And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations

Rutuja Chitra-Tarak [a,1], Laurent Ruiz [b,c], Sandeep Pulla [a], H.S. Dattaraja [a], H.S. Suresh [a], Raman Sukumar [a,d,*]

[a] Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India
[b] INRA, Agrocampus Ouest, UMR1069, Sol Agro et hydrosystème Spatialisation, 35000 Rennes, France
[c] Indo-French Cell for Water Sciences, IISc-IRD Joint Laboratory, Indian Institute of Science, Bangalore 560012, India
[d] Divecha Centre for Climate Change, Indian Institute of Science, Bangalore 560012, India

ABSTRACT

Accuracy in tree woody growth estimates is important to global carbon budget estimation and climate-change science. Tree growth in permanent sampling plots (PSPs) is commonly estimated by measuring stem diameter changes, but this method is susceptible to bias resulting from water-induced reversible stem shrinkage. In the absence of bias correction, temporal variability in growth is likely to be overestimated and incorrectly attributed to fluctuations in resource availability, especially in forests with high seasonal and inter-annual variability in water. We propose and test a novel approach for estimating and correcting this bias at the community level.

In a 50-ha PSP from a seasonally dry tropical forest in southern India, where tape measurements have been taken every four years from 1988 to 2012, for nine trees we estimated bias due to reversible stem shrinkage as the difference between woody growth measured using tree rings and that estimated from tape. We tested if the bias estimated from these trees could be used as a proxy to correct bias in tape-based growth estimates at the PSP scale.

We observed significant shrinkage-related bias in the growth estimates of the nine trees in some censuses. This bias was strongly linearly related to tape-based growth estimates at the level of the PSP, and could be used as a proxy. After bias was corrected, temporal variance in growth rates of the PSP decreased, while the effect of exceptionally dry or wet periods was retained, indicating that at least a part of the temporal variability arose from reversible shrinkage-related bias. We also suggest that the efficacy of the bias correction could be improved by measuring the proxy on trees that belong to different size classes and census timing, but not necessarily to different species.

Our approach allows for reanalysis – and possible reinterpretation – of temporal trends in tree growth, above ground biomass change, or carbon fluxes in forests, and their relationships with resource availability in the context of climate change.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Accuracy in tree woody growth estimates is critical to global carbon budget estimation and climate-change science (Clark and Kellner, 2012; Malhi, 2012). The most commonly and widely used method for estimating tree growth in permanent sampling plots (PSPs) involves the measurement of successive stem diameter changes using a graduated tape or a dendrometer band, and is followed by the use of allometric equations (Chave et al., 2014, 2005) to estimate the above-ground biomass (AGB) or carbon of the plot and changes therein (Condit, 1998; Marthews et al., 2012). However, potentially biases and uncertainties in the measurements in PSPs can substantially affect estimates of forest tree growth, and thus AGB and carbon pools and fluxes (Cushman et al., 2014; Muller-Landau et al., 2014; Sheil, 1995; Talbot et al., 2014).

Water-induced expansion and shrinkage of tree trunks poses a major challenge in the accurate measurement of woody diameter change (Sheil, 2003, 1997). This is because diameter change as

* Corresponding author at: Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India. Tel.: +91 80 23600382 (Direct), +91 80 22933102 (Office); Fax: +91 80 23602280.

E-mail addresses: arutuj@gmail.com (R. Chitra-Tarak), ruiz@rennes.inra.fr (L. Ruiz), sandeep@ces.iisc.ernet.in (S. Pulla), dattaraj@ces.iisc.ernet.in (H.S. Dattaraja), suresh@ces.iisc.ernet.in (H.S. Suresh), rsuku@ces.iisc.ernet.in (R. Sukumar).

[1] Co-corresponding author. Tel.: +91 94831 90581.

measured by a tape or a dendrometer band not only arises from irreversible woody growth (cell wall extension and cell division), but also from reversible expansion and shrinkage in the stem due to water-induced fluctuations. Bias in woody growth estimates due to this reversible stem flexing occurs if the water status of the tree is different across successive measurements (Baker et al., 2002; Sheil, 1995). In the absence of bias correction, temporal variability in growth rates is likely to be overestimated and wrongly attributed to fluctuations in resource (e.g. water) availability. To our knowledge, such biases have not been satisfactorily estimated so far, as no study has measured and separated actual woody growth from water-induced fluctuations at the level of forest community, and no satisfactory method of correcting this bias at this scale is currently available.

Diameter change due to reversible stem flexing occurs as the stem tissues storing water reversibly constrict due to dehydration. This is induced by reduced xylem water potential (Worrall, 1966, Kozlowski, 1990), which is determined by transpiration demand and below-ground water availability. Depending on the species, the largest fraction of the reversible stem flexing is known to occur in the bark (Zweifel and Häsler, 2001) or in the outer parenchyma – the tissues in between the cambium and the cork (Scholz et al., 2008). A water potential difference between xylem and bark causes a radial flow of water from the stem storage compartment towards the xylem, causing the stem bark diameter and consequently the stem diameter, to shrink. The xylem contributes much less to the reversible flexing, although it likely stores and supplies water for about 10–50% of daily transpiration demand (Holbrook and Zwieniecki, 2011).

Much variation in reversible stem flexing occurs with respect to species and in time due to variations in environmental factors affecting water stress, as reviewed by Baker et al. (2002). Temporal variation occurs at a diurnal scale as tree stems typically contract during the day when leaves transpire, and rehydrate during the night (Karling, 1934; Klepper et al., 1971). At a seasonal scale, stem shrinkage during the dry season occurs due to high transpiration demands and depletion of the soil water reserve. Species differ in the extent and timing of reversible stem flexing (Kozlowski and Winget, 1964; Scholz et al., 2008). This is possibly due to differences in timing of leaf flush, flowering or fruiting (Baker et al., 2002), and differences in tissue structures, and/or in relative proportions of various tissues – causing differences in water storage capacity and/or volume change per unit change in water content (Scholz et al., 2008). In the absence of leaves, water stored in the trunk may last across seasons, enabling rehydration of stem tissues and subsequent flowering or flushing (Borchert, 1994a, 1994b; Holbrook and Zwieniecki, 2011). The extent and timing of shrinkage within a species can differ according to topographic position and rooting depth, which influences access to water (Borchert, 1994b; Markesteijn et al., 2010; Meinzer et al., 1999). The effect of tree size on the direction and extent of reversible flexing is debated (Baker et al., 2002). In summary, diameter change in stems can arise not only from woody growth, but also from water-induced reversible flexing, which we hereafter refer to as "water growth".

The case that biases in growth estimates of PSPs could arise from short term – diurnal and seasonal – water-induced fluctuations was first made by Sheil (1997). Negative tree growth estimates are commonly reported in dry forests, which are attributed to water growth and are considered biases (Sheil, 1995). Reversible stem flexing has long since known to be substantial compared to irreversible woody growth and thermal changes (Kozlowski, 1971). The extent of seasonal shrinkage varies from year to year (Baker et al., 2002; Pélissier and Pascal, 2000), and is likely to lead to substantial biases in growth estimates based on annual or supra-annual censuses (Baker et al., 2002; Pélissier and Pascal, 2000). We expect that the largest biases in growth are likely

in forests where both high seasonal and inter-annual variability in water is observed, as often found in seasonally dry tropical forests (SDTFs) (Maas and Burgos, 2011).

A few studies have tried to use a measure of short-term water availability such as rainfall or soil moisture and transpiration demand to account for water growth. Sheil (1997) observed that growth rates of most stems in an Ugandan semi-deciduous forest showed an apparent reduction when measured over wetter seasonal periods, presumably due to measurements during the wetter season being typically made on drier, bright, sunny days when trees are in full leaf and diurnal shrinkage is high. Soil water potential at the time of measurement explained the bias in annual growth estimates in a two year study in a semi-deciduous forest in Ghana (Baker et al., 2002).

Prescriptions for the optimal timing of annual diameter measurements to minimize bias due to diurnal and seasonal water growth have been controversial for seasonally dry forests. For example, Pélissier and Pascal (2000) suggested that inter-annual variation in dry season shrinkage might be stronger than wet season expansion, and therefore recommended measuring growth in the wet season in order to minimize bias in annual growth measurements. Baker et al. (2002) observed greater inter-annual variability in diameter change during the dry season, and also prescribed the wet season for measuring annual growth. However, Sheil (2003) claimed that observations by Baker et al. (2002) of higher variability in diameter change in dry season was debatable, given measurement errors of dendrometer bands and exceptional drought conditions in that study. Sheil (2003) suggested that "wet season measures are more perturbed by moisture (deficits and availability) and by phenological events (flowers, fruit, etc.) impacting true growth. Dry season quiescence reduces growth variance".

However, these hypotheses have remained untested in the absence of actual measurements of the two components of diameter change – woody growth and water growth. Tree ring widths can provide a measure of actual woody growth at annual scale. However this method is invasive, and also expensive in terms of required expertise and resources. Thus estimating bias at the community level needs other approaches.

In this study we propose a novel approach for estimating and correcting bias in growth estimates due to water-induced fluctuations at the community level. We used long-term diameter census data from a PSP in a southern Indian seasonally dry tropical forest. Comparing woody growth using tree rings and observed growth using a tape in a small number of trees, we check whether significant biases in tree growth estimates were due to water growth. We then test whether biases in this small number of trees can be used as a proxy to correct biases in tree growth at the community level. We also suggest ways to improve this approach.

2. Materials and methods

2.1. Study site, climate and forest plot

We used data from a 50-ha Mudumalai Forest Dynamics Plot (MFDP) located in a seasonally dry tropical forest in the Western Ghats, southern India (Latitude: 11.5989, Longitude: 76.5338). Detailed information on this forest and the 50-ha plot can be found elsewhere (Sukumar et al., 1998, 1992; Suresh et al., 2013, 2010). The average annual precipitation 4 km from the site is 1200 (±280 SD) mm from 1988 to 2013 (Fig. 1).

About 80% of annual precipitation occurs during the monsoon from June to November. The dry period (<100 mm precipitation/month) lasts for about 6–8 months, with four months of less than 50 mm precipitation/month from December to March. Average monthly maximum and minimum temperatures are 27.4 °C (±2.7