Testing implicit assumptions regarding the age vs. size dependence of stem biomechanics using *Pittocaulon* (~*Senecio*) *praecox* (Asteraceae)[1]

Julieta A. Rosell and Mark E. Olson[2]

Instituto de Biología, Universidad Nacional Autónoma de México, Departamento de Botánica, Tercer Circuito s/n, Ciudad Universitaria, Copilco, Coyoacán A.P. 70–367, México, Distrito Federal, C.P. 04510, Mexico

Strong covariation between organismal traits is often taken as an indication of a potentially adaptively significant relationship. Because one of the main functions of woody stems is mechanical support, identifying the factors that covary with biomechanics is essential for inference of adaptation. To date in such studies, stem biomechanics is plotted against stem age or size, thus with implicit assumptions regarding the importance of each in determining mechanics. Likewise, comparing ontogenies between individuals is central to the study of ontogenetic evolution (e.g., heterochrony). Both absolute age and size have been used, but the rationale for choosing one over the other has not been examined. Sampling a plant of simple architecture across microsites with differing sizes for the same absolute age, we compared regressions of stem length, mechanics, and tissue areas against age and size. Stem length was predicted by diameter but not by age, and stem biomechanics and tissue areas were better explained by stem length rather than age. We show that the allometric and mechanical properties observed across microsites are uniform despite great plasticity in other features (e.g., size and wood anatomy) and suggest that this uniformity is an example of developmental homeostasis. Finally, we discuss reasons for preferring size over absolute age as a basis for comparing ontogenies between individuals.

Key words: adaptation; allometry; Asteraceae; developmental homeostasis; heterochrony; ontogenetic autocorrelation; plasticity; Young's modulus.

Covariation between morphological characters has often been interpreted as an indication of functional relationships that may be of adaptive significance. From this point of view, close correlations suggest selectively important relationships, whereas a lack of covariation between characters suggests that their synergy is not essential for survival (cf. Berg, 1960; Frankino et al., 2005). For example, the observation that many tree species have constant trunk–crown allometric relationships throughout ontogeny (Sterck and Bongers, 1998) thus could be interpreted as indicating that the maintenance of specific allometric relationships may be of strong functional significance. The same reasoning leads to the idea that dissociation between characters such as the lack of phenotypic integration between vegetative and reproductive characters (e.g., Pigliucci et al., 1991) implies that strong covariation between these features is not essential for organismal function and thus not favored by natural selection. Covariation between features in ontogeny or across the adults of a clade has also been interpreted as an indication of developmental constraint (e.g., Zelditch et al., 1990; Marroig and Cheverud, 2005). To begin to unravel the causes of trait covariation and to identify relationships of adaptive significance, we first need to identify the characters involved and the strength and direction of their covariation.

The stems of woody plants are studied from many points of view such as anatomical, hydraulic, biomechanical, allometric, yet many assumptions remain untested regarding the covariation of these traits with stem size and age. For example, on what basis can it be said that the wood of species A is stiffer than the wood of species B, that the xylem of one is more vulnerable to cavitation than another, or that the libriform fibers have thicker walls in one than the other? Such ranking of traits is based on some standard, but what standard best predicts the traits of interest has not been widely addressed. Some workers prefer to compare features between stems of similar size (e.g., Tyree and Yang, 1992; Kavanaugh et al., 1999; Carlquist and Grant, 2005), whereas others have reason to favor comparisons between stem segments of similar absolute age (e.g., Bailey and Tupper, 1918; Panshin and de Zeeuw, 1980; Moltenberg and Hoibo, 2006). A notable exception is the work of Spicer and Gartner (2001), who found that tree ring age was not sufficient to explain the specific conductivity (k_s) of a given sample of xylem but that position within the stem was strongly associated with k_s. The use of stem age vs. stem size as a basis for the comparison of stem properties between individuals (whether anatomical, hydraulic, mechanical, or otherwise) implies differing scenarios regarding the adaptive significance of these variables. Plotting stem characteristics against age invokes the implicit hypothesis that certain features are dependably associated with the same age between individuals. In contrast, comparing stem features in the context of stem size between individuals involves the notion that, regardless of its age, the structure and function of a stem must keep pace with its proportions.

In this article, we focus on the biomechanical behavior of stems and ask whether mechanics are best predicted by the

absolute age or by the size of a stem segment. Because one of the major functions of woody plant stems is mechanical support, stem biomechanical data provide crucial information for inferences of adaptation in these organisms. Despite the importance of understanding the interrelationship between mechanics, size, and age, in most biomechanical studies of woody plant stems, variation in mechanical behavior has been considered either in the context of absolute age or growth rates (e.g., Bhat and Priya, 2004) or of stem allometry (e.g., Niklas and Buchman, 1994) but not both simultaneously. Similarly, in various studies the relationship between allometry in relation to size or age has been considered, but the mechanical parameters were not examined or were inferred indirectly (e.g., Sterck and Bongers, 1998; Briand et al., 1999; Poorter et al., 2003). Taken together, these studies imply that the mechanical behavior of a stem is related to its size, age, and allometry, but to what extent each plays a part cannot be determined when these factors are considered separately. Identifying whether or not woody stem features are more strongly predicted by stem size or age would permit a biologically justified selection of one or the other for a given study. To provide information to guide the inference of woody plant stem evolution and to distinguish between these very different implicit visions of ontogeny, it is vital to understand the ways that structure, size, age, and allometry interact to produce mechanical behavior.

It might be argued that age and size are clearly and necessarily related in woody stems, an assertion that highlights the differences between within-stem and between-individual comparisons. Within individual stems, age and size vary predictably in that the direction of the correlation between size and age can always be predicted; because woody stems grow via the accretion of xylem layers, an older stem segment will inevitably have accumulated more layers than a more distal and therefore younger segment. Greater stem segment diameter implies greater second moment of area I, the mechanical parameter that describes the geometric arrangement and size of a given beam in cross section and mathematically reflects how well this arrangement of material can resist bending. As a result, larger, more basal segments can confidently be predicted to be less flexible than more distal segments, although the magnitude of this difference cannot be predicted (see Niklas, 1995, 1997a–c, 1999a). However, the relationship of mechanics with size and age in comparisons between individuals is less clear, because stems of the same age growing in different environments or microsites can have differing sizes (e.g., Rozas, 2003; Parish and Antos, 2004; Brienen and Zuidema, 2006). For example, a stem growing slowly in a dry environment will be much smaller than a rapidly growing stem in a moist one, even though they may be clones of the same age (cf. Weiner, 2004). Thus, in contrast to comparisons of segments within the same stem, larger stem size does not necessarily indicate greater age between individuals. It is precisely this plasticity that gives rise to the problem of whether size or age better reflects stem properties, mechanical and otherwise. To test the relative importance of each requires a model system in which age can be readily determined.

We compare the relationship of mechanical behavior to both size and age using the Asteraceous "broomstick tree" Pittocaulon (~Senecio) praecox (Cav.) H. Rob. and Brettell, endemic to seasonally dry tropical areas of southern central Mexico. This species is ideal for such tests for several reasons. First, the pattern of leaf scars on the stem permits the inference of the age of any segment (Pérez and Franco, 2000). Early in the yearly rainy season, the internodes are long, and the leaf scars on the stem are well separated, but as the rains dwindle, the internodes become so short that the scars of the final leaves produced nearly touch one another, leaving a conspicuous ring of scars around the stem (Fig. 1B, C). Each scar ring thus indicates the growth of one season. We are not aware of other woody dicots in which these annual scars can be so readily detected, even in stems decades old. Second, detailed anatomical information is available for P. praecox and its relatives (Olson, 2005), which allows us to pinpoint the anatomical features responsible for some of the ontogenetic changes in biomechanical behavior observed. Finally, P. praecox has relatively simple architecture, consisting of thick stems that branch only occasionally, thus providing long, straight beams ideal for mechanical bending tests (Fig. 1A). There is relatively little xylem in the stems of Pittocaulon, with the bulk taken up by thick, water-storing pith and bark that fuel flowering and fruiting at the end of the 6-month dry season (Fig. 1A inset, D; Olson, 2005).

By sampling a variety of situations, from old, slow-growing individuals atop exposed lava boulders to younger trees of rapid growth in shady hollows, we tested stems spanning an array of size–age relations (Fig. 2; cf. Niklas, 1995). Our general strategy to address whether the mechanical properties of a stem are better explained by its absolute age or by its size was to compare the fit of a linear regression that included age as a covariable with one using stem length. First, we asked whether or not stem length-diameter proportions should resemble each other more strongly between stems of similar size or between those of similar absolute ages. Likewise, are similar materials properties, i.e., tissue and structural Young's moduli (E), observed between stems of similar sizes or between stems of similar absolute ages? We also examined the changes in areas occupied by bark, wood, and pith along the length of the stems studied. These tissue areas are important because, in addition to E, the mechanical behavior of a structure is also determined by the amount and arrangement of its materials, as reflected by the second moment of area I. Therefore, we determined whether the percentage of the cross-sectional area of the stem occupied by bark, wood, and pith were best predicted by segment age or by stem diameter. Furthermore, because it is the performance of the entire branch that is of greatest adaptive relevance, we examined flexural stiffness EI. Because I is related directly to stem diameter, then stem size would be expected to predict EI well. However, it is not clear to what extent age should be associated with stem EI. We therefore also examined how well the age of a given stem segment predicts its flexural stiffness. Finally, many studies have suggested that differences between environments or growth rates result in differences in mechanical properties (Kliger et al., 1998; Bhat and Priya, 2004). We examined which features change with the great differences in environments and growth rates sampled and how these are involved in the interplay between size, allometry, and mechanics. Finally, we highlight which stem features appear to be of chief adaptative importance in woody stems and discuss the merits of size vs. age in studies of ontogenetic evolution.

MATERIALS AND METHODS

Plants were collected from a highland, dry tropical scrub community on the Pedregal de San Ángel lava field in the southwestern part of the Valley of
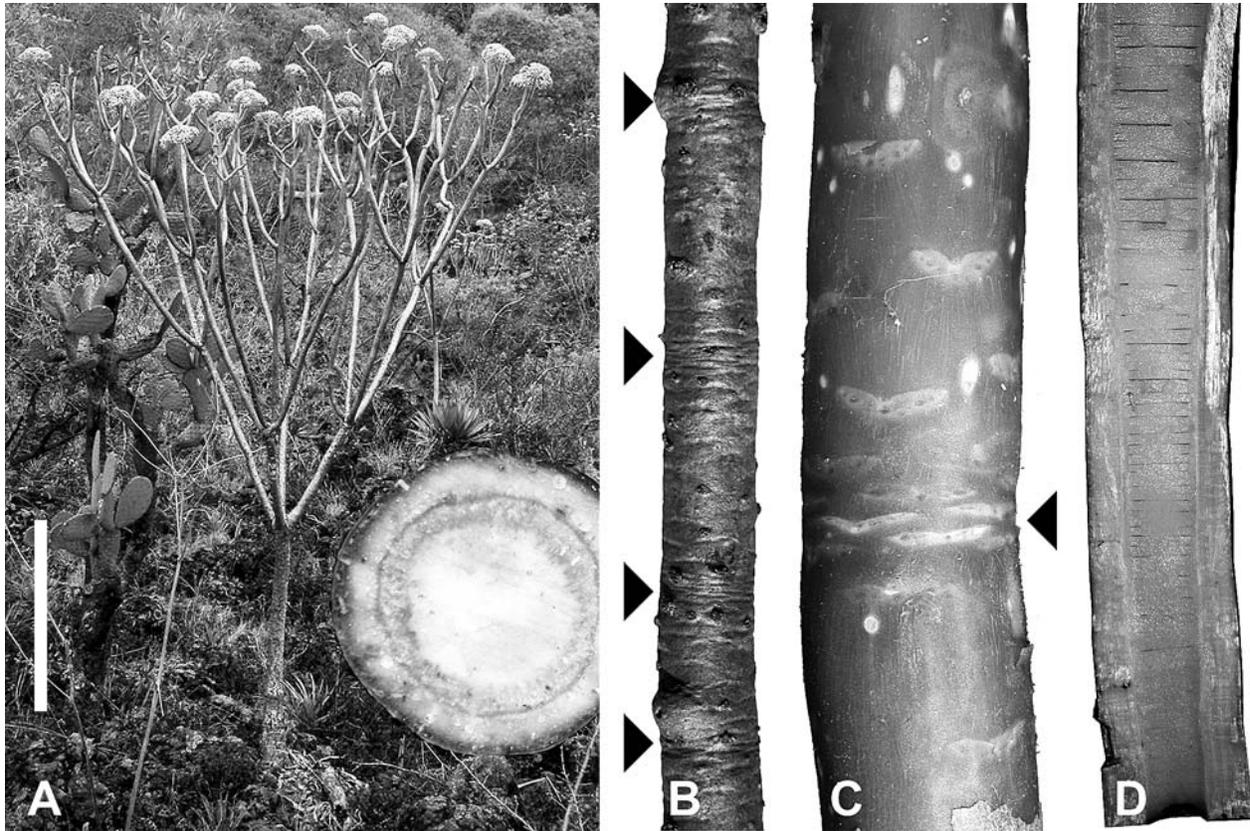
Fig. 1. *Pittocaulon* habit and stem construction. (A) Habit, with thick stems and sparse branching. Scale bar = 1 m. Inset, 6.5 cm diameter stem in transection to show the very wide pith, thin xylem cylinder, and bark with thick, water-storing cortex. (B) Stem with annular scars left at the end of each growing season. Four such rings are shown here (arrows). Stem = 1.5 cm in diameter. (C) In older stems, the annular scars can become obscured by the phellem, but they are preserved and readily detected by exposing the phelloderm. A large amount of phellem was removed from this stem to show separated mid-season leaf scars and the aggregated end-of-season scars (arrow); only a very small amount was removed from stems subjected to mechanical testing. Stem = 5.5 cm in diameter. (D) Stem split lengthwise to show very wide pith replete with water at the end of the wet season. Stem = 6 cm in diameter.

Mexico (19°19′14″ N 99°11′40″ W) at an elevation of 2315 m a.s.l. Vouchers are deposited as *Olson 1020* in the MEXU herbarium. We selected a single branch from each of 16 individuals from microsites describing a range of water availability within a single 0.5 km^2 locality. The driest habitats were exposed lava outcrops, and the moistest were areas of deeper soil where the natural vegetation was shaded by native and invasive trees. To provide optimal beams for mechanical testing, we selected stems that branched well above the base, had fewer than three orders of branching, and had long, straight segments. Like many water-storing dryland plants, *Pittocaulon* stem water content changes drastically throughout the year (Olson, 2005); mechanical tests could produce differing results between dry and wet seasons (see Jacobsen et al., 2005). To eliminate any such possibility, all allometric measurements and mechanical tests were conducted at the same time of the year, at the end of the 2005 rainy season. The collected stems were immediately taken to the laboratory for processing.

Data were analyzed using simple and multiple linear regressions, checking all assumptions. All variables were log$_{10}$ transformed to meet assumptions and/ or to increase model fit. Statistical analyses employed Statistica v.6.0. (StatSoft, Inc., Tulsa, Oklahoma, USA) and S-Plus 2000 (MathSoft, Inc., Cambridge, Massachusetts, USA).

Stem age—The age of stems was determined by counting the annual growth increment scars (Fig. 1B). These scars were no longer apparent on the older phellem of some lower stems. In these cases, we removed small amounts of phellem to expose the phelloderm, where these scars are clearly preserved (a stem with a large amount of phellem removed is shown in Fig. 1C).

Allometric relationships: variation of stem length with diameter and age—We sampled plants of very different heights that were of similar ages and plants of differing ages but similar heights (cf. Niklas, 1995). To test our hypothesis that length is better predicted by its relationship with basal diameter than absolute age, we used linear regressions to estimate the relationships between these variables.

Bending tests and variation of mechanical properties with size and age—For mechanical testing, the branches were divided into segments with a 1 : 20 diameter to length ratio to minimize shear (Vincent, 1992). Each segment was submitted to three-point bending tests using a digital micrometer to measure the deflection of the stem caused by adding weights to a bucket suspended at the midpoint of the tested segment (Vincent, 1990). The taper of each segment was less than 10% of its mean diameter, except for a few terminal segments, which tapered ~20%. The flexural stiffness for each segment (structural flexural stiffness, EI_{struct}) was computed from the formula (Gere, 2002):

$$EI_{struct} = \frac{L^3}{48m},$$

where m is the slope of the linear relationship resulting from observed deflections of stem segments upon adding a sequence of weights and L is the length between the supports on which the segment ends rested. After testing, each segment was debarked to repeat the bending test and to compute the flexural stiffness of the wood (EI_{wood}). The flexural stiffness of the bark (EI_{bark}) was inferred by taking the difference of EI_{struct} and EI_{wood} (Niklas, 1999b). For most of the terminal segments of the stems, EI_{wood} and thus EI_{bark} could not be
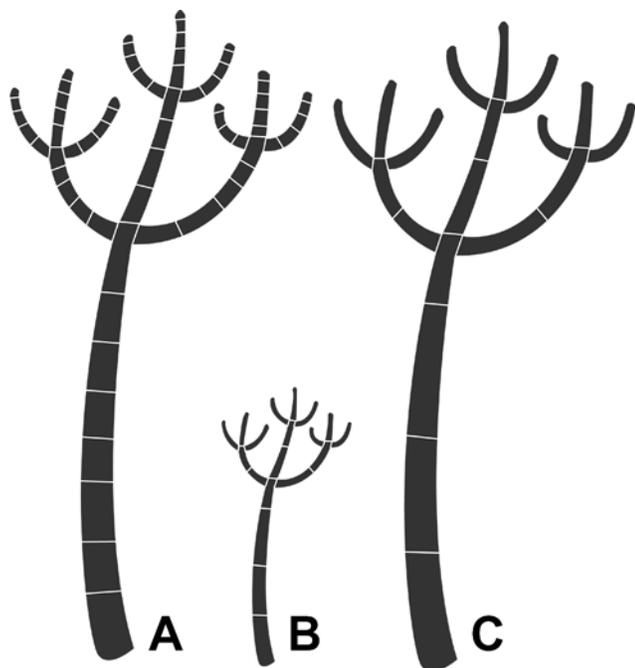
Fig. 2. Age and size in *Pittocaulon*. The black silhouettes represent three individuals of *Pittocaulon*; ages can be determined by annual scars (white lines). All three have flowered twice and thus have undergone two branching events. Despite having similar architecture, the three plants have very different age–size relationships. (A) Tall individual; annual scars show it is 17 years old. (B) Small individual, 7 years old. (C) Tall individual, 7 years old.

computed, because the xylem fascicular areas were not yet united into a continuous cylinder (see Olson, 2005; cf. Esau, 1977, p. 297), making removal of the bark impossible without damaging the xylem. Because the cross sections of the tested segments were nearly circular, the second moments of area (I) were calculated with the formulas of Pisarenko et al. (1979) for circles and hollow circles. To obtain the measurements necessary for calculating I, apical and basal diameters of the bark, wood cylinder, and pith were measured before bending tests for each segment and averaged for computing I_{struct}, I_{wood}, and I_{bark}. After calculating both flexural stiffness (EI) and second moment of area (I), the computation of the different Young's moduli (E_{struct}, E_{wood}, and E_{bark}) was straightforward. The structural Young's modulus (E_{struct}) refers to the heterogeneous composite material formed by the bark and wood when the whole stem is mechanically tested. In tests both with the pith and with the pith removed with a rod, the pith contributes minimally to the flexural stiffness of older stems (data not shown). As a result, we ignored this tissue, although in the terminal segments it likely makes a significant mechanical contribution. The measurements of each segment used for computing I were used to calculate areas occupied by bark, wood, and pith in stem transection.

We regressed the mechanical characteristics EI_{struct}, EI_{wood}, EI_{bark}, E_{struct}, E_{wood}, and E_{bark} on the stem segment midpoint–stem tip distance. We selected this distance as a measure of size based on the expectation that it should reflect the amount of load that a given segment has to bear. We compared these results with regressions of the same mechanical characteristics against stem age. The number of stems tested (16) exceeded the average number of segments per stem (3.6), which made it seem unlikely that similarity between segments due to membership in the same stem would influence our results (i.e., that mechanical data would be ontogenetically autocorrelated, because samples were taken from along the same stem). To check this supposition, in all regressions, "individual" was entered as a random effect to check for its potential influence in the fitting of the model (Longford, 1993). All regressions with distance from the tip and "individual" as independent variables resulted in estimated coefficients and associated standard errors that were practically identical to those estimated in the models without individual as a variable. In contrast, some of the regressions with age as an independent variable had a significant effect of

individual, with the fit slightly increasing. This increase can be attributed to the markedly poor fit of the regressions with age as an explanatory variable. Therefore, we report the fitting of simple models with only distance from the tip or age as independent variables, thus allowing direct comparisons between all models.

Growth rate as a proxy environmental variable—The marked differences in age and size observed (Fig. 2) in plants from a range of environments imply differing growth rates, an observation that is of interest because growth rate has been implicated in many plants as being associated with mechanical differences. We assumed that the average growth rate of a stem should reflect the long-term water availability of a microsite, and we thus considered growth rate a stand-in for water availability, referred to here as "environment." The plants sampled were collected from the same general area, climate, and soils. However, fine-grained microsite differences led to extreme situations, such as short, old plants on exposed sites on bare rock growing adjacent to tall, young ones in sheltered spots.

To calculate growth rates, stem age was determined, the length of each annual growth increment was measured with a tape measure, and the diameter of the base of each growth increment was measured with digital calipers. Growth rate in length was calculated for each individual as the slope of the simple linear regression line defined by the relationship between annual cumulative length (distance from tip to annual scars) and age. Because we were dealing with cumulative lengths along the same stem, one value could not be considered entirely independent of another. This autocorrelation was taken into account in a variance–covariance matrix ($\mathbf{W}$), which was incorporated into the estimation process of the regression coefficients as follows (Kutner et al., 2005):

$$\boldsymbol{\beta} = (\mathbf{X}'\mathbf{W}\mathbf{X})^{-1}\mathbf{X}'\mathbf{W}\mathbf{Y},$$

where $\boldsymbol{\beta}$ is the vector of the least-squares regression coefficients (β_0 and β_1), $\mathbf{X}$ is the matrix that contains the explanatory variable (age in yr), and $\mathbf{Y}$ is the vector of the response variable (annual cumulative length). To construct $\mathbf{W}$, we performed a preliminary regression of annual cumulative length vs. age to estimate the residuals. Using these residuals, we then estimated the average autocovariance between age difference categories, that is, between all pairs of residuals that differed by 1 year, then between all that differed by 2 years, and so on, until the maximum distance of the total branch age minus one was reached. These values were placed in the off-diagonal cells of the matrix. For example, for a 5-year-old branch, the autocovariance for the 1-year age difference category would be the average autocovariance between the residuals for years 1 and 2, 2 and 3, 3 and 4, and 4 and 5. This value would be placed in all cells that represent a difference of 1 year between segments. The autocovariance for the 2-year category would correspond to the average autocovariance between residuals for years 1 and 3, 2 and 4, and 3 and 5; that for the 3-year category would correspond to the average between years 1 and 4 and 2 and 5, whereas the 4-year category would consist only of the value between years 1 and 5. For the diagonal elements of the matrix, we calculated the average variance for the annual cumulative length of each stem age. That is, the length from the stem tip to the first annual scar was measured and the average variance across all stems calculated. Similarly, the average variance in length from the second annual scar to the stem tip was calculated using data from all stems. This procedure was followed for all ages. The same approach was followed with respect to growth rates in diameter.

To examine whether or not different environmental situations were associated with differences in allometry and mechanics, we used multiple regression models introducing growth rate as an explanatory variable to 13 of the 26 simple regressions in Table 1. These 13 models were selected because they did not include age, which is closely related to growth rate ($r = -0.87$; $P < 0.05$) and could therefore be a source of collinearity. As for simple regressions of mechanical parameters vs. distance from the tip or age, in these multiple models the effect of the "individual" was tested and was also not significant. We inferred a significant environmental effect when $\beta_{growth\ rate}$ differed from zero and when the adjusted coefficient of multiple determination r_a^2 increased with respect to the simple model without growth rate. The strength of the contribution of environment to explaining allometric or mechanical response variables was evaluated using semipartial correlations. We preferred semipartial over partial correlations because they readily identified which variable explained more of the variation in the response variable in each multiple model and were thus useful indicators of the relevance of growth rate (Etxeberria, 1999).

TABLE 1. Simple ordinary least-squares regressions of *Pittocaulon* stem length, tissue areas, and mechanical parameters vs. size and age, showing that dimensional variables in all cases predict far more effectively than age. Regressions for stem allometry (a), tissue area (b–d), flexural stiffness (e–g), Young's modulus (h–j), and moment of inertia (k–m). All variables are $\log_{10}$ transformed. Diameter = basal diameter of the stem (m); Distance = distance from tip of stem to midpoint of segment (m); Age = average age of segment (yr). F test for lack of fit of model; β_0 = intercept; β_1 = slope. * = significant at $P < 0.05$; ** = significant at $P < 0.01$; ns = not significant, $P > 0.05$.

	Response	Explanatory	r^2	N	F test	$\beta_0 \pm$ SE	$\beta_1 \pm$ SE
(a)	Stem length	Diameter	0.69	16	$F_{1,14} = 31.16$**	2.20 ± 0.36**	1.33 ± 0.24**
	(m)	Age	<0.1	16	$F_{1,14} < 0.01$, ns	ns	ns
(b)	Bark area	Distance	0.69	54	$F_{1,52} = 114.01$**	-3.61 ± 0.02**	0.60 ± 0.05**
	(m^2)	Age	0.13	58	$F_{1,56} = 7.99$**	-3.90 ± 0.08**	0.28 ± 0.10**
(c)	Wood area	Distance	0.75	53	$F_{1,51} = 154.03$**	-3.92 ± 0.04**	1.15 ± 0.09**
	(m^2)	Age	0.26	57	$F_{1,55} = 19.77$**	-4.61 ± 0.13**	0.76 ± 0.17**
(d)	Pith area	Distance	0.55	54	$F_{1,52} = 62.28$**	-3.70 ± 0.05**	0.87 ± 0.11**
	(m^2)	Age	<0.1	58	$F_{1,56} = 0.76$, ns	-3.93 ± 0.14**	ns
(e)	EI_{struct}	Distance	0.86	54	$F_{1,52} = 322.60$**	1.11 ± 0.06**	2.5 ± 0.14**
	(GN·m^2)	Age	0.19	58	$F_{1,56} = 12.714$**	ns	1.34 ± 0.38**
(f)	EI_{wood}	Distance	0.91	45	$F_{1,43} = 450.30$**	1.05 ± 0.05**	2.95 ± 0.14**
	(GN·m^2)	Age	<0.1	46	$F_{1,44} = 4.37$*	ns	1.03 ± 0.49*
(g)	EI_{bark}	Distance	0.63	39	$F_{1,37} = 63.19$**	ns	1.63 ± 0.21**
	(GN·m^2)	Age	<0.1	41	$F_{1,39} = 1.02$, ns	ns	ns
(h)	E_{struct}	Distance	0.8	54	$F_{1,52} = 213.82$**	-0.36 ± 0.03**	1.02 ± 0.07**
	(GN/m^2)	Age	0.34	58	$F_{1,56} = 28.08$**	-1.06 ± 0.11**	0.76 ± 0.14**
(i)	E_{wood}	Distance	0.74	44	$F_{1,42} = 117.04$**	0.30 ± 0.03**	0.85 ± 0.08**
	(GN/m^2)	Age	0.12	46	$F_{1,44} = 5.95$*	ns	0.38 ± 0.15*
(j)	E_{bark}	Distance	<0.1	39	$F_{1,37} = 0.30$, ns	-1.18 ± 0.06**	0.09 ± 0.1706
	(GN/m^2)	Age	<0.1	41	$F_{1,39} = 0.08$, ns	-1.14 ± 0.15**	-0.05 ± 0.1763
(k)	I_{struct}	Distance	0.75	54	$F_{1,52} = 156.64$**	-7.53 ± 0.05**	1.49 ± 0.12**
	(m^4)	Age	<0.1	58	$F_{1,56} = 5.16$*	-8.15 ± 0.20**	0.57 ± 0.25**
(l)	I_{wood}	Distance	0.8	53	$F_{1,51} = 199.20$**	-8.26 ± 0.06**	2.00 ± 0.14**
	(m^4)	Age	0.15	57	$F_{1,55} = 9.80$**	-9.21 ± 0.24**	0.97 ± 0.31**
(m)	I_{bark}	Distance	0.76	54	$F_{1,52} = 159.90$**	-7.72 ± 0.05**	1.36 ± 0.11**
	(m^4)	Age	<0.1	58	$F_{1,56} = 5.96$*	-8.32 ± 0.18**	0.55 ± 0.23*

RESULTS

The 16 measured stems ranged in age from 5 to 26 yr old, in total length from 1.2 to 3.4 m and from 2.2 to 4.5 cm in diameter. Branches were divided into an average of 3.6 segments for a total of 58 segments tested mechanically.

Allometry: stem dimensions and areas of bark, wood, and pith—To compare how stem length is related to diameter and age, we performed two regressions, which showed that the length of a stem cannot be predicted from its age, but is well explained by its diameter (Table 1a, Fig. 3A, B). The model with diameter as an explanatory variable takes the form of a Huxley-type allometric equation ($\log_{10}$ length = β + $\alpha\log_{10}$ diameter; Niklas, 1994), that explains variation in length reasonably well (Table 1a, Fig. 3A). Because the confidence interval of its scaling exponent α includes unity (0.82–1.84), the allometric relationship of branch length and diameter does not deviate significantly from isometry, with large plants showing the same proportions as small ones. Areas of bark, wood, and pith were also better predicted by distance from the tip of the stem than age (Table 1b–d, Fig. 3C, D).

Stem mechanical properties—The mechanical parameters E, I, and EI decreased from the stem bases to the tips in all situations but in Young's modulus of the bark. As was observed for allometry, a size variable was a better predictor of the mechanical parameters than was age (Table 1e–m). E_{struct} ranged from a minimum of 0.27 GN/m^2 near the branch tips to 1.82 GN/m^2 at the stem base ($N = 58$). Likewise, E_{wood} varied from 0.2 GN/m^2 in terminal segments to 5.31 GN/m^2 in segments 2 m or more from the stem tips ($N = 46$). In contrast, the Young's modulus of the bark (E_{bark}) was more or less constant, showing no trend with age or with distance to the tip (Table 1j) and an average of 0.083 GN/m^2 ($N = 40$, SE = 0.009) at any given point. With respect to the flexural stiffness of the stem (EI_{struct}), the data ranged from 0.02 to 320.52 GN·m^2 ($N = 58$), whereas EI_{wood} varied from 0.03 to 312.11 GN·m^2 ($N = 46$) and EI_{bark} between 0.03 and 8.93 GN·m^2 ($N = 41$). Table 1 gives the regressions modelling EI (Table 1e–g, Fig. 4), E (Table 1h–j, Fig. 5), as well as the second moments of area (I) (Table 1k–m) based on the distance from the tip of the stem or age. Except for E_{bark}, which remained constant along the stem, mechanical variables were better explained by the size variables than by age, which in all cases yielded very poor regression models (cf. Fig. 4A, C vs. 4B, D and Fig. 5A, C vs. 5B, D).

Effect of environment on allometry and mechanical properties—The wide variety of environments occupied by *Pittocaulon* was reflected in the range of growth rates in length observed, which varied from 0.060 m/yr in the most highly
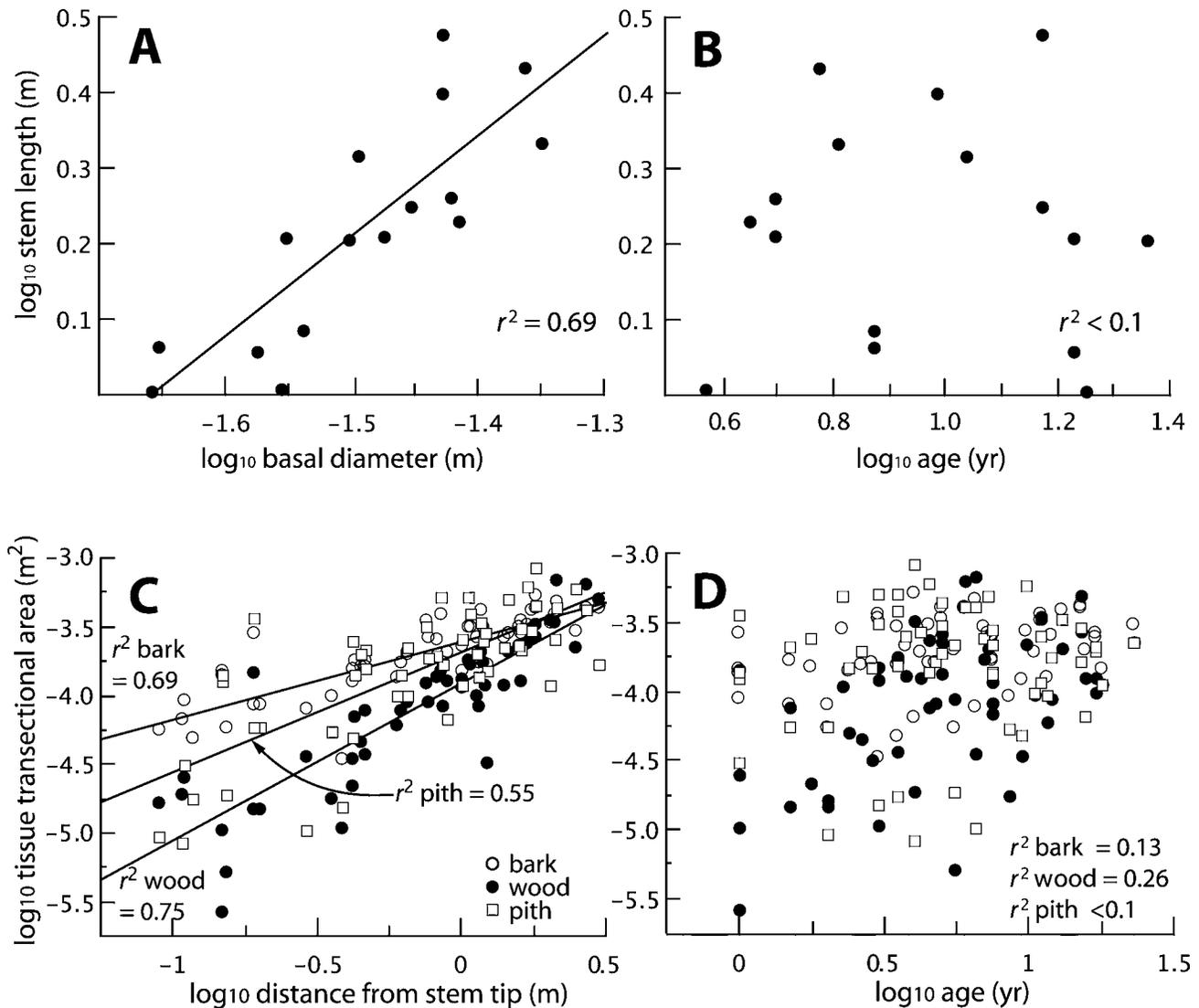
Fig. 3. Size vs. age in *Pittocaulon* allometry and proportions of bark, wood, and pith. (A, B) Stem length is better explained by diameter than by age. (A) Total stem length is predicted well by basal diameter. (B) Stem length has no statistical relationship to total stem age. (C–D) Similarly, areas of bark, wood, and pith per unit of stem transectional area are predicted better by stem size than by stem age. (C) Wood and bark, the tissues with greatest mechanical contributions, are predicted better than the pith. (D) Bark, wood, and pith plotted against segment age, showing that age is a poor predictor.

exposed location to 0.496 m/yr in the most sheltered, with a mean of 0.237 (SE = 0.018). The high uniformity in diameter along the length of *P. praecox* stems prevented in most cases the calculation of a growth rate in diameter.

Multiple regressions that included growth rate showed that stem length to diameter relations apparently do not vary across environments but that environment does play a role, albeit very slight, in explaining bark and pith areas. When stem length was explained by diameter and growth rate, the coefficient associated with growth rate was not significant ($N = 16$, $\beta_{\log_{10} \text{growth rate}} \pm \text{SE} = -0.10 \pm 0.10$, $P = 0.38$), showing that the same allometric relationship is maintained regardless of habitat. In contrast, the environment was significant in the multiple regressions explaining both bark and pith areas based on distance from the tip and growth rate (Table 2a, b). Despite these significant coefficients, the contribution of growth rate is slight, with semipartial correlations showing that the distance

from the tip explains much more of the total variation in bark or pith areas than growth rate (Table 2a, b). The effect of environment was also detected in the regressions involving flexural stiffness and moment of inertia, but it was again slight. EI_{struct}, EI_{wood}, and EI_{bark} increased with distance from the tip of the stem and also with environment, tending very slightly to be greater in faster-growing plants in moister locations (Table 2c–e). The same pattern applied to I_{struct}, I_{wood}, and I_{bark} (Table 2f–h). In contrast, no influence of environment on the elastic moduli was detected (E_{struct} $N = 54$, $\beta_{\log_{10} \text{growth rate}} \pm \text{SE} = 0.01 \pm 0.11$, $P = 0.94$; E_{wood} $N = 44$, $\beta_{\log_{10} \text{growth rate}} \pm \text{SE} = 0.14 \pm 0.10$, $P = 0.18$; E_{bark} $N = 39$, $\beta_{\log_{10} \text{growth rate}} \pm \text{SE} = 0.12 \pm 0.21$, $P = 0.59$). As a result, the pattern of increase in EI with increased growth rate must be attributed only to the increase observed in I. When the environment had any effect on the models, the effect was very slight, as shown by the low semipartial correlations associated with growth rate in Table 2.
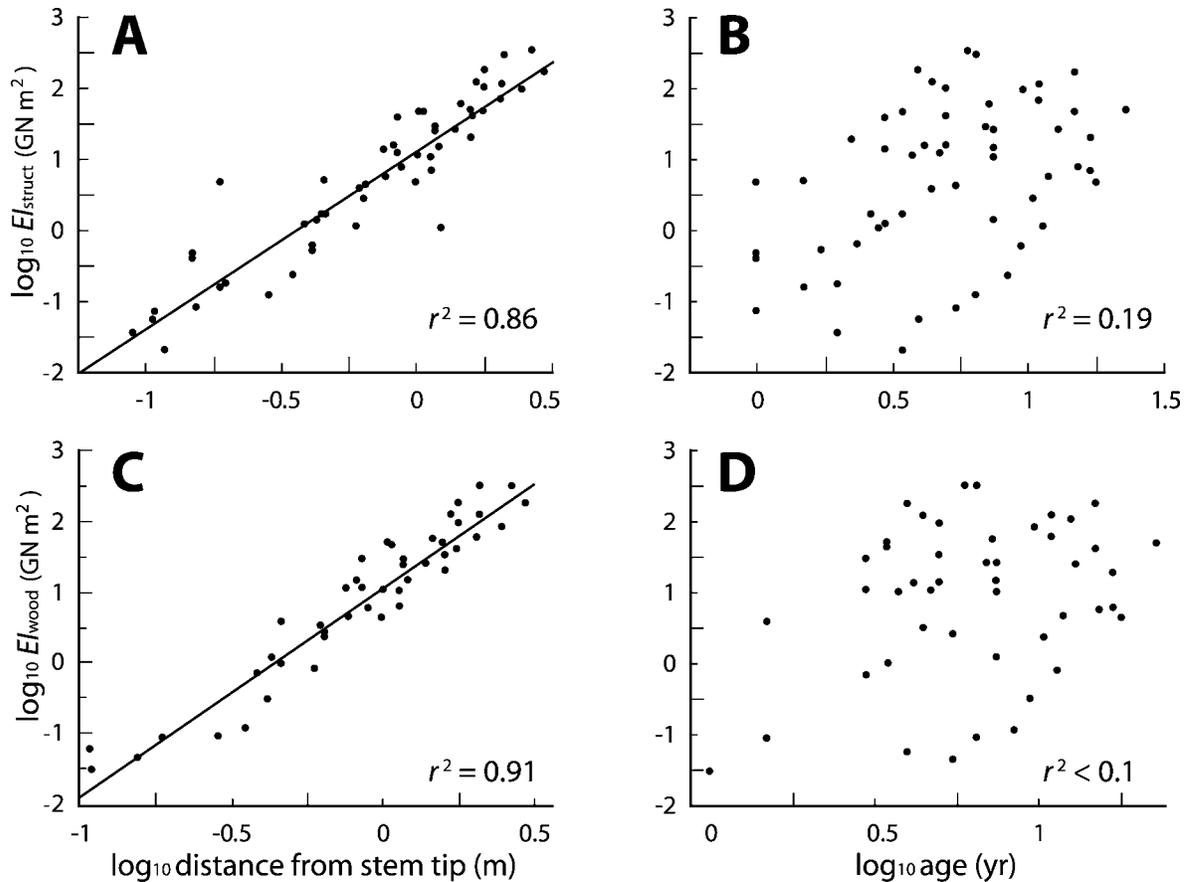
Fig. 4. Structural (EI_{struct}) and wood flexural stiffness (EI_{wood}) are poorly explained by stem age. (A) As could be expected given the allometric relationship between stem length and diameter, the EI_{struct} of a stem segment is predicted very well based only on the distance of the midpoint of the segment to the tip of the stem. (B) In striking contrast, the average age of the segment is a poor predictor of EI_{struct}. (C) Likewise, EI_{wood} of a stem segment is largely explained by the distance from the tip of the stem, whereas (D) it is not explained at all by age.

For example, for EI_{struct} (Table 2c), the semipartial correlation for distance was 0.85, more than four times that for the growth rate at 0.19. Also, the increase in the coefficient of determination when growth rate was added to the simple model that included only distance from the tip was minimal, changing from 0.86 to 0.89 (Table 1e and 2c). The very slight association between growth rate and tissue areas or mechanical parameters was readily evident in scatter plots (Fig. 6).

DISCUSSION

The allometric and biomechanical attributes of a given section of *P. praecox* stem were far better predicted by stem size than by age. Stems of the same size could have very different ages and come from very different environments, but they maintained very similar length to diameter proportions (Fig. 3). Likewise, mechanical parameters of similarly sized segments and their tissues were comparable regardless of absolute age (Figs. 4, 5). Our results thus support the notion that time can be rejected as a meaningful basis for comparison for many evolutionary studies, and with it the implicit assumption of plant ontogeny characterized by particular developmental events occurring at particular absolute times. In contrast, the correlation of mechanics with size could be

expected based on basic mechanical theory, which predicts that the stress experienced by a given sector of a beam is directly related to the amount of material that must be supported and its distribution (Niklas, 1999a; Gere, 2002; cf. Holbrook and Putz, 1989). As a result, the mechanical needs of a stem of a given length by diameter proportion would be the same regardless of age. We discuss the implications of these findings for inferring variables of adaptive importance in woody plants and argue that variables describing stem size are more appropriate for comparing ontogenies between individuals than are those that represent absolute ages.

The Pittocaulon allometric and biomechanical "model," adaptation, and plasticity—Perhaps the most surprising result of our study was the observation that, although they were collected across a marked amplitude of microhabitats and displayed a greater than eightfold range in growth rate, the stems measured were for the most part mechanically and allometrically interchangeable. In other words, there was no way to distinguish an old stem covered with annual scars (Fig. 2A) from similarly sized stems produced in just one or a few seasons (Fig. 2B) based on allometry or mechanics. To predict the flexural stiffness of a stem segment (EI_{struct}), it was necessary only to know the length of stem that the segment must support (i.e., its distance from the tip of the stem; cf. Fig.
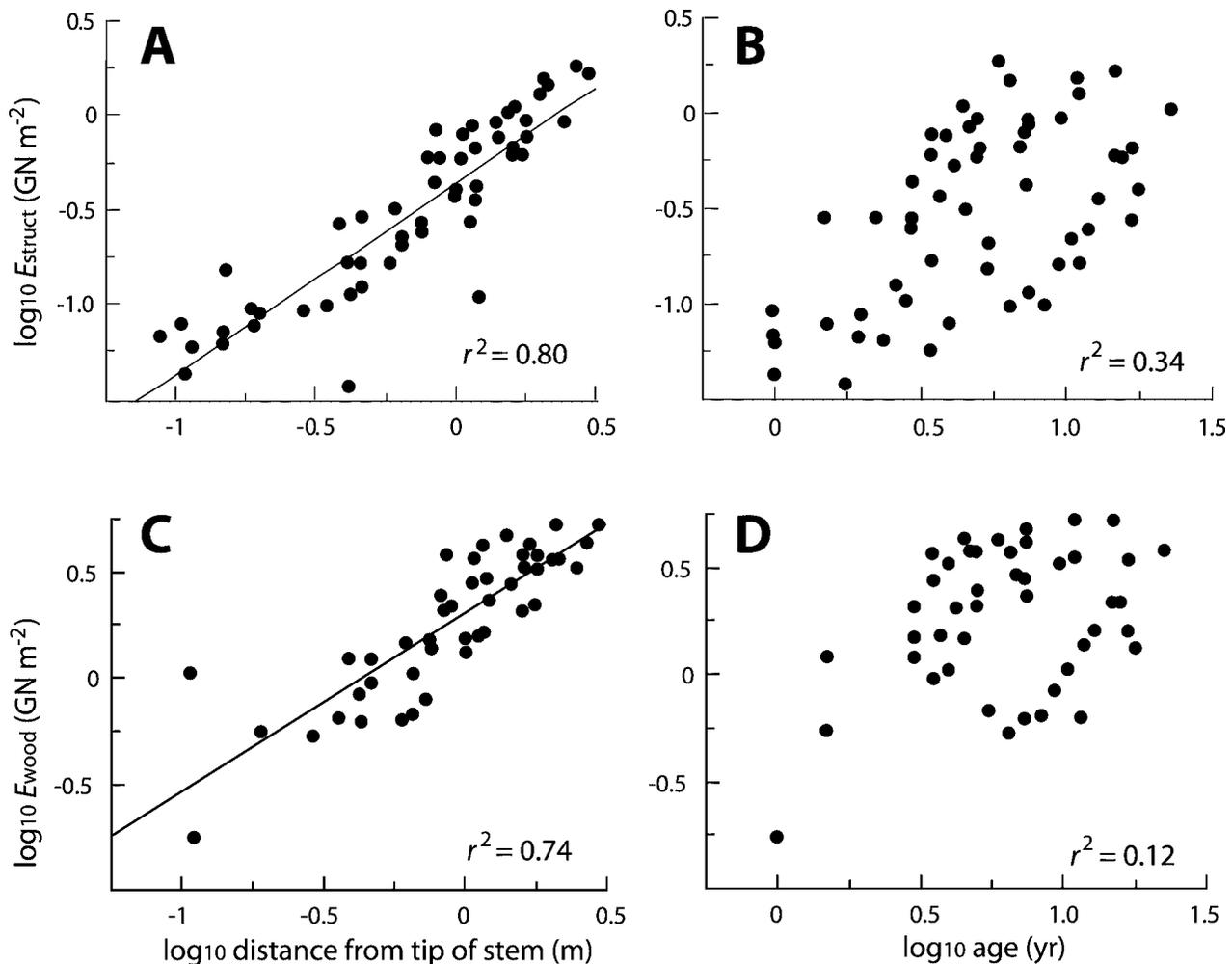
Fig. 5.   Structural (E_{struct}) and wood Young's moduli (E_{wood}) are closely related to size and not to stem age. (A) The E_{struct} of a segment correlates remarkably well with the distance of the midpoint of the segment to the tip of the stem. (B) In contrast, E_{struct} is only very loosely correlated with the average age of the same stem segments. (C) Likewise, E_{wood} is explained in large part by the distance from the tip of the stem, whereas (D) E_{wood} cannot be explained by age.

4A, B). Likewise, at the tissue level, the Young's modulus of the wood was associated to a striking degree with the distance to the stem tip (Fig. 5C), regardless of age (Fig. 5D).

The production of a relatively invariant phenotype despite internal or external perturbing factors, as in *Pittocaulon* allometry and mechanics, has been referred to as developmental homeostasis. Developmental homeostasis is commonly explained as a result of natural selection favoring ontogenetic systems capable of producing a specific, perhaps even optimal, phenotype (Fenster and Galloway, 1997; Møller and Shykoff, 1999). Our study thus directs attention to allometry and mechanics as factors that are likely under strong selection. But what features are of primary selective importance? In most situations, allometry seems unlikely to be the direct object of selection. Instead, we suggest that the most plausible hypothesis is that allometry follows selection for storage, mechanics, conduction, or size. For example, given constant materials properties (e.g., wood and bark E), selection for increased stature will require concomitant changes in allometry to maintain a mechanically viable structure (Niklas, 1992;

Vogel, 2003). In the case of *Pittocaulon*, selection for storage has clearly played a role in shaping its allometric and biomechanical syndrome. In Asteraceae and in many other plants, selection for increased stem water storage has led to massive zones of parenchyma in pith and bark (e.g., *Kleinia, Pachythamnus*); parenchymatized xylem does not seem to be a typical mode of water storage in asters (cf. Carlquist, 1966). Many ways could be imagined to arrange a given cross-sectional area of xylem within a stem. Nevertheless, in all plants with extensive stem water storage outside of the xylem, the xylem is not in a central rod-like cylinder with a conventional tiny pith. Instead, the pith is always greatly enlarged, and the xylem cylinder is close to the stem periphery, where it is better located to resist tension and compression (that is, with higher I) as compared to a central rod (cf. Fig. 1A and structures such as the vertebrate femur). Selection for storage thus almost certainly results not only in a thick stem, but also in an arrangement of tissues that accommodates water storage while at the same time providing mechanical adequacy. More detailed testing of these hypotheses will require examination of

TABLE 2. Multiple regressions of *Pittocaulon* tissue areas and mechanical parameters predicted by the inclusion of environment (growth rate) with distance from the stem tip, showing that the effect of environment is slight in all cases. Multiple regressions for tissue areas (a–b), flexural stiffness (c–e), and moments of inertia (f–h). All variables are $\log_{10}$ transformed. r_a^2 = adjusted coefficient of multiple determination; β_D = coefficient associated with distance from the tip of the stem; β_{GR} = coefficient associated with growth rate (proxy environmental variable). The semipartial correlations indicate the relative contribution of stem diameter (PD) and growth rate (PGR) in predicting the response variable of interest. Distance from the tip never has partial correlations less than 0.60, whereas those for environment never are above 0.4. Other abbreviations and units are as in Table 1.

Response	r_a^2	N	F test	$\beta_0 \pm$ SE	$\beta_D \pm$ SE	$\beta_{GR} \pm$ SE	PD	PGR
(a) Bark area	0.72	54	$F_{2,51} = 68.49**$	$-3.46 \pm 0.57**$	$0.53 \pm 0.05**$	$0.21 \pm 0.08**$	0.75	0.21
(b) Pith area	0.69	54	$F_{2,51} = 59.06**$	$-3.21 \pm 0.10**$	$0.75 \pm 0.10**$	$0.70 \pm 0.14**$	0.62	0.39
(c) EI_{struct}	0.89	54	$F_{2,51} = 224.64**$	$1.66 \pm 0.14**$	$2.37 \pm 0.13**$	$0.79 \pm 0.18**$	0.85	0.19
(d) EI_{wood}	0.95	45	$F_{2,42} = 398.74**$	$1.65 \pm 0.11**$	$2.69 \pm 0.12**$	$0.81 \pm 0.15**$	0.80	0.19
(e) EI_{bark}	0.68	39	$F_{2,36} = 40.38**$	$0.54 \pm 0.19**$	$1.46 \pm 0.20**$	$0.63 \pm 0.24*$	0.68	0.25
(f) I_{struct}	0.83	54	$F_{2,51} = 133.85**$	$-6.99 \pm 0.11**$	$1.35 \pm 0.10**$	$0.78 \pm 0.15**$	0.76	0.30
(g) I_{wood}	0.83	53	$F_{2,50} = 128.29**$	$-7.80 \pm 0.14**$	$1.89 \pm 0.13**$	$0.67 \pm 0.19**$	0.82	0.20
(h) I_{bark}	0.83	54	$F_{2,51} = 126.78**$	$-7.26 \pm 0.10**$	$1.24 \pm 0.09**$	$0.66 \pm 0.14**$	0.77	0.28

more than one species, preferably in a clade of broad anatomical, biomechanical, and ecological diversity.

The mechanical properties of *Pittocaulon* wood (as reflected by E) could also be expected to differ with respect to non

water-storing plants. Selection pressure for bark and pith storage could lead to pressure for a xylem cylinder of great diameter but minimal wall thickness, thereby maximizing pith diameter. Given the mass of such thick, water-filled stems, the
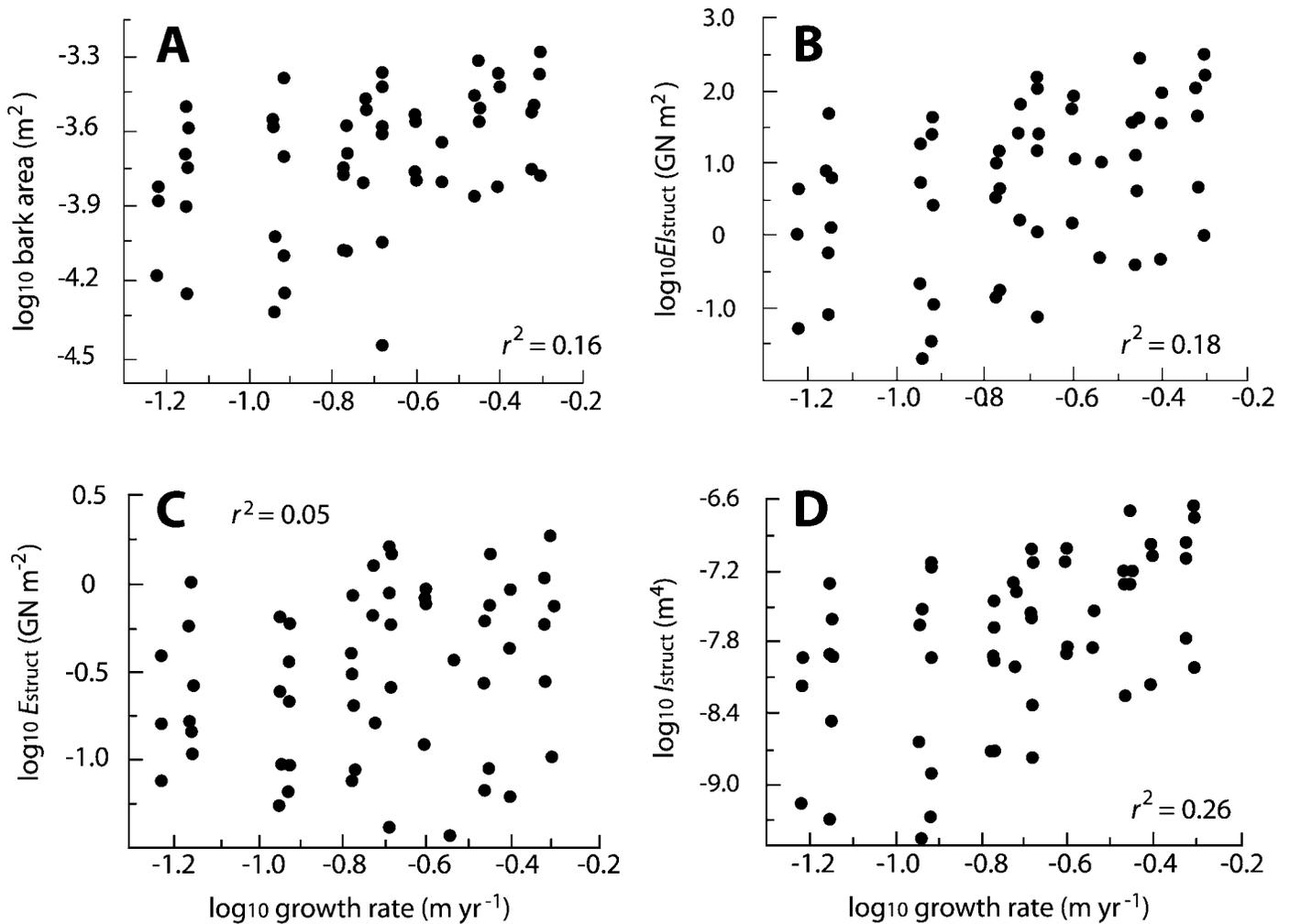
Fig. 6.   Growth rate is only very slightly correlated with tissue areas and mechanical parameters; its contribution to their prediction is very poor. (A) Growth rate is poorly correlated with bark area, (B) structural flexural stiffness (EI_{struct}), (C) structural Young's modulus (E_{struct}), and (D) structural second moment of area (I_{struct}). No relationship between environment and Young's modulus (E) was detected.

little xylem that is present would be expected to be relatively stiff. Congruent with this expectation, *Pittocaulon* wood is comparable with plants of much larger stature (see Niklas, 1992).

The relatively constant allometric and mechanical phenotype observed in *Pittocaulon* is all the more striking given the host of other characters with high levels of plasticity. The most obvious plastic response is represented by the strong differences in size that were observed between individuals. Plants on exposed lava ridges were short, slender-stemmed, and branched far below the height at which more sheltered plants did. In the allometric and mechanical characteristics examined, the only exception to the pattern of uniformity across habitats was a tendency for stems in moister environments to have marginally larger pith and bark areas (Table 2a, b). Greater pith area implies higher I_{pith} and also higher I_{wood} and I_{bark} (Table 2f–h) because the xylem-bark cylinder lies farther from the neutral axis if pith area increases. This environmental effect on I seems to be responsible for the minor tendency for EI to increase with growth rate (Table 2c–e), because E had no environmental differences (cf. Kliger et al., 1998). Similarly, in a previous anatomical study (Olson, 2005), cellular features thought to be of great functional importance varied substantially. For example, both vessel wall diameter and libriform fiber length and diameter had coefficients of variation on the order of 20–25%, whereas variation in vessel wall thickness and the number of vessels per group was even broader at 40%. The cambium thus appears to modulate the mechanical properties and the arrangement of tissues it produces in such a way that the *Pittocaulon* "model" is produced despite a remarkable degree of variation in growth rate and cellular level variation. This pattern of higher-level uniformity despite lower-level variation corresponds exactly with what would be expected if developmental homeostasis were responsible for the constancy of the *Pittocaulon* "model."

Size and stem properties—Because the mechanical properties of a stem are the result of its characteristics at lower hierarchical levels (Niklas, 1992; cf. Alfaro et al., 2004), size attributes should correlate not only with mechanical characteristics at the whole-structure level but also with lower-level features such as anatomy and hydraulics. The correlation of cell size with stem size within species, well known to wood anatomists and foresters (Carlquist, 1975; Panshin and De Zeeuw, 1980; Gartner, 1995; Carlquist and Grant, 2005; Olson and Rosell, 2006), would seem to bear out this expectation, as does the observation that *Pittocaulon* bark, wood, and xylem proportions can be predicted based on stem size (Fig. 3A). Similarly, authors such as Tyree and Yang (1992) and Tyree and Zimmermann (2002) have shown that features of hydraulic architecture are well predicted by stem size.

If comparisons between individuals are based on size rather than age, then the interpretation of phenomena such as dwarfing could differ from conventional interpretations. For example, Bailey and Tupper (1918) present tracheid lengths from "vigorous" and "stunted" individuals plotted against growth ring age. In all cases, the cells for stunted individuals are smaller for a given growth ring age. Authors such as Baas et al. (1984) and Moltenberg and Hoibo (2006) also reported smaller cell sizes for suboptimal individuals. It seems likely that comparisons between similar distances from the pith rather than age would reveal cell sizes that more closely resemble one another (cf. Mäkinen et al., 2002).

Comparing ontogenies—Explicitly identifying whether stem mechanics are better predicted by size or age can also inform studies of the evolution of ontogeny in woody plants. Morphology is produced via ontogeny, and as a result, morphological differences between species are associated with ontogenetic differences (Gould, 1977; Raff, 1996; West-Eberhard, 2003). Comparing ontogenies between species can thus serve as a means of inferring the evolutionary mechanisms responsible for the differences observed. To accomplish these comparisons, a suitable common axis is needed against which ontogenetic data from different species can be plotted in the same space. The most commonly studied evolutionary alteration to ontogeny is heterochrony, which involves interspecific differences in the timing of developmental events (Alberch et al., 1979). The very name implies differences with respect to time, and indeed those working with animals are often emphatic that ontogenetic data from different individuals must be plotted against absolute time (e.g., Godfrey and Sutherland, 1995). As we show here, woody plant stems may have different sizes and be at different ontogenetic stages at similar ages (see also Parish and Antos, 2004; Brienen and Zuidema, 2006). As a result, mechanical and other features are unlikely to correlate well with age between individuals. The identification of an axis with points corresponding to comparable events in different individuals is thus a significant challenge in studies of ontogenetic evolution in woody plants.

For many organisms, there may be measures of "biological time" that are more relevant than absolute time (Strauss, 1987). From our results in *Pittocaulon*, absolute time can be rejected as a meaningful axis for comparisons between individuals (e.g., Figs. 3B, D; 4B, D; 5B, D), whereas size is clearly correlated with crucial characteristics such as proportions of tissues and mechanical attributes (e.g., Figs. 3A, C; 4A, C; 5A, C; Olson and Rosell, 2006; Olson, in press). It could be argued that simply observing a correlation is not sufficient justification for the use of size as a basis for comparison between species. However, size is of prime biological relevance in woody stems because stems increase in girth as the result of the accumulation of new layers of wood and bark; the diameter of a stem reflects how many layers it has accumulated. Thus, across species that share similar allometry (cf. Müller et al., 2000), variables such as diameter would appear to offer a more biologically defensible measure of "biological time" than would absolute age (Strauss, 1987; Olson and Rosell, 2006).

Conclusion—We suggest that there is reason to justify the selection of stem size as a basis for comparing stem structure and function between individuals over absolute age. Conversely, the degree of fit when modelling wood properties, whether mechanical, hydraulic, or structural, based on age is likely to vary to the extent that age and size are decoupled. Results from *Pittocaulon* can be used to generate hypotheses regarding woody plants generally. For example, a prediction meriting examination is that allometry and mechanical characteristics always respond to stem size more than absolute age in plants in general. The stem of *Pittocaulon* has a somewhat unusual stem construction resembling a columnar cactus in having more water-storing cortex and pith than xylem (Gibson and Nobel, 1986; Niklas et al., 2000; Olson, 2005). It could be argued that the results we obtained might not apply to a typical arborescent dicot in which the xylem predominates. However, the need for the mechanical characteristics of a structure to meet the demands imposed by its size would seem to apply to any

structure regardless of its construction, and thus we feel that results similar to those in *Pittocaulon* could be expected in most if not all woody plant stems. In fact, finding that there is a lack of correspondence between mechanics or allometry and size would be noteworthy and perhaps point to factors such as developmental constraint. Similarly, the hypothesis that woody plants in general have ontogenetic systems that produce a narrow, perhaps optimal, range of allometry and mechanics warrants examination.

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