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Autocorrelated growth of tropical forest trees: Unraveling patterns and quantifying consequences

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Abstract

Tropical trees show considerable variation in growth rates. Often this variation is not random, as some trees perform better than others and as growth may be temporally correlated. Using long-term growth data obtained from tree ring analysis, we studied the degree to which growth rates of four Bolivian rainforest tree species were autocorrelated and how this affected the output of growth simulations.

Autocorrelated growth is commonly defined as the correlation between growth in one time interval with that in a subsequent interval calculated over all individuals of the population. We termed this *total autocorrelated growth* and identified its two components: temporally correlated growth rates of individual trees (*within-tree autocorrelated growth*) and persistent growth differences between trees (*among-tree autocorrelated growth*).

Total autocorrelated growth was high (Pearson's $r \sim 0.75$) between growth rates of subsequent years and decreased gradually at larger time lags. At time lags of 20 years growth rates were still positively autocorrelated in some species.

Juvenile trees tend to have strong within-tree autocorrelated growth (Pearson's $r \sim 0.4$–0.5), probably mainly caused by temporally correlated variation in light availability due to canopy dynamics. The within-tree autocorrelation was considerably lower in larger trees (Pearson's $r < 0.2$), and did – in contrast to juvenile trees – not contribute much to total autocorrelation. In larger trees total autocorrelation originated mostly from persistent growth differences among trees, caused by factors as site-specific differences or differences among trees in crown area or liana infestations. Among-tree autocorrelated growth was strong and long-lasting: differences between fast and slow growing trees were maintained for long periods.

Incorporation of autocorrelated growth in bootstrap simulation models led to higher variation in age estimates compared to simulations without autocorrelation. Still, this variation was lower than that observed in tree rings. By using 5-year growth steps instead of the 1-year growth steps the observed variation increased and closely matched those in tree rings.

Our findings emphasize the importance of incorporating autocorrelated growth in tree growth simulation models, for obtaining more realistic estimates of long-term growth and tree ages.

Keywords: Bootstrapped simulations; Size-dependent growth; Size variability; Tree age; Temporal autocorrelation

1. Introduction

Growth rates of tropical forest trees show considerable variation both among and within trees (Clark and Clark, 1992, 2001). In demographic studies and population models this variation is often neglected or considered to be random (Fox et al., 2001). Variation in growth rates, however, is often not randomly distributed. Some trees are better performers than others and temporal correlations may be found between growth rates in subsequent years (Kohyama and Hara, 1989; Terborgh et al., 1997; Kammescheidt et al., 2003; Landis and Peart, 2005). This temporal autocorrelation may strongly influence the variation in growth trajectories and thus size–age variation in tree populations (Bullock et al., 2004).

Autocorrelated growth is commonly defined as the correlation between growth in one time interval with that in a subsequent interval, calculated over all individuals of a population. This measure is referred to as 'growth autocorrelation' (DeAngelis et al., 1993; Pfister and Stevens, 2002; Fujiwara et al., 2004) or

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'temporal autocorrelation' (Terborgh et al., 1997; Fox et al., 2001; Bullock et al., 2004; Kohyama et al., 2005). In this paper we will use the term *total autocorrelated growth*, and distinguish two different components (Fig. 1). The first component is the temporally correlated growth of an individual tree, which we term *within-tree autocorrelated growth*. A positive within-tree autocorrelation is obtained if a tree that grows at a low rate in a given year (compared to its long-term average growth) is likely to do so again the next year (Fig. 1B). The second component concerns the differences in growth between trees that may persist over time, which we term *among-tree autocorrelated growth*. This can be calculated as the correlation of growth values between trees, after removing the component of within-tree autocorrelated growth by randomization (Fig. 1C). Positive among-tree autocorrelated growth is found when the fast growers in a population remain fast growers over time. Although the terms might suggest that the two components are additive, they are not. We apply these terms for maintaining clarity.

Separating within-tree and among-tree autocorrelated growth is ecologically meaningful, as they reflect different growth-determining factors. Within-tree autocorrelated growth is the result of temporally correlated environmental factors acting on individual trees, e.g. light availability, while among-tree autocorrelated growth mainly results from differences among all trees within the population in site conditions, crown area, or genetic setup. The relative importance of both types of autocorrelated growth is likely to vary among life-phases. For instance, juvenile trees in the forest understory are subject to periods of suppression and release, which may cause long-lasting within-tree autocorrelated growth, while large trees probably lack such long-lasting within-tree autocorrelated growth. Growth of canopy trees, on the other hand, is more likely influenced by local water availability, crown area or degree of liana infestation that causes strong among-tree autocorrelated growth.

So far, most autocorrelation studies on tropical forest trees included several species (cf. Swaine et al., 1987; Kohyama and Hara, 1989; Clark and Clark, 1992; Sheil, 1995; Kammesheidt et al., 2003). Positive correlations in such cases are likely to reflect interspecific differences in growth rates more than among-tree or within-tree autocorrelated growth. Other studies treated species separately, but combined trees of different size, and therefore yielded estimates of total autocorrelated growth, which may be biased as trees of different size intrinsically differ in growth (e.g. Terborgh et al., 1997). Very few studies (Clark and Clark, 2001) separated effects of size and species. Within-tree autocorrelated growth has only been quantified in dendrochronological studies with the purpose of extracting climate information from tree ring series (Fritts, 1976; Monserud, 1986; Woollons and Norton, 1990). To our knowledge, this is the first study to disentangle within-tree and among-tree autocorrelated growth, and quantify their importance for tree growth.

Autocorrelated growth may strongly influence the output of growth simulations models (e.g. Pfister and Stevens, 2002) and population models (e.g. Pfister and Stevens, 2003). Strong among-tree autocorrelated growth leads to large differences in long-term growth rates between trees and consequently to large

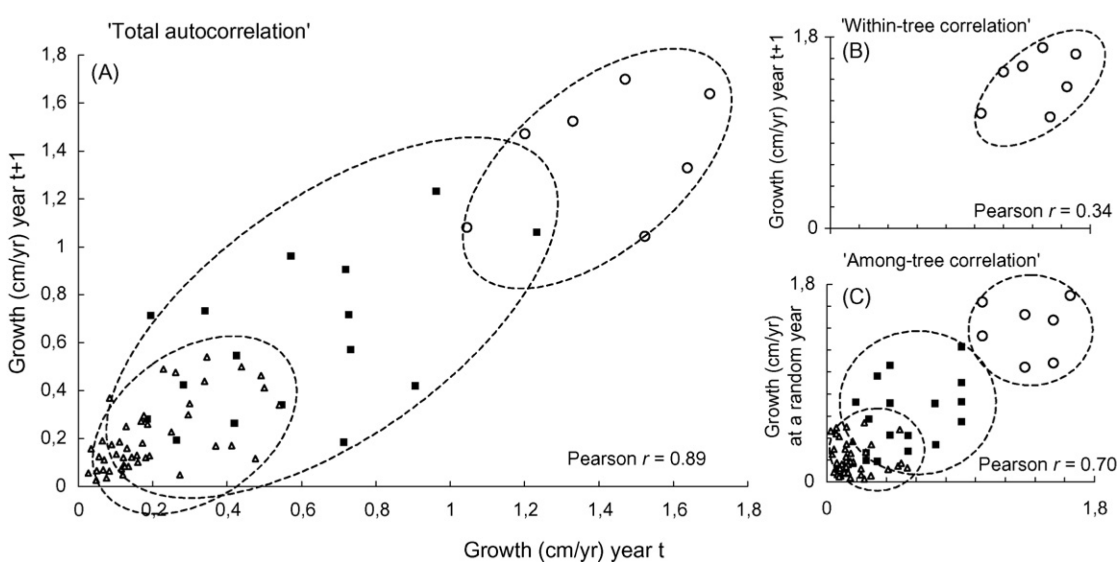

Fig. 1. Schematic representation of the three types of autocorrelation distinguished in this study, illustrated by three trees of *Cedrela odorata* for the growth trajectory from 0 to 10 cm in diameter. 'Total autocorrelation' (A) is the correlation of all datapoints from all trees (identified by different symbols) in two consecutive years. This is the type of autocorrelation that is commonly presented in tree growth studies. We unraveled total autocorrelation in two components. 'Within-tree autocorrelation' (B) is the correlation of the growth rate for one tree with that during the next year, calculated over its entire life or over a shorter period. A tree that experiences periods of continuous above-average growth (e.g. a release), and periods of continuous below-average growth (a suppression) will have high values for within-tree autocorrelation. Such a tree is represented by datapoints that have a strongly ellipsoid shape depicted as in (B). The second component is 'among-tree autocorrelation' (C). This represents the persistent differences in growth among individuals: if these differences are strong, high values of among-tree autocorrelation are found. In our analyses, we calculated among-tree autocorrelation by removing the within-tree autocorrelation from the dataset. We did so by randomizing the growth data of each tree at $t + 1$, thus disconnecting the growth rates of subsequent years. The result of this randomization is shown by the circle-shaped clouds of datapoints in (C), compared to the ellipsoid-shaped data in (A) and (B). The correlation that remains in the data for the three example trees is that among individuals.