

# Interannual variability of growth and reproduction in *Bursera simaruba*: the role of allometry and resource variability

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**Abstract.** Plants are expected to differentially allocate resources to reproduction, growth, and survival in order to maximize overall fitness. Life history theory predicts that the allocation of resources to reproduction should occur at the expense of vegetative growth. Although it is known that both organism size and resource availability can influence life history traits, few studies have addressed how size dependencies of growth and reproduction and variation in resource supply jointly affect the coupling between growth and reproduction. In order to understand the relationship between growth and reproduction in the context of resource variability, we utilize a long-term observational data set consisting of 670 individual trees over a 10-year period within a local population of *Bursera simaruba* (L.) Sarg. We (1) quantify the functional form and variability in the growth–reproduction relationship at the population and individual-tree level and (2) develop a theoretical framework to understand the allometric dependence of growth and reproduction. Our findings suggest that the differential responses of allometric growth and reproduction to resource availability, both between years and between microsites, underlie the apparent relationship between growth and reproduction. Finally, we offer an alternative approach for quantifying the relationship between growth and reproduction that accounts for variation in allometries.

**Key words:** allocation; allometry; *Bursera simaruba*; Costa Rica; life history theory; tropical dry forest.

## INTRODUCTION

The principle of allocation states that resources devoted to growth, maintenance, and reproduction are constrained by the rate of acquisition of limiting resources from the environment (Cody 1966, Levins 1968). That is, variation in growth and reproduction are linked and the allocation of resources is a zero sum whereby allocation to one function should come at the cost of allocation to other functions. A key assumption underlying this trade-off hypothesis is that reproduction is costly and reduces resources available for growth (Roff 1992). However, the central prediction linking reproduction and vegetative growth has received mixed empirical support (e.g., Fox and Stevens 1991, Knops et al. 2007, Koenig et al. 2009). Further, positive correlations are known between many life history traits (see Stearns 1977, van Noordwijk and de Jong 1986) suggesting that a general negative relationship between

growth and reproduction remains questionable. Studies have also argued that variation in growth and reproduction may be more strongly driven by other factors including: (1) photosynthetic reproductive structures; (2) increased resource uptake during reproduction (i.e., the compensation hypothesis; Tuomi et al. 1983); (3) excess resources above some threshold are used for sexual reproduction without added costs to somatic growth (i.e., the threshold hypothesis; Tuomi et al. 1983); (4) inability of the methods used to accurately detect reproductive costs (Bazzaz et al. 2000); and (5) confounding environmental factors that underlie the negative correlation between life history traits (Knops et al. 2007). Together, these findings may call into question whether the trade-off between growth and reproduction is actually an important driver of the observed variation in growth and reproduction in natural populations.

Deconstructing the factors that differentially affect growth and reproduction is central to discovering the mechanistic underpinnings of the relationship between growth and reproduction. Empirical evidence and theoretical arguments show that reproductive investment and other life history traits are moderated by the

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environment (e.g., Grime 1979), and some empirical studies have demonstrated the effects of growing conditions on patterns of resource production and allocation (Harper and Ogden 1970, Bazzaz and Reekie 1985). For example, in perennial species, both reproductive allocation (the proportion of aboveground biomass in reproductive structures) and community-wide fruit production have been shown to decrease in response to resource limitation (Chiariello and Gulmon 1991, Wright et al. 1999, respectively). Environmental conditions can also influence the cost of reproduction, independent of growth. For example, reproductive costs have been observed to vary spatially as a result of differing soil, water availability, growing season length, and altitude (Obeso 2002). Furthermore, theoretical work has suggested that both environmental and genetic factors can result in a nonexistent or weak correlation between growth and reproduction (Reznick et al. 2000).

There are two methodological and practical issues that limit our understanding of the factors that influence the growth–reproduction relationship. First, while variation in growth and reproduction are often linked to variation in abiotic conditions, it is unclear how reproduction and growth are both influenced by resource supply. Our lack of knowledge is particularly acute in long-lived trees due, in part, to the impracticality of experimental manipulations. Second, body size is a primary factor underlying variability in life history strategies (Calder 1984, Niklas 1994). Indeed, it is crucial to take into account allometric effects when assessing the impact of environmental factors on life history (Samson and Werk 1986); yet studies detailing the size dependency of life history traits in woody perennials are relatively few (Hubbell 1980, Peters et al. 1988, Acosta et al. 1993, Wheelwright and Logan 2004).

Here, we use a long-term intraspecific study of over 600 individual trees to assess the primary factors influencing variation in tree growth and reproduction. We test the principle of allocation in a natural population of the tropical tree species *Bursera simaruba* (L.) Sarg., by examining 10 years of reproduction and growth. In order to parse the various factors that can influence variation in growth and reproduction, we derive a theoretical framework that allows the allometries of growth and reproduction to vary independently from each other. Our model allows us to assess the relative importance of opposing factors controlling variation in plant growth and reproduction. We empirically test the analytical link between the growth and reproduction allometries and the growth–reproduction relationship itself and assess the role of annual variation in a key resource, water (i.e., precipitation). After accounting for size-dependent growth and reproduction, we further provide an alternative method for quantifying the true nature of the relationship between growth and reproduction.

## METHODS

### *Site description*

The 15-ha San Emilio Long Term Forest Dynamics Plot (SE-LFDP) is located in Sector Santa Rosa of Área de Conservación Guanacaste (ACG) in northwestern Costa Rica (10°45' N, 85°40' W). The larger area encompassing the SE-LFDP is a mosaic of old growth (>200 years) and younger, secondary forests (>80 years) that have regenerated from abandoned banana plantations, pastures, and selective logging (Janzen 1988). The area is characterized as seasonally dry tropical forest (Holdridge et al. 1971) with the dry season beginning in late December and lasting until early May. Annual rainfall ranges from 900–2600 mm with an average of 1500 mm, though annual variation in precipitation is known to be quite high (Hartshorn 1983). During the dry season, much of the vegetation, including *Bursera simaruba*, is drought deciduous.

### *Natural history and other characteristics of *Bursera simaruba**

This study focused on a population of the tropical tree species, *Bursera simaruba*, in the SE-LFDP. *Bursera simaruba* is a tropical, dioecious, perennial, canopy tree and is characterized by a single cylindrical stem. Staminate and pistillate individuals, referred to onward as male and female for simplicity, flower at the end of the dry season and flowers retain color and turgor for a single day (Greenberg et al. 1995). Within three weeks of pollination by moths, bees, and flies, the newly formed fruit expands to full size and will remain on the tree for up to 12 months before they are dispersed (Stevens 1983). The major dispersers of *B. simaruba* are primate species and more than 40 species of frugivorous and insectivorous birds (Scott and Martin 1984). Fruits ripen asynchronously within a tree throughout the rainy season and ripening can extend up until the time of the following years' flowering. Fruits that are not dispersed are dropped en masse by the female at the time of new fruit production (Stevens 1983). The fruit consists of an aril, a capsule, and seeds. The mean dry mass of the fruit is ~0.20 g, with the capsule comprising approximately 50% of the total mean dry mass of the fruit (Greenberg et al. 1995). Individual female trees appear to have some control on reproductive allocation. For example, Dunphy and Hamrick (2007) found that seed abortion was common and suggested that it was related to the amount of outcrossing.

### *Data collection*

We utilized a unique long-term demographic record for *Bursera simaruba* collected by George C. Stevens (see Stevens 1987). Each January, during 1976–1986, the circumference at breast height was measured in 1-cm increments for approximately 500 male and 170 female *B. simaruba* individuals within the 15-ha SE-LFDP. Diameter at breast height (dbh; circumference/ $\pi$ ) ranged

from approximately 2 to 60 cm. Similarly, each January, for each female tree, the total number of fruits was counted from the ground by eye (Stevens 1987). The accuracy of fruit counts was checked by comparing fruit counts made on the ground to counts made by an observer in the tree crown (Stevens 1987). In this previous study, five trees were selected for experimental manipulation. We excluded these five female trees for the present analyses. Across years, the percentage of total population tree biomass in fruit varied considerably, ranging from 1.6% to 17%, with an average of 5.7%.

To assess the linkage between climate, growth, and reproduction, we used annual rainfall for the years 1979–1986 from the Meteorological Station in Sector Santa Rosa de Área de Conservación Guanacaste (data available online).<sup>10</sup> The station is located a few kilometers from the SE-LFDP. Rainfall records for the years 1976–1978 were not available; thus, rainfall for these years was taken from Hagnauer (1993) for Cañas, Guanacaste, Costa Rica, approximately 60 km southeast of Sector Santa Rosa. Mean annual rainfalls at Cañas and Sector Santa Rosa for 1979–1986 were similar ( $r^2 = 0.75$ ,  $P < 0.01$ ). This decade-long study provides an extensive growth and reproduction data set that encompasses one La Niña (1975) and three El Niño events (1976, 1977, and 1983), according to the United States Department of Commerce National Oceanic and Atmospheric Administration (data available online).<sup>11</sup>

We utilize the Stevens data set to quantify (1) the functional relationship between aboveground tree biomass, annual reproduction, and annual growth rate and (2) the variability in the annual growth–reproduction relationship. Using a theoretical framework to derive the allometric dependence of growth and reproduction, we then (3) quantify how the growth–reproduction relationship and the size dependencies of growth and reproduction respond to variability in annual precipitation.

#### Data analyses

Aboveground biomass (AGB, kg) was estimated for each individual ( $n$ ), for each year ( $t$ ), according to the following equation for tropical dry forest trees (Chave et al. 2005):

$$\text{AGB}_{i,n} = \rho \times \exp\left(-0.667 + 1.784 \times \ln(D_t)\right) + 0.207 \times \ln(D_t)^2 - 0.0281 \times \ln(D_t)^3 \quad (1)$$

where  $D_t$  is the stem diameter of the tree (dbh in cm) in a given year and  $\rho$  is the mean wood density of the plant species ( $\text{g/cm}^3$ ). For *B. simaruba*,  $\rho = 0.307 \text{ g/cm}^3$  (Williamson 1984). Here, we assume that wood density

is constant across all trees and all years. On a population level, the total increment in AGB, or total growth ( $\text{Tot}G_t$ , kg), for all individuals for a given year  $t$ , can then be expressed by

$$\text{Tot}G_t = \sum_{n=1}^{n=x} G_{n,t} = \sum_{n=1}^{n=x} (\text{AGB}_{n,t+1} - \text{AGB}_{n,t}) \quad (2)$$

where  $x$  is the total number of individuals. Here,  $G_{n,t}$  can be defined as an individual-level variable to describe the growth of an individual in one year. Similarly, the population total reproductive biomass ( $\text{TotRB}_t$ , kg) was estimated by

$$\text{TotRB}_t = \sum_{n=1}^{n=x} \text{RB}_{n,t} = \sum_{n=1}^{n=x} (N_{\text{Fruit},t} \times M_{\text{Fruit}}) \quad (3)$$

where,  $N_{\text{Fruit},t}$  is the total number of fruit produced by an individual at time  $t$  and  $M_{\text{Fruit}}$  is the average mass of an individual fruit. Likewise,  $\text{RB}_{n,t}$  can be defined as an individual-level variable to describe the reproductive production in one year. While the magnitude of variation in fruit mass for *B. simaruba* was not measured in this study, the variation in length and width of whole fruits was small for *B. simaruba* populations in tropical dry forests of Mexico (Greenberg et al. 1995). Further, variation in fruit mass is small compared to the large variation in fruit number between trees and between years. Thus, assuming a constant fruit mass is reasonable. Finally, total biomass production ( $\text{Tot}B_t$ , kg) for all individuals in a given year can be represented by

$$\text{Tot}B_t = \text{Tot}G_t + \text{TotRB}_t \quad (4)$$

For each year, we quantified (1)  $\text{TotRB}_t$  and  $\text{Tot}G_t$  and (2) the percentage of total biomass production,  $\text{Tot}B_t$ , represented by  $\text{TotRB}_t$  and  $\text{Tot}G_t$ , and evaluated each as a function of precipitation (Appendix A). This provides a population-wide summary of the influence of annual precipitation on total growth and the fractions of total growth due to somatic and reproductive biomass. Community-wide fruit production in tropical trees has been shown to respond to extreme drought events (e.g., Wright et al. 1999), and we wanted to test whether population-level growth and reproduction of *B. simaruba* were affected by annual precipitation.

The use of population-level measures provides an aggregate measure across individuals and summarizes the influence of annual precipitation on growth patterns. However, these measures average out the variation in growth and allocation among individual trees. This is particularly important when assessing direct environmental effects on phenotypic traits and reproductive fitness. Further, the absolute size of the pool from which resources are allocated to reproductive and somatic growth may vary with tree size, as well as natural variation in the environment (Chapin et al. 1987). In order to characterize the relationship between growth and reproduction across individuals that differ in size as well as to fully understand phenotypic variation, it is

<sup>10</sup> <http://www.investigadoresacg.org/sections/databases/databases.html>

<sup>11</sup> <http://www.pmel.noaa.gov/tao/elnino/nino-home.html>

necessary to examine proportional changes in biomass on an individual tree level (Enquist et al. 1999, Kerkhoff and Enquist 2009). Thus, for all male and female individuals, relative growth rate (RGR) and reproductive allocation (RA) were quantified as

$$\text{RGR}_{n,t} = \frac{(\text{AGB}_{n,t+1} - \text{AGB}_{n,t})}{\text{AGB}_{n,t}} \quad (5)$$

$$\text{RA}_{n,t} = \frac{(N_{\text{Fruit}} \times M_{\text{Fruit}})}{\text{AGB}_{n,t}}. \quad (6)$$

Both RGR and RA represent the change in somatic biomass and the production of reproductive biomass, respectively, over one year relative to the standing somatic biomass at the start of the year. Interpretations of RA assume that reproductive parts make no energetic contribution to their own production (Thompson and Stewart 1981), an important tenet of Cody's principle of allocation (Cody 1966). As with many plant species, this is likely violated in *B. simaruba* as fruit are likely to be photosynthetic; the developing fruit is bright green with a darker green layer underneath the cuticle. Eq. 6 can be modified to account for reproductive tissue contribution to reproduction as

$$\text{RA}_{n,t} = \frac{(N_{\text{Fruit}}) \left[ \left( M_{\text{Fruit}} - (\vartheta) \right) \right]}{\text{AGB}_{n,t}}. \quad (7)$$

Here  $\vartheta$  is the mass of the fruit that originated from photosynthetic contributions from the reproductive tissue. The value of  $\vartheta$  is unknown for *B. simaruba*. However, it is reasonable to assume that  $\vartheta < M_{\text{Fruit}}$  and that  $\vartheta$  does not appreciably vary between individuals, years, or with  $\text{AGB}_t$ . Thus, using Eq. 6 to calculate RA in *B. simaruba*, is a reasonable comparative measure.

#### Decomposing the allometry of growth and reproduction

Next, we derive the functional relationship between RA and RGR. In doing so, we show that an assessment of the drivers behind variation in growth and reproduction must first assess the role of allometry because plant growth and seed/fruit production are directly related to plant size (Niklas 1994, Niklas and Enquist 2003, Moles et al. 2004, Enquist et al. 2007, Weiner et al. 2009). We begin by allowing rates of allometric growth and reproduction to vary independently from each other. The simplest model of plant net growth rate (kg/time) is related to plant size ( $M$ ) as a power function:

$$\frac{dM}{dt} = c_1 M^a = G_t. \quad (8)$$

The total plant fruit production (kg/time) can also be expressed as a power function of plant size:

$$\frac{d\text{RB}}{dt} = c_2 M^b = \text{RB}_t. \quad (9)$$

Here, on log-log axes,  $c_1$  and  $c_2$  are the intercepts and  $a$  and  $b$  are the exponents of the mass-dependence of plant net growth rate and total plant fruit production (see Appendix B). Note, Eqs. 8 and 9 are annual rates that describe net plant growth rate (kg/yr) and total plant fruit production (kg/yr), respectively. We can use Eqs. 8 and 9 to define  $c_1$  and  $c_2$  on an individual tree level where  $c_1 = (dM/dt)/M^a$  and  $c_2 = (d\text{RB}/dt)/M^b$ . In this case,  $c_1$  and  $c_2$  can then be defined as allometrically normalized measures of the relationships between growth and reproduction across years. Thus, comparing values of  $c_1$  and  $c_2$  across individuals within and between years provides a quantitative measure of growth and reproduction that is standardized for allometric effects. Further, Eq. 8 implicitly includes reproductive allocation. To explicitly include reproduction in the growth equation, we can define RA as the quotient of fruit production ( $\text{RB}_t$ ) and plant mass such that

$$\text{RA} = \frac{c_2 M^b}{M} = c_2 M^{b-1} \quad (10)$$

where RA has the units of  $\text{kg} \cdot \text{kg}^{-1} \cdot \text{yr}^{-1}$ . Second, the relative growth rate of a plant can be defined by the growth rate divided by the mass such that

$$\text{RGR} = \frac{dM/dt}{M} = \frac{c_1 M^a}{M} = c_1 M^{a-1}. \quad (11)$$

One can relate RA to RGR by noting that

$$M = \left( \frac{1}{c_1} \text{RGR} \right)^{1/(a-1)} \quad (12)$$

so that substituting Eq. 12 into Eq. 10 provides the functional relationship between reproductive allocation and relative growth rate, where

$$\text{RA} = \left( \frac{c_2}{c_1^{(b-1)/(a-1)}} \right) \text{RGR}^{(b-1)/(a-1)}. \quad (13)$$

Eq. 13 shows that a plot of RA and RGR is governed by the allometric dependency of growth and reproduction. Specifically, the functional relationship between growth and reproduction is determined by the relative magnitudes of  $a$  and  $b$  as well as  $c_1$  and  $c_2$ .

Our model makes three critical predictions when assessing the primary drivers of variation in growth and reproduction. First, a plot of RA and RGR does not necessarily imply a trade-off in the classic sense but instead represents a function that is dependent upon the magnitude of the allometric exponents that govern growth and reproduction. The functional relationship between RA and RGR can be positive, negative, or even flat depending on the relative magnitudes of  $a$  and  $b$ . If the allometric normalizations  $c_1$  and  $c_2$  are approximately independent of plant size, then a negative relationship is predicted to be observed if either  $b$  or  $a$ , but not both, are greater than 1. If both  $a$  and  $b$  are less than 1 but greater than zero, or if  $a$  and  $b$  are both

TABLE 1. Growth intercept  $c_1$ , reproduction intercept  $c_2$ , growth exponent  $a$ , and reproduction exponent  $b$  calculated using Eqs. 8–11 and the RA–RGR regressions.

Year	Precipitation (mm)	$c_1$	$c_2$	$a$	$b$	Slope
1976	986	-0.56 (0.12)	-4.96 (0.27)	0.68 (0.05)	2.11 (0.12)	-2.17 (0.33)
1977	948	-0.48 (0.10)	-5.42 (0.43)	0.69 (0.04)	1.80 (0.18)	1.65 (0.27)
1978	1366	-0.40 (0.10)	-4.73 (0.38)	0.72 (0.05)	1.78 (0.16)	-1.29 (0.19)
1979	1979	-0.34 (0.07)	-6.20 (0.39)	0.60 (0.04)	2.23 (0.17)	-1.61 (0.19)
1980	1708	-0.42 (0.07)	-4.63 (0.26)	0.64 (0.03)	1.78 (0.11)	-1.31 (0.24)
1981	2240	-0.73 (0.04)	-5.38 (0.23)	0.75 (0.03)	1.88 (0.10)	-2.24 (0.29)
1982	1821	-0.44 (0.06)	-4.55 (0.21)	0.59 (0.04)	1.74 (0.09)	-1.47 (0.15)
1983	915	-0.51 (0.07)	-4.88 (0.23)	0.70 (0.03)	1.66 (0.10)	-1.12 (0.13)
1984	1721	-0.35 (0.06)	-5.37 (0.25)	0.62 (0.03)	1.68 (0.11)	-1.38 (0.11)
1985	1431	-0.60 (0.07)	-4.16 (0.20)	0.70 (0.04)	1.54 (0.09)	-1.60 (0.20)
1986	1306	NA	-4.80 (0.25)	NA	1.86 (0.11)	NA

Notes: The standard error is given in parentheses. NA indicates that growth data for calculations of  $c_1$  and  $a$  were unavailable after the January 1986 census. Note that, on log axes,  $c_1$  and  $c_2$  are the allometric normalizations and are the mass-normalized geometric mean responses of growth and reproduction, respectively, of the population, and  $a$  and  $b$  are the slopes of the mass dependence of plant net growth rate and total plant fruit production (see Appendix B). The slope of the RA–RGR regression is also noted for each year.

greater than 1, then the slope between RA and RGR should be positive. Further, if  $a$  and  $b$  are equal to each other, the slope should take on a value of 1. In sum, variation in the relationship between growth and reproduction critically depends on variability in the allometry of growth and reproduction.

Second, our framework shows that assessing relationships between growth and reproduction are best reflected in the residual variation in Eqs. 8 and 9. In the case where variation in growth and reproduction are governed primarily by a trade-off, and do not respond strongly to resource availability, a positive allometric residual for fruit production (a tree that is producing more fruit than expected for its size) will be followed by a negative residual for vegetative production (that same tree will produce less biomass than expected for its size). In other words,  $c_1$  and  $c_2$  will be inversely related. However, the above critically assumes that  $c_1$  and  $c_2$  are governed by internal resource allocation and are a constant across resource levels: either across space, reflecting differences in microsites, or across time, reflecting differences in resource supply.

A third prediction from Eq. 13 comes from relaxing the assumption that  $c_1$  and  $c_2$  are independent of resource supply across time or across microsites. If both of these allometric variables are strongly influenced by microsite variation or differences across years (i.e., if both reproduction and/or growth are resource limited; see Chiariello and Gulmon 1991, Wright et al. 1999) then a plot of  $c_1$  and  $c_2$  will *not* show a negative relationship. Instead, there are two possible outcomes. If microsites strongly differ in resources, and growth and reproduction are strongly tied to external resource levels, then individuals in high resource sites will, for their size, grow and reproduce to a greater degree than individuals in poor resource sites. As a result, the relationship between  $c_1$  and  $c_2$  will be positive. If such a relationship were observed, we could infer that microsite resource variation is a stronger constraint shaping

variation in growth and reproduction than individuals trading off growth and reproduction. Finally, if the relationship between  $c_1$  and  $c_2$  is flat, we can infer that the trade-off and microsite resource variation have about the same effect on growth and reproduction.

To quantify the allometries of RGR and RA and the RA–RGR relationship (Table 1), ordinary least squares bisector (OLSB) regression analyses were performed between log-log-transformed female and male  $G$  and AGB (Fig. 1A and Appendix C), female RB and AGB (Fig. 1B and Appendix D), and female RA and RGR (Fig. 2A and Appendix E). Because it is not clear which variable is the dependent variable, RMA and OLSB measures are preferable (see Isobe et al. 1990, Warton et al. 2006). Also, because the log-log linear regression models can produce low  $r^2$  values, RMA regression can lead to highly unstable slope estimates (O’Conner et al. 2007). The OLSB method has been shown to be less biased than ordinary least squares regression and more stable than RMA regression when there is a large degree of scatter in the data (Isobe et al. 1990). For completeness, the OLSB results are compared to results from ordinary least squares and RMA regression (see Appendices C–E). Finally, annual slopes from the RA–RGR regressions were evaluated as a linear function of precipitation for each year (Fig. 2B).

For each year, we also quantified the allometric variables  $a$ ,  $b$ ,  $c_1$ , and  $c_2$  as the slopes and intercepts of the OLSB regressions relating log-transformed  $G$  and RB, respectively, to log-transformed AGB (Appendix B). We then regressed  $a$  as a function of  $b$  and  $c_1$  as a function of  $c_2$ , as well as  $a$ ,  $b$ ,  $c_1$ , and  $c_2$  as functions of precipitation in linear model regressions (Fig. 3). Last, we calculated  $c_1$  and  $c_2$  for each individual using coefficients  $a$  and  $b$  and Eqs. 8 and 9, and plotted  $c_1$  against  $c_2$  between years to account for variation in interannual precipitation (Fig. 3F). We also plotted  $c_1$  and  $c_2$  within years to account for variation in microsite resource availability (Fig. 3G). All analyses were

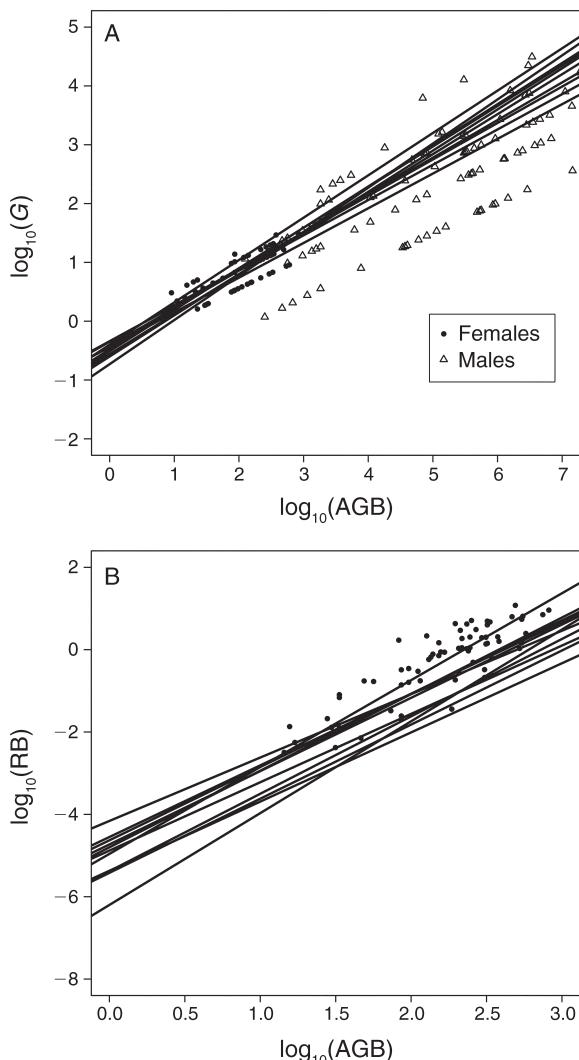


FIG. 1. Ordinary least squares bisector (OLSB) regressions of  $\log_{10}$ - $\log_{10}$ -transformed (A)  $G$  (woody biomass increment; kg) and (B)  $RB$  (reproductive biomass; kg) against  $AGB$  (aboveground biomass; kg) for females during 1976–1986. Each line represents a single regression of  $G$  or  $RB$  onto  $AGB$  for all individuals in a given year for each of 10 years. Individual trees for males (open triangles) and females (solid circles) are shown in panel A and for females in panel B for one year, 1976. Note that the data points line up in panel A due to the rounding of circumference. Circumference was measured in 1-cm increments so that all  $G$  values for a 1-cm increase fall along a single line across  $AGB$  values. Each “line” of data points is due to a discrete amount of increase (e.g., 1, 2, or 3 cm, etc.) on the log scale.

performed using R (R Development Core Team 2011), including the SMATR and slope.s packages (Isobe et al. 1990, Warton et al. 2006).

RESULTS

Population-level analyses

For *B. simaruba* females, population growth and reproduction responded differently to precipitation. While the total population woody growth did not

change significantly (Appendix A;  $r^2 = 0.31$ ,  $P = 0.1$ ), the total population reproductive biomass was greater in years with greater rainfall (Appendix A; ( $r^2 = 0.44$ ,  $P = 0.03$ ). Further, the percentage of population woody growth decreased while the percentage of population reproductive biomass increased with increasing precipitation (Appendix A;  $r^2 = 0.51$ ,  $P = 0.02$ ). The percentage allocation of biomass to reproduction varied from 2% in dry years to 20% in wet years.

Individual-level analyses: relative growth rate, reproductive allocation, and size

For both *B. simaruba* females and males, growth of an individual in one year ( $G$ ; in kg of woody biomass

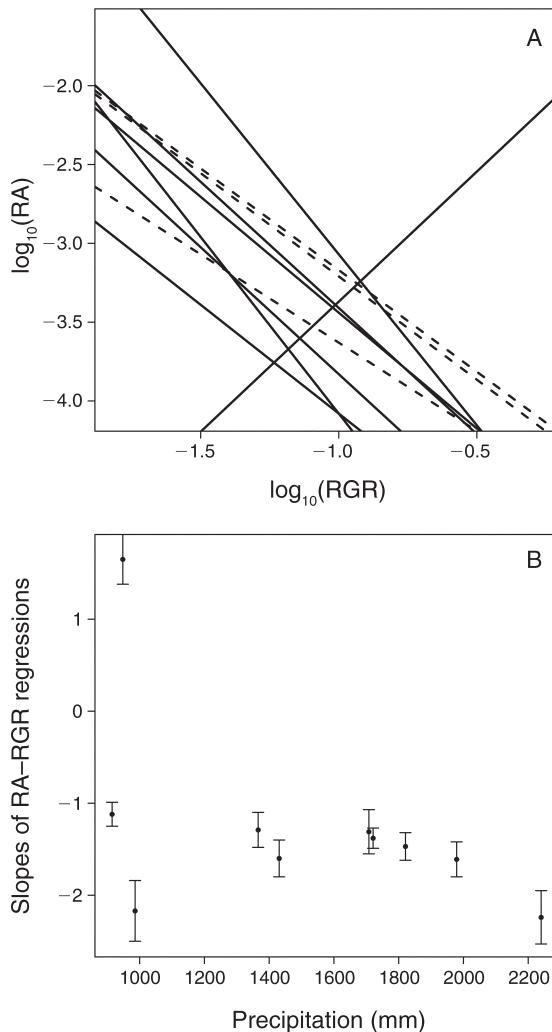


FIG. 2. (A) OLSB regressions of  $\log_{10}$ - $\log_{10}$ -transformed  $RA$  (reproductive allocation) and  $RGR$  (relative growth rate) for female individuals, showing the expected negative relationship between  $RA$  and  $RGR$  for 7 of the 10 years of the study. Dashed lines represent years with no statistical significance between  $RA$  and  $RGR$ ; solid lines represent years with a significant relationship between  $RA$  and  $RGR$ . (B) Scatterplot of the  $RA$ - $RGR$  regressions against annual precipitation for 1976–1986 for all years ( $r^2 = 0.14$ ,  $P = 0.15$ ).

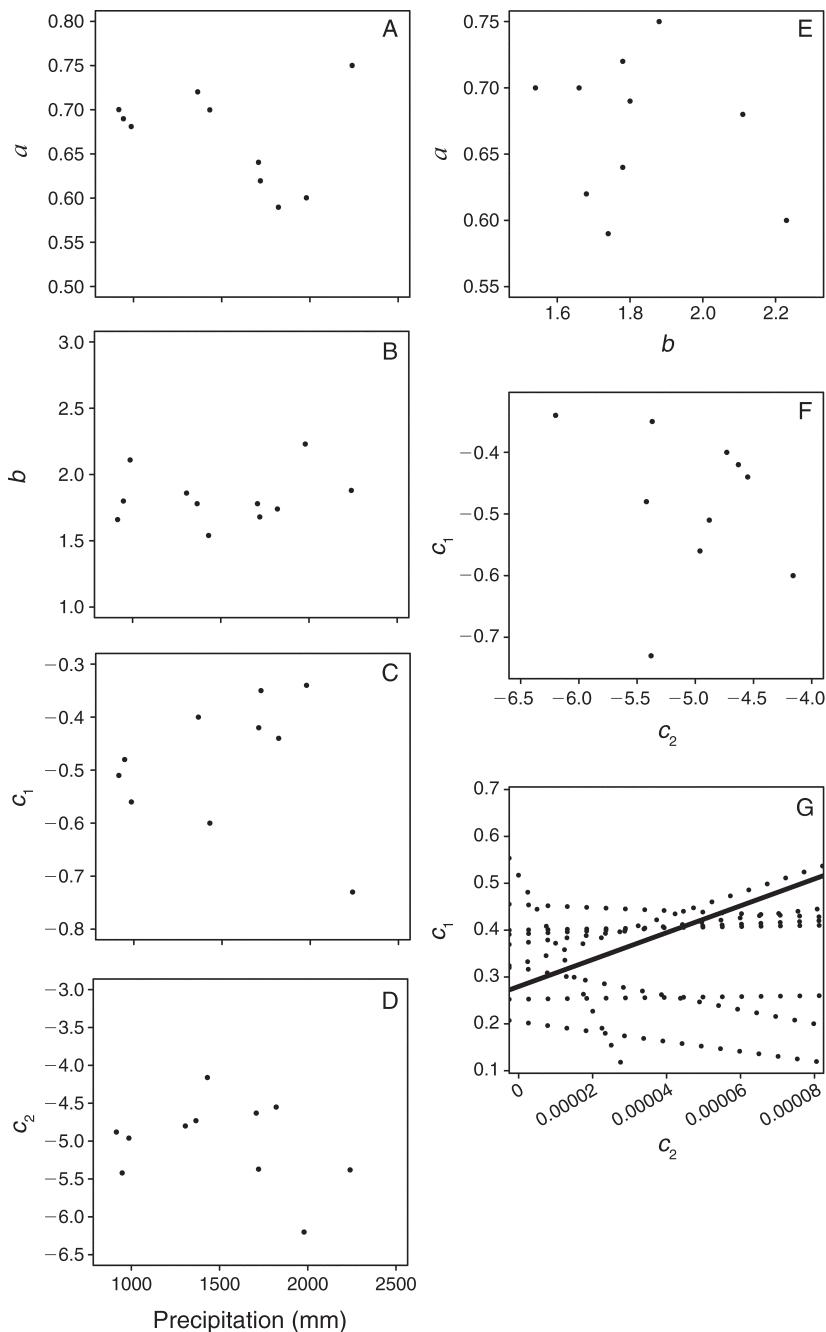


FIG. 3. Scatterplots of (A) the growth exponent  $a$  on precipitation for all years ( $r^2 = 0.10$ ,  $P = 0.45$ ), (B) the reproduction exponent  $b$  on precipitation for all years ( $r^2 = 0.02$ ,  $P = 0.66$ ), (C) the growth intercept  $c_1$  on precipitation for all years ( $r^2 = 0$ ,  $P = 0.97$ ), (D) the reproduction intercept  $c_2$  on precipitation for all years ( $r^2 = 0.08$ ,  $P = 0.39$ ), (E)  $a$  against  $b$  for all years ( $r^2 = 0.18$ ,  $P = 0.22$ ), (F)  $c_1$  against  $c_2$  between years ( $r^2 = 0.07$ ,  $P = 0.46$ ), and (G)  $c_1$  against  $c_2$  within years. In panel G, dashed lines represent years with no statistical significance between  $c_1$  and  $c_2$ ; solid lines represent years with a significant relationship. Here, on log axes,  $c_1$  and  $c_2$  are the allometric normalizations and are the mass-normalized geometric mean responses of growth and reproduction, respectively, of the population, and  $a$  and  $b$  are the regression slopes of the mass-dependence of plant net growth rate and total plant fruit production (see Appendix B).

produced) significantly increased with aboveground biomass (Fig. 1A and Appendix C) and female reproductive biomass (RB; in kilograms of fruit produced) significantly increased with aboveground

biomass (Fig. 1B and Appendix D). In sum,  $a$  (the scaling exponent between growth and mass) was found to be positive and less than 1 and  $b$  (the scaling exponent between reproductive biomass and mass) was found to

be positive and greater than 1 (Table 1). According to Eq. 13, the observed values of  $a$  and  $b$  are then predicted to yield a negative relationship between RA and RGR. Indeed, for 7 of the 10 years of the study, RA did significantly decrease with increases in RGR (Fig. 2A and Appendix E) supporting a central prediction of the model. Assessing variation in the RA–RGR regression slopes across years reveals that they do not vary with precipitation (Fig. 2B;  $r^2 = 0.14$ ,  $P = 0.15$ ).

#### *RA, RGR, and allometry*

There was no response to precipitation for the scaling exponent of reproduction,  $b$  (Fig. 3B;  $r^2 = 0.02$ ,  $P = 0.66$ ), or the allometrically normalized reproduction rate,  $c_2$  (Fig. 3D;  $r^2 = 0.08$ ,  $P = 0.39$ ). Similarly, there was no response to precipitation for the scaling exponent of growth,  $a$ , (Fig. 3A;  $r^2 = 0.10$ ,  $P = 0.45$ ) or the allometrically normalized growth rate,  $c_1$  (Fig. 3C;  $r^2 = 0$ ,  $P = 0.97$ ). Further, the allometric slopes of growth and reproduction were independent of each other as plotting  $a$  vs.  $b$  revealed no significant relationship between these two scaling exponents (Fig. 3E;  $r^2 = 0.05$ ,  $P = 0.54$ ). Finally, between years,  $c_1$  was not significantly correlated with  $c_2$  (Fig. 3G;  $r^2 = 0.38$ ,  $P = 0.08$ ). This finding is consistent with our prediction that microsite variation in resource supply is as important as the trade-off between growth and reproduction. Interestingly, within years,  $c_1$  was not significantly correlated with  $c_2$  (Fig. 3F) except for one strong El Niño year (1983) during which  $c_1$  was positively correlated with  $c_2$  (solid line;  $r^2 = 0.20$ ,  $P < 0.001$ ) indicating that in dry years, resource differences govern growth and reproduction to a greater extent than does a trade-off between growth and reproduction.

#### DISCUSSION

The first focus of our study was to determine the relationship between growth and reproduction in this population of *B. simaruba*. We show that, at the population level, growth and reproduction are influenced by precipitation in opposing ways. Population-level growth decreases and population-level reproduction increases with increasing precipitation. Thus, it appears that when resources are scarce individuals preferentially invest in somatic growth and when resources are abundant (during high-precipitation years) investment in reproductive biomass increases at the cost of somatic growth. Selection, for example, may adjust reproductive effort to anticipate conditions favorable for future seedling establishment (Wright et al. 1999). The abundance of resources may thus invoke higher investment in reproduction as more seeds are likely to survive following germination during a high-resource year. However, this hypothesis critically assumes that the resource pool is finite, equivalent across microenvironments, and does not change with tree size: important components for understanding phenotypic variation in growth and reproduction (Kerkhoff and Enquist 2009).

While the use of population-level measures summarizes the influence of annual precipitation on growth patterns, these measures can average out much of the variation in growth and allocation among individual trees. This is particularly true when the absolute size of the pool from which resources are allocated to reproductive and somatic growth varies between sites, between years, and with tree size. Thus we examined proportional changes in biomass on an individual tree level in order to characterize the relationship between growth and reproduction across individuals that differ in size as well as in variable resource environments. First, across individuals, we found evidence for a negative relationship between growth (RGR) and reproduction (RA) for 7 of the 10 years of the study. Again, this is consistent with individuals investing in reproductive biomass at the cost of somatic growth. Yet 3 of the 10 years of the study show no significant relationship between RA and RGR. We hypothesized that extreme conditions (i.e., El Niño/La Niña events) could potentially cause a decoupling of growth and reproduction; however, two of the three years had a precipitation level just below the 10-year average and one of the three years was just above the 10-year average annual precipitation. Also, tree size and location could influence the availability of microsite resource levels so that even during drought years individuals with access to deep or easily accessible water (i.e., a large individual with deep roots or an individual in a valley) could still grow and reproduce at a higher rate than a similar sized individual in a drier microenvironment. Thus, we suspected that there were further influences on growth and reproduction that neither our population nor individual-level analyses captured.

In order to explore the ultimate cause for variation in growth and reproduction, we then turned to the scaling exponents,  $a$  and  $b$ , and their effects on the RA–RGR relationship. Although plant size may explain many plant allocation patterns (Niklas 1994) and is an important determinant of absolute and proportional reproductive allocation, relatively few studies have assessed the effect of size dependency of reproduction (Hubbell 1980, Wheelwright and Logan 2004, Weiner et al. 2009). Coupling our model and empirical results suggests that the relationship between RA and RGR is not due to a trade-off per se, but instead emerges from allometric relationships that govern both growth and reproduction. In particular, the difference between size dependencies of growth and reproduction within females is primarily responsible for the negative correlation between RA and RGR. In accordance with our model (Eq. 13), a negative relationship between RGR and RA will emerge if either  $a$  or  $b$  (allometric growth and reproduction, respectively), but not both, are less than 1 and both are positive. Indeed, our results show that  $b$  is greater than 1 while  $a$  is less than 1 and both greater than 0 (Table 1). This suggests that the fraction of total production allocated to growth and reproduction

changes with tree size. Thus, even though RGR and RA are mass corrected, the RA–RGR relationship does not evaluate the nature of the trade-off since growth and reproduction are not isometric with tree size.

It is often argued that evidence of trade-offs derived from phenotypic correlations among individuals in nature can be ambiguous and that such correlations may be caused by variation in the environment rather than being primarily generated by trade-offs (Fox and Stevens 1991, Knops et al. 2007). The issue is not whether a trade-off between growth and reproduction exists or not. Allocation is ultimately a zero-sum game; allocation of the total net energy production of an organism to any one function must, by definition, come at the expense to other functions. Instead, the issue is whether observed variation in growth and reproduction is governed more by variation in other factors (e.g., spatial and temporal variation in resource availability) that can mask trade-offs.

To evaluate the relative influence of a growth–reproduction trade-off, the size dependence of growth and reproduction must first be accounted for. It is not enough, however, to simply normalize growth and reproduction by size because the size dependence of both variables is not isometric. To factor out the influence of size, one must instead normalize growth and reproduction by their estimated allometries. Size-corrected growth and reproduction can subsequently be related to each other, and the observed relationship can be compared to predictions based on the relative influence of the growth–reproduction trade-off. That is, comparing  $c_1$  and  $c_2$ , the allometrically normalized measures of growth and reproduction, respectively, will reveal the influence of the growth–reproduction trade-off in comparison to the influence of resource availability on growth and reproduction. This is the only approach we are aware of that can use observational data to appropriately assess trade-offs in growth and reproduction.

Recall that if growth and reproduction are governed primarily by a trade-off rather than resource availability, then  $c_1$  and  $c_2$  will be inversely related. On the other hand, if microsites strongly differ in resources, and growth and reproduction are strongly tied to external resource levels, then individuals in high resource sites will, for their size, grow *and* reproduce to a greater degree than individuals in poor resource sites. As a result, the relationship between  $c_1$  and  $c_2$  will be positive. If such a relationship was observed, we could infer that microsite resource variation is a much stronger constraint shaping variation in growth and reproduction than individuals trading off growth and reproduction. Finally, if the relationship between  $c_1$  and  $c_2$  is flat, we can infer that the trade-off and microsite resource variation have similar effects on growth and reproduction. The finding that, within years,  $c_1$  was not significantly correlated with  $c_2$  except for in one strong El Niño year (1983) during which  $c_1$  was positively

correlated with  $c_2$  (solid line in Fig. 3F), might suggest that average levels of precipitation are sufficient to cancel out differences in microsite conditions. However, the positive correlation between  $c_1$  and  $c_2$  during the extreme drought in 1983 suggests when resources are scarce, microsite differences may be intensified whereby only those individuals with access to deep soil water can both effectively grow and reproduce. Further, the finding that, between years,  $c_1$  was not significantly correlated with  $c_2$  supports the hypothesis that variation in growth and reproduction across females is governed by spatial variation in resource supply and a resource allocation trade-off. Though more statistical power may reveal a directional relationship between  $c_1$  and  $c_2$ , this relationship would presumably be quite weak as there is no evidence to suggest increasing statistical power would substantially change our ultimate conclusions. To further explore the effects of microsite differences and between year variability in resources, future efforts could be made to investigate whether individuals of the same size located in contrasting microhabitats differ in allocation to growth and reproduction (e.g., Pitelka et al. 1980, Young 1984, Denslow et al. 1990, Sugiyama and Bazzaz 1998). Manipulating resource availability between years and between sites in an experimental design could help tease apart the interactive effects of microsite and interannual variability of resource availability on growth and reproduction (see Obeso 2002).

We propose that our theoretical derivation for the allometric size dependency of growth and reproduction is appropriate for understanding the primary origin of the RA–RGR relationship. Thus, a positive or negative relationship between RA and RGR does not necessarily signify that reproduction slows or improves plant growth rate and is not necessarily a measure of a trade-off. This is due to the fact that the functional relationship between RA and RGR is influenced by the allometries of growth rate and reproduction. A plot of RA as a function of RGR can most usefully be used to assess a trade-off between vegetative and reproductive production if there is no variation in size or resource availability among individuals. However, a plot of RA vs. RGR is often used to look for a trade-off between vegetative and reproductive growth without holding tree size and resource availability constant (Calder 1984, Samson and Werk 1986, Bonser and Aarssen 2008). We recommend that future experimental studies eliminate variation in tree size and resource supply and that these experiments be coupled with observational studies that take an allometric approach similar to that developed here.

In this study, we quantified the relationship between two important life history traits: growth and reproduction. We asked how this relationship varies across time and how it is influenced by underlying allometries and resource supply. Our results support and underscore the findings of several recent papers (see Knops et al. 2007). Specifically, a negative correlation between growth and

reproduction is not a strong test of the processes that underlie variation in growth and reproduction. In particular, in *B. simaruba*, after controlling for allometric growth and reproduction, both growth and reproduction reveal three important patterns. First, we show that growth and reproduction are not isometric and thus do not scale similarly with size. Second, the relationship between RA and RGR is ultimately governed by the underlying allometries of growth and reproduction. Third, observed variation in growth and reproduction is consistent with resource variation and trade-off mechanisms each playing important roles in the observed patterns. To better understand the processes governing individual growth and reproduction, we suggest that more emphasis be placed on studying the dual effects of size and variation in resource supply across microsites, particularly within long-lived trees.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Simple linear regressions of total population woody growth, reproductive biomass, percentage of population woody growth, and percentage of reproductive biomass as functions of precipitation for each year (*Ecological Archives* E093-017-A1).

##### Appendix B

Conceptual figure describing the calculation of  $a$ ,  $b$ ,  $c_1$ , and  $c_2$  (*Ecological Archives* E093-017-A2).

##### Appendix C

Tabular results for female and male growth as a function of mass from log–log-transformed ordinary least squares, ordinary least squares bisector, and reduced major axis regressions (*Ecological Archives* E093-017-A3).

##### Appendix D

Tabular results for female reproductive biomass as a function of mass from log–log-transformed ordinary least squares, ordinary least squares bisector, and reduced major axis regressions (*Ecological Archives* E093-017-A4).

##### Appendix E

Tabular results for female reproductive allocation as a function of relative growth rate from log–log-transformed ordinary least squares, ordinary least squares bisector, and reduced major axis regressions (*Ecological Archives* E093-017-A5).