increase continental river runoff as plants reduce stomatal conductance to decrease evapotranspiration (Gedney *et al.*, 2006; Betts *et al.*, 2007; Cao *et al.*, 2010). In Africa, this concerns major rivers basins, such as those of the Congo, Nile, Niger, Chad, and Zambezi upon which 44% of the African population are reliant for sustenance (Desanker *et al.*, 2001). Understanding of trends in iWUE is also important to assess to what extent the terrestrial biosphere will be able to act as a net carbon sink and what climate feedbacks can be expected from the interactions between terrestrial biosphere and atmosphere (Heimann and Reichstein, 2008).

**Methods:** Five *Juniperus procera* trees were cored at the compound of Kuskuam church in Gondar, Ethiopia (12°37'N, 37°27'E) (Wils *et al.*, 2010). One *Juniperus procera* tree was cored in Hugumburda forest on the north-western escarpment of the Ethiopian Rift Valley (12°15'N, 39°30'E). Discs were obtained for a *Mimusops caffra* growing in KwaZulu-Natal in South Africa (29°43'S, 31°05'E) (Hall *et al.*, 2009) and an *Acacia erioloba* growing in the Koichab Valley in Namibia (26°13'S, 15°52'E) (Figure 1). Cross-dating of the *Juniperus*



**Fig. 1.** Location of the trees sampled throughout Africa from Gondar in the north-western Ethiopian Highlands, the Hugumburda State Forest on the north-western escarpment of the Ethiopian Rift Valley in Ethiopia, the Koichab Valley in Namibia and Kwazulu-Natal in South Africa.

*procera* trees to ensure absolute dates was achieved using skeleton plotting and the computer program COFECHA (Wils *et al.*, 2011; Grissino-Mayer, 2001; Stokes and Smiley, 1968). Dating of *Juniperus procera* tree rings from Gondar (Wils *et al.*, 2010), the *Mimusops caffra* (Hall *et al.*, 2009) and the *Acacia erioloba* was confirmed using high precision ‘bomb’ radiocarbon dating. In this case, juvenile rings from approximately the first forty years of growth were excluded from the study (Hall *et al.*, 2009; Gagen *et al.*, 2007).

Annual  $\delta^{13}\text{C}$  values were measured on resin-extracted ground *Acacia erioloba* and *Mimusops caffra* wholewood samples using a Thermoquest EA1110 elemental analyser interfaced to a VG Isogas SIRA 24 stable isotope mass spectrometer with an average precision of 0.2‰ (CSIR, Pretoria). Annual  $\delta^{13}\text{C}$  values were measured on absolutely-dated ground *Juniperus procera* wholewood (Gondar) and homogenised  $\alpha$ -cellulose (Hugumburda Forest) (Loader *et al.*, 1997) using a PDZ Europa 20-20 mass spectrometer interfaced to an ANCA elemental analyser with a precision of  $\pm 0.09\text{‰}$  (Swansea University).  $\delta^{13}\text{C}$  values were expressed relative to the VPDB standard (Coplen *et al.*, 1995). To ensure consistency,  $\delta^{13}\text{C}$  values measured on annually-resolved  $\alpha$ -cellulose (*Juniperus procera* from Hugumburda forest) were transformed into wholewood values. For Anthropocene samples that have been subjected to minimal diagenesis, this pragmatic approach is based upon the premise that although the major wood constituents may have different absolute isotopic values, they exhibit similar trends (Wils, 2012; Robertson *et al.*, 2004; Loader *et al.*, 2003; Borella *et al.*, 1999). Values of intrinsic water-use efficiency (iWUE) were calculated from the tree-ring  $\delta^{13}\text{C}$  values using the following equations describing fractionation during plant  $\text{CO}_2$  uptake and iWUE:

$$\delta^{13}\text{C}_{tree} \approx \delta^{13}\text{C}_{atm} - (a + (b - a) \cdot (c_i / c_a)) \quad (\text{Farquhar } et al., 1982), \quad (2)$$

and

$$iWUE \approx \frac{c_a - c_i}{1.6} \quad (\text{Ehleringer } et al., 1993), \quad (3)$$

where

$\delta^{13}\text{C}_{tree}$  = observed  $\delta^{13}\text{C}$  in a tree ring;

$\delta^{13}\text{C}_{atm}$  = atmospheric  $\delta^{13}\text{C}$  value (records from McCarroll and Loader, 2004);

$a$  = discrimination against  $^{13}\text{CO}_2$  during diffusion through stomata ( $\approx 4.4\text{‰}$ );

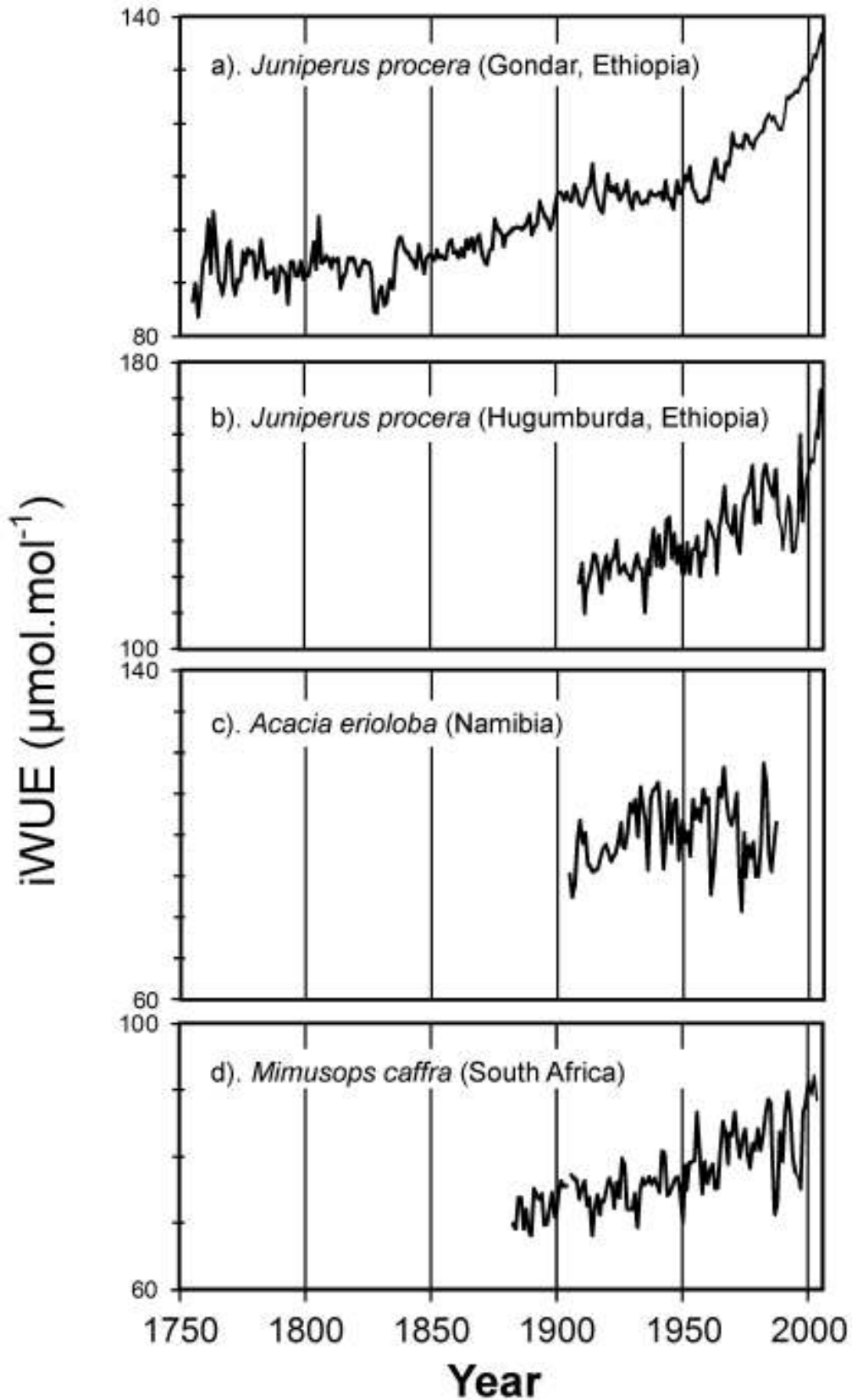
- $b$  = net discrimination against  $^{13}\text{CO}_2$  due to carboxylation ( $\approx 27\%$ );
- $c_i$  = intercellular  $\text{CO}_2$  concentration;
- $c_a$  = atmospheric  $\text{CO}_2$  concentration (records from McCarroll and Loader, 2004);
- $i\text{WUE}$  = intrinsic water-use efficiency.

## Results

In Africa, long, high-resolution tree ring records are scarce due to a lack of trees that produce distinct annual growth rings (De Ridder *et al.*, 2013; Therrell *et al.*, 2006; Dunwiddie PW and LaMarche VC Jr., 1980). Here, we present annually-resolved  $i\text{WUE}$  records for African trees inferred from tree-ring  $\delta^{13}\text{C}$  values (Figure 2). Over the common period (1909-2003), the mean  $i\text{WUE}$  was calculated by taking the 5-year average centred upon the midpoint. The mean  $i\text{WUE}$  for African trees was found to increase: 22.9% for *Juniperus procera* from Gondar, Ethiopia (106.2 to 130.5  $\mu\text{mol}\cdot\text{mol}^{-1}$ ); 29.9% for *Juniperus procera* from Hugumburda, Ethiopia (117.3 to 152.3  $\mu\text{mol}\cdot\text{mol}^{-1}$ ), and 21.0% for *Mimusops caffra* growing in KwaZulu-Natal, South Africa (74.3 to 89.9  $\mu\text{mol}\cdot\text{mol}^{-1}$ ). The *Acacia erioloba* from the Koichab Valley in Namibia showed a small increase in  $i\text{WUE}$  (97.5 to 99.9  $\mu\text{mol}\cdot\text{mol}^{-1}$ ). Excluding this latter sample, the overall increase in  $i\text{WUE}$  for African trees over the common period 1909-2003 was 24.6%.

## Discussion

In the late nineteenth century, the Swedish scientist Svante Arrhenius showed remarkable vision when he determined that an increase in the concentration of atmospheric  $\text{CO}_2$  could increase the Earth's temperature (Arrhenius, 1896). It is now a well-established fact that increasing atmospheric  $\text{CO}_2$  concentrations will affect climate directly through radiative effects but the indirect influences upon climate, through biological influences, such as changes of the water use efficiency of plants are less well understood. Under global warming scenarios, models show that increased atmospheric greenhouse gas concentrations have a substantial impact on climate, hydrological cycles, future bush encroachment, crop yields and river flow. However, the influence of carbon dioxide influenced physiological forcing is not adequately taken into consideration in most models; partly because long-term physiological effects are difficult to quantify.



**Fig. 2.** Annual intrinsic water-use efficiency (iWUE) from eight African trees calculated over the period 1755-2006. (A) Mean iWUE from five *Juniperus procera* individual trees growing in a church compound at Gondar in the north-western Ethiopian Highlands (B) iWUE from *Juniperus procera* growing at Hugumburda on the north-western escarpment of the Ethiopian Rift Valley (C) iWUE from *Acacia erioloba* growing in the Koichab Valley in Namibia and (D) iWUE from *Mimusops caffra* growing in KwaZulu-Natal in South Africa.

Although iWUE-values derived from tree-ring could be overestimated (Silva *et al.*, 2013), there is general agreement that the effective ratio of assimilation to stomatal conductance increases as atmospheric CO<sub>2</sub> concentrations increases. Elevated atmospheric CO<sub>2</sub> levels could increase assimilation (La Marche *et al.*, 1984) but there is generally little direct evidence for this under natural conditions (Jacoby and D'Arrigo, 1997) even if there is an increase in iWUE (Andreu-Hayles *et al.*, 2011; Peñuelas *et al.*, 2011). The magnitude of the increase in African iWUE values is similar to that reported elsewhere (Frank *et al.*, 2015; Saurer *et al.*, 2015; Wang and Feng, 2012; Loader *et al.*, 2011). The overall 24.6% increase in iWUE over the period 1909-2003 suggests that these species are initially adopting a homeostatically active response to increasing atmospheric CO<sub>2</sub> concentration with a relatively constant  $c_i/c_a$  (intercellular CO<sub>2</sub> concentration /atmospheric CO<sub>2</sub> concentration) resulting in higher iWUE values. However, the complex nature of iWUE trends (Wang and Feng, 2012) is confirmed by the uncorrected tree-ring  $\delta^{13}\text{C}$  values (Wils *et al.*, 2010; Hall *et al.*, 2009). Over shorter timescales, Keenan *et al.* (2013) used eddy-covariance techniques to determine carbon uptake and water use from 21 flux towers across northern temperate and boreal forest ecosystems. They found that for almost two decades, forest water-use efficiency increased but as the observed trend was larger than that predicted by theory, coupled vegetation-climate models may need re-evaluation.

In response to increasing atmospheric CO<sub>2</sub> concentrations, species-specific differences in iWUE were found (Figure 2) in a similar manner to those reported under natural conditions (Soulé and Knapp, 2015) and at Free-Air CO<sub>2</sub> Enrichment (FACE) sites (Battipaglia *et al.*, 2012). The *Acacia erioloba* from the Koichab Valley in Namibia showed a small increase in iWUE which is a passive response to increasing  $c_a$  caused by a general resilience to changes in water availability as a result of its extraordinarily deep tap root with access to groundwater (Barnes *et al.*, 2007).

The 24.6% increase in iWUE over the twentieth century highlights the importance of taking indirect physiological forcing, such as CO<sub>2</sub> fertilisation, into account when modelling anthropogenic changes to the climate system as coupled global atmosphere-land surface models that only incorporate radiative forcing may underestimate future environmental impacts (Andrews *et al.*, 2011; Cao *et al.*, 2010). However, the inability of several stomatal conductance models to replicate stomatal response to increased atmospheric CO<sub>2</sub> levels makes the quantification of physiological forcing far from a trivial task (Boden *et al.*, 2013).

Climate models that include radiative and physiological forcing have generally reported an increase in surface temperatures and a complex change to the hydrological cycle as increased runoff partly compensates for reduced precipitation. The effects of physiological forcing are widespread with the forest of central Africa being modelled as one of the regions of greatest change (Andrews *et al.*, 2011).

Intensification of the global water cycle generally results in “*dry areas becoming drier (generally throughout the subtropics) and wet areas becoming wetter, especially in the mid-to high latitudes*” (Trenberth, 2011). However, the system is complex and it is difficult to identify the contributions of individual factors. In particular, is it possible to detect if the reported increase in iWUE from physiological forcing could have a direct influence upon runoff? Globally, there is some evidence that increased atmospheric CO<sub>2</sub> concentration have caused a small increase in river discharge (Gedney *et al.*, 2006) even if vegetation changes weren't fully considered (Kundzewicz and Gerten, 2014). Although future modelled scenarios with increased temperatures and reduced precipitation show a general increase in evapotranspiration (Pan *et al.*, 2015) that may subsequently be reduced through physiological forcing with a net increase in runoff, the attribution of these modifications to physiological forcing is controversial (Huntington, 2008). Consequently, other factors influencing runoff should also be taken into account. When the effects on nitrogen limitation and atmospheric ozone exposure were also taken into account together with physiological forcing, it was found that modelled runoff could be underestimated by as much as 17% for forests in the eastern United States (Felzer *et al.*, 2009). In the northern extra-tropics, as air quality improves future runoff may actually decrease as solar dimming from aerosols may have increased historical river flows as reduced sunlight limited surface evaporation (Gedney *et al.*, 2014).

## **Conclusion**

The presented iWUE records originate from semi-arid to sub-humid regions in Africa (Figure 2). The 24.6% increase in mean iWUE confirms that African trees are already adapting to increasing atmospheric CO<sub>2</sub> concentrations. Compared to the size of the continent, the spatial coverage is low. In Africa, long, high-resolution tree ring records are scarce, as the abundance of trees that produce annual growth rings is limited (Woodborne *et al.*, 2015). These results indicate that more work is required to develop a network of tree ring records in Africa and to understand the as yet uncertain effects of increasing iWUE on crop yield, river flow and to constrain global climate models.



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