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Research

Exploring the bark thickness–stem diameter relationship: clues from lianas, successive cambia, monocots and gymnosperms

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Summary

- Bark thickness is ecologically crucial, affecting functions from fire protection to photosynthesis. Bark thickness scales predictably with stem diameter, but there is little consensus on whether this scaling is a passive consequence of growth or an important adaptive phenomenon requiring explanation.
- With a comparative study across 913 species, we test the expectation that, if bark thickness–stem diameter scaling is adaptive, it should be possible to find ecological situations in which scaling is predictably altered, in this case between species with different types and deployments of phloem.
- 'Dicots' with successive cambia and monocots, which have phloem-free bark, had predictably thinner inner (mostly living) bark than plants with single cambia. Lianas, which supply large leaf areas with limited stem area, had much thicker inner bark than self-supporting plants. Gymnosperms had thicker outer bark than angiosperms.
- Inner bark probably scales with plant metabolic demands, for example with leaf area. Outer bark scales with stem diameter less predictably, probably reflecting diverse adaptive factors; for example, it tends to be thicker in fire-prone species and very thin when bark photosynthesis is favored. Predictable bark thickness–stem diameter scaling across plants with different photosynthate translocation demands and modes strongly supports the idea that this relationship is functionally important and adaptively significant.

Introduction

Thickness is regarded as one of the most ecologically important traits of bark. Bark thickness is most commonly regarded as an adaptive response to fire regime (Uhl & Kauffman, 1990; Hoffmann *et al.*, 2003; Lawes *et al.*, 2013; Pausas, 2015), but is also affected by precipitation, temperature, soil fertility (Scholz *et al.*, 2007; Rosell & Olson, 2014; Richardson *et al.*, 2015; Rosell, 2016), mechanical support needs (Niklas, 1999) and bark photosynthesis (Pfanz *et al.*, 2002; Rosell *et al.*, 2015). Although these and other factors affect bark thickness, it is becoming increasingly clear that by far the main driver of variation in this trait globally is stem size (Rosell, 2016). Stem diameter (SD) has been shown to explain 72% of total bark thickness (TBT) variation globally, meaning that relatively little variation is available for explanation by environmental factors (Rosell, 2016). Although the TBT–SD relationship is so marked, the cause of this relationship has received relatively little attention.

In part, this lack of attention may stem from the view that TBT is largely the result of the passive accumulation of dead cells. Because conductive secondary phloem cells are short lived and continually crushed and replaced (Evert & Eichhorn, 2006), larger stems, which have accumulated more cell layers, naturally have thicker bark. From this point of view, the TBT–SD relationship can be simply factored out in ecological studies of bark, for example via residuals (Paine *et al.*, 2010) or other methods (Hempson *et al.*, 2014), with little need to understand the causes of the relationship. However, TBT–SD allometry could be an adaptively significant relationship, intimately linked to stem size, as are key traits, such as leaf area (Mokany *et al.*, 2003; Buckley & Roberts, 2006), vessel diameter (Anfodillo *et al.*, 2006; Olson *et al.*, 2014) and sapwood area (Vertessy *et al.*, 1995; Wullschleger & King, 2000). If so, then it should be possible to find situations in which selection should favor different TBT–SD allometries. Finding such situations would suggest that TBT–SD allometry is not simply a passive consequence of tissue accumulation given the stem size. Instead, this result would focus the attention of ecologists on the TBT–SD relationship as an adaptive one requiring functional explanation.

In searching for situations in which the TBT–SD relationship is predictably different, we distinguish between outer and inner bark (Fig. 1; Romero, 2014). The outer portion of bark includes an accumulation of dead cells, known as phellem (produced by the cork cambium) or rhytidome (produced by more than one cork cambium plus products of the vascular cambium, Supporting Information Fig. S1; Roth, 1981). The amount of outer bark in a stem has been shown to be associated with protection from fire and other agents (Graves *et al.*, 2014; Schafer *et al.*, 2015; Rosell, 2016), and with bark photosynthesis (Rosell *et al.*, 2015). In turn, the inner and mostly living portion of bark includes the active and crushed secondary phloem, the tissue that translocates photosynthates from the leaves to the rest of the plant, the cortex (when rhytidome is not present), a mostly parenchymatous tissue, and the phelloderm, a usually thin layer of living cells produced by the cork cambium (Fig. 1). In accordance with its large percentage of living cells, inner bark stores water and other compounds (Srivastava, 1964; Scholz *et al.*, 2007), and translocates photosynthates (Roth, 1981). Although this translocation has been the focus of recent physiological studies (Jensen *et al.*, 2012; Knoblauch & Oparka, 2012; De Schepper *et al.*, 2013; Ryan & Asao, 2014; Savage *et al.*, 2016), it is still unclear whether different levels of translocation demands or differences in physiology or placement of phloem affect the thickness of bark in seed plants, especially of the inner and mostly living bark.

Because they are thought to vary in photosynthate translocation demand for their SD, climbing and self-supporting plants

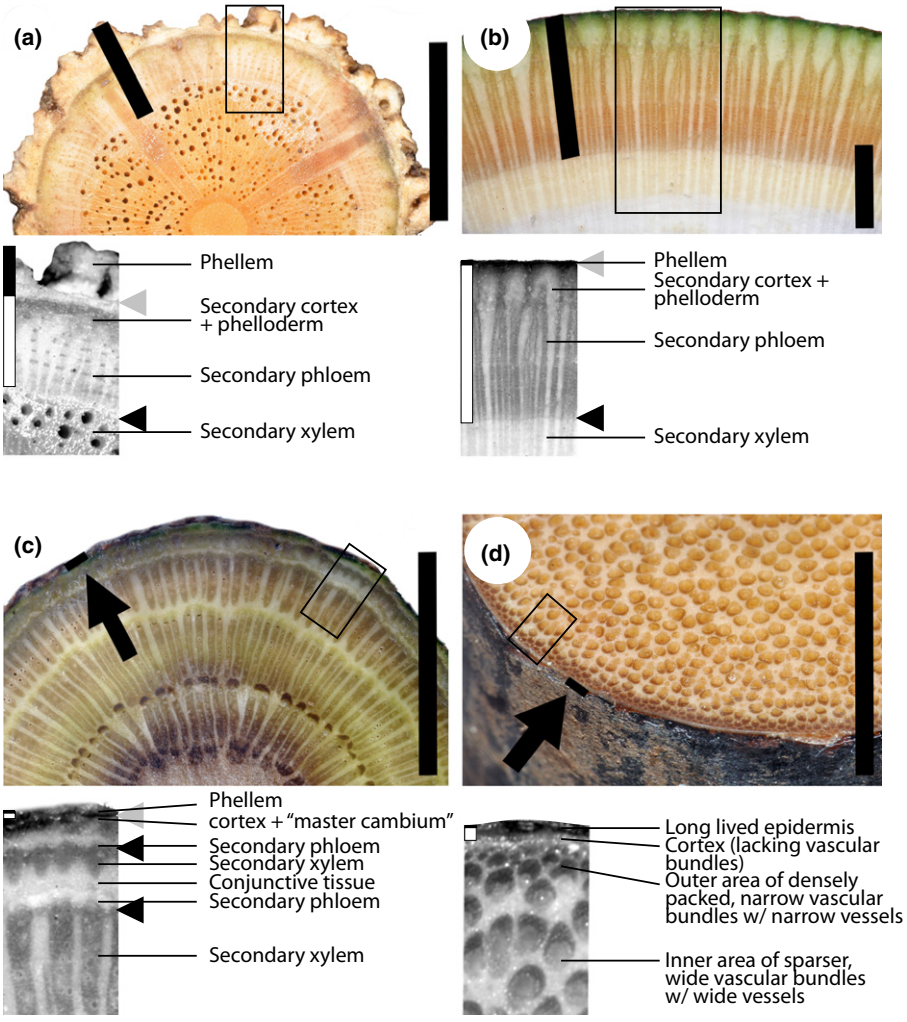

Fig. 1 Variation in bark construction and inner and outer bark proportions. Total bark is shown in stem cross-sections with a black rectangle, whose position is indicated with a black arrow when very thin. Insets show locations of the phellogen (gray arrowheads), the vascular cambium (black arrowheads) and the major anatomical regions of bark. Rectangles at the left of the insets indicate the thicknesses of the inner (white) and outer (black) bark. (a) Bark is thick for a given stem diameter in lianas, as in this Bignoniaceae, with bark divided into thick phellem and thick inner bark with conspicuous banded wedges of phloem fibers; the four large rays are storage phloem. (b) The phellem is very thin in the self-supporting *Carica papaya* (Caricaceae), and is underlain by a photosynthetic phelloderm and secondary cortex. The single cambium has produced thick secondary phloem with abundant fibers. (c) By contrast, stems with successive cambia are innervated with phloem and have relatively thin, phloem-free bark, as in *Hyperbaena ilicifolia* (Menispermaceae), a self-supporting tree. The bark in this species consists only of the periderm and the secondary cortex. It is underlain by a 'master cambium', an area that produces to the inside vascular cambia surrounded by conjunctive tissue, in this case thick-walled parenchyma. The vascular cambia, in turn, produce phloem abaxially and xylem adaxially. (d) Monocot stems are also innervated with phloem and have thin 'bark', as in *Calamus australis,* in which each vascular bundle (darker circular spot) has both xylem and phloem. Monocot bark may or may not (as in this case) have a periderm. Bars, 1 cm.

would seem likely to have differing inner bark thickness (IBT) standardizing for SD. IBT would be expected to be thicker in lianas than in trees and shrubs (Fig. 1a). Lianas, and nonself-supporting plants in general, maintain a given area of crown via stems that are narrower than those of self-supporting plants (Putz, 1983; Zhu & Cao, 2010; Santiago *et al.*, 2015). Higher metabolic demand for a given area of stem seems to be coupled with a higher amount of phloem per unit xylem cross-sectional area, wider phloem sieve tubes and longer lived phloem (Carlquist, 1991; Ewers & Fisher, 1991; León-Gómez & Monroy-Ata, 2005; Angyalossy *et al.*, 2015). These phloem features seem a likely response to the limited tangential extent of cambium available for phloem production in lianas, coupled with very long stems with abundant metabolically active xylem and leaves (Wyka *et al.*, 2013; Ewers *et al.*, 2015). Given that selection should favor greater phloem transectional area for a given SD in lianas, we tested the prediction that lianas should have relatively thicker inner bark than their self-supporting counterparts. Finding that stems of similar diameters, but different habits, have predictably different IBT would highlight the need to understand the cause of IBT–SD allometry.

In addition to photosynthate translocation demands, the deployment of the translocating tissue in the stem (Spicer & Groover, 2010) could lead to variation in IBT. We compared IBT in species that included secondary phloem in their inner bark (phloem-bearing bark) with those that did not (phloem-free bark). It has been suggested that TBT is the most important factor in protecting the thickening meristem and the conductive xylem from agents such as fire (Vines, 1968; Hoffmann *et al.*, 2003; Brando *et al.*, 2012; Pausas, 2015). If this were the case, both phloem-bearing and phloem-free barks would have similar TBT, because damage to the thickening meristem and the conductive xylem would be equally damaging and would require protection in either case. However, if phloem-bearing inner barks were predictably thicker, this would suggest that thickness is also a function of the space allocated to photosynthate translocation, in addition to protection and other functions of bark. Phloem-bearing barks are formed in species with conventional cambia, which produce secondary phloem to the outside, as part of the bark, and secondary xylem to the inside (Fig. 1a,b; Table 1). In this stem type, secondary phloem can be a significant percentage of TBT (Roth, 1981). By contrast, species with successive cambia produce phloem-free barks. These species can be thought of as having a 'master cambium' that produces secondary cortex to the outside, not phloem, and to the inside vascular cambia and the conjunctive tissue that surrounds the cambia and their products (Carlquist, 2007). The vascular cambia produce xylem and phloem (Fig. 1c). This means that stems with successive cambia are comprehensively innervated with phloem, obviating the need for phloem in the bark. Like plants with successive cambia, monocot stems are also innervated with phloem (Evert & Eichhorn, 2006; Figs 1d, S2). Although bark refers to all the tissues outside the vascular cambium (Roth, 1981), in monocots, 'bark' refers to the stem layers external to the outermost vascular bundles, which may or may not include a periderm. Here, we tested whether species with phloem-free bark (those with successive cambia and monocots) had thinner inner bark than conventional woody plants, potentially caused by the placement of translocating tissue within the xylem. Finding thinner inner bark in plants with successive cambia and monocots would highlight the need to include factors other than fire in explanations of bark thickness variation.

It would be expected that not only would the position of photosynthate translocation tissue affect IBT, but also the nature of the translocating cells themselves. Along these lines, differences could be expected between gymnosperms and angiosperms. Gymnosperms have phloem conducting elements known as sieve cells, which are analogous to xylem tracheids in that they lack sieve plates, having, instead, lateral sieve areas (Cronshaw, 1981; Evert & Eichhorn, 2006). Angiosperms have sieve elements that form tubes, reminiscent of the elements forming xylem vessels (Roth, 1981). Although both gymnosperms and angiosperms seem to translocate photosynthates through a similar active transport mechanism, gymnosperm sieve cells offer greater resistance, slowing flow (Jensen *et al.*, 2012). Compensating for slower flow, gymnosperms might be expected to have higher transectional area

Table 1 Mean annual precipitation, precipitation of the driest quarter of the year, precipitation of the driest month, mean annual temperature and sample size (*n*) across angiosperm habits, angiosperm stem constructions and angiosperm vs gymnosperm phloem cells (only self-supporting species included) in our dataset

	n	Mean annual precipitation (mm)	Precipitation of the driest quarter (mm)	Precipitation of the driest month (mm)	Mean annual temperature (°C)
All species	913	1169 (90–4312)	92 (0–907)	26 (0–265)	19.9 (1.7–27.3)
Habit (angiosperms)					
Nonself-supporting	134	1169 (217–3484)	92 (2–299)	26 (0–93)	24.5 (7.2–26.9)
Self-supporting	712	1155 (90–4312)	92 (0–907)	26 (0–265)	19.3 (4.5–27.3)
Stem construction (angiosperms)					
Monocot	53	1521 (213–3484)	123 (2–330)	34 (0–106)	23.2 (8.8–27.3)
Single cambium	757	1155 (90–4312)	92 (0–907)	26 (0–265)	19.9 (4.5–27.3)
Successive cambia	36	792 (217–3437)	16 (2–232)	3 (0–71)	24.5 (15.6–26.5)
Phloem cells (self-supporting species)					
Angiosperm	712	1155 (90–4312)	92 (0–907)	26 (0–265)	19.3 (4.5–27.3)
Gymnosperm	67	1238 (324–2552)	121 (2–391)	35 (0–118)	13.7 (1.7–27.3)

Medians are shown with ranges in parentheses.

dedicated to phloem, and thus thicker inner bark, than angiosperms of similar SD, a hypothesis we tested with our dataset.

Although our main hypotheses were focused on photosynthate translocation, and thus on inner bark, we also compared TBT and outer bark thickness (OBT) across habits, stem constructions and angiosperm vs gymnosperm phloem cells. It has been shown that the amounts of inner and outer bark are drivers of TBT variation (Rosell, 2016). Given that outer bark has a very important role in protection, but not translocation (Graves *et al.*, 2014; Romero, 2014), predictions regarding translocation would not apply to outer bark. Therefore, we examined whether the patterns observed in IBT could also be recovered when examining TBT, or whether the thickness of outer bark obscured these patterns. We also examined the phylogenetic lability of all bark traits measured. To test our predictions, we assembled the largest dataset on TBT, IBT and OBT to date, including 2720 samples in 913 species from virtually all bark-bearing 'dicot', monocot and gymnosperm orders, and spanning most woody plant habits and environments. Our results suggest that the different ways in which phloem is deployed in a stem, as well as photosynthate demand for a given SD, do seem to affect bark thickness variation and bark thickness–plant size allometry. Thus, photosynthate translocation is another function that needs to be considered in an effort to understand the ecology of bark at a geographically and phylogenetically global scale, and highlights the bark thickness–stem size relationship as one demanding explanation in and of itself.

Materials and Methods

Sampling and measurements

Our dataset included 2720 samples from 913 species in 199 families, including 846 species of angiosperms and 67 gymnosperms covering most seed plant orders and bark morphologies (Fig. S3). Gymnosperm sampling included gnetophytes, cycads, Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae and Taxaceae. We included species from the 'basal' angiosperms, spanning *Amborella*, Austrobaileyales, Canellales, Chloranthales, Laurales, Magnoliales and Piperales. Samples also included 53 monocot species spanning eight orders and 13 families, non-core eudicots including Ranunculales, Sabiales, Proteales and *Trochodendron*, and virtually all orders within the core eudicots. Samples were collected from a wide range of habitats spanning alpine freezing-prone vegetation, a gradient of very dry to very wet tropical and temperate forests, savannas, and frost-free and frost-prone deserts (Table 1). We sampled fire-free wet forests and tropical dry forests, as well as the most fire-prone habitats on earth, savannas that burn biennially. In fire-prone areas, species sampling included those with persistent stems as well as those that resprout from the base or from lignotubers and reseeders. Of the 913 species, 640 self-supporting angiosperms with conventional vascular cambia had been examined previously for bark thickness variation across environments (Rosell, 2016). The 43% of species (273) added here include gymnosperms, species with successive cambia and lianas. The very wide ecological variation, in combination with the phylogenetic span of our sampling, makes this the most comprehensive dataset on TBT, IBT and OBT of seed plants to date.

Our data have three important strengths compared with literature-assembled trait datasets. First, most specimens were collected from the wild with well-documented locations; second, sampling was designed to span diverse clades and ecological settings; and third, all measurements were carried out by the authors, ensuring consistency of trait definitions and methods. Bark thickness traits were measured at the bases of trees and shrubs, above buttresses, roots or basal swellings. For stems larger than 5 cm in diameter, we removed a section of bark by making two parallel transverse cuts reaching the secondary xylem, and then dislodging the bark segment with a hammer and screwdriver. For smaller stems, we collected whole basal stem segments. Stem circumference was measured at the point at which the sample was collected, and SD was calculated from the circumference. We measured TBT on fresh material in the field or on samples fixed in 70% aqueous ethanol in the laboratory. In species with a single conventional vascular cambium, we measured TBT with a digital caliper as the distance from the outermost surface of the stem to the cambium (Fig. 1a,b), using a hand lens or a light microscope and thin sections when needed. In species with successive cambia, we measured TBT as the distance from the outermost surface of the stem to the innermost cortex, the site of the master cambium, an area that produces secondary cortex to the outside and vascular cambia and conjunctive tissue to the inside (Carlquist, 2007; Fig. 1c). In monocots, TBT was the distance from the surface to the outermost limit of the area in which vascular bundles were present (Fig. 1d; further examples of the diversity of monocot bark are shown in Fig. S2). Some lianas had wedges of phloem that extended nearly to the pith, separating vascular areas, or included several xylem cylinders bundled together, each with its own vascular cambium. In these cases, we measured from the stem surface to the outermost vascular cambium. In all cases, thickness was measured at the point at which TBT was maximum.

We measured IBT at the site at which TBT was measured, identifying inner bark by the presence of living tissue based on color, texture and cell types (Fig. 1), using a light microscope when necessary. IBT was available for 92% (843) of species. For 879 species, we also measured stem length (SL) with a tape, a Tru-Pulse 200B laser rangefinder (Laser Technology Inc., Centennial, CO, USA) or extracted the height from the literature. Liana SL was measured following the longest stem through the canopy with rappelling equipment when necessary. Two to five adults per species were collected from the majority of species, although, for 13% of species, only one sample was available, usually as a result of rarity or conservation concerns. We calculated mean TBT, SD and SL means per species. When a species was collected from different sites, we calculated per-site means to reflect potential differences in TBT between sites. To summarize IBT per species, we calculated the percentage of TBT represented by IBT per sample and averaged this percentage per species. We then used this species IBT percentage and the mean species TBT to calculate mean species IBT. OBT was the difference between

mean TBT and mean IBT per species. Our dataset was uploaded to the TRY Plant Trait Database (Kattge *et al.*, 2011).

Bark thickness variation between self- and nonself-supporting plants

To examine TBT variation across self- vs nonself-supporting plants, we included only angiosperms, given that all sampled gymnosperms were self-supporting. We included 134 non self-supporting and 712 self-supporting angiosperms (Table 1) and compared mean TBT between habits through a model predicting $\log_{10}$TBT based on $\log_{10}$SD, the variable 'habit' (with levels 'nonself-' and 'self-supporting') and an SD–habit interaction. This interaction tested for differences in TBT–SD scaling between habits, and was not significant. We thus compared mean TBT between habits through intercepts (Quinn & Keough, 2002). We fitted similar models for mean IBT and OBT. To assess the potential effect of intraspecific variability on our analyses, we re-fitted models based on a single, randomly selected sample per species (instead of species means), and repeated this procedure 1000 times. We compared coefficients and goodness-of-fit indices with those of the models based on species means, and tested for equal slopes and intercepts in each fit (Table S1). In addition, we performed variance component analyses to compare the variance within and across species (Manly, 1997; Messier *et al.*, 2010). Models for variance component analyses were fitted using the R packages Ape (Paradis *et al.*, 2004) and Nlme (Pinheiro *et al.*, 2017). All analyses were performed in R v.3.3.1 (R Development Core Team, 2016).

Bark thickness variation between species with phloem-bearing and phloem-free bark

To examine differences in TBT between species with conventional single cambia, successive cambia and monocots, we focused again on angiosperms, given the low number of gymnosperms with successive cambia. Thus, we included 757 angiosperm species with conventional single cambia, 36 with successive cambia (terminology follows Carlquist, 2007) and 53 species of monocots (Table 1). We compared TBT across stem constructions through a model predicting $\log_{10}$TBT based on $\log_{10}$SD, the variable 'stem construction' (with levels 'monocot', 'single cambium' and 'successive cambia') and an SD–stem construction interaction. Similar models were fitted to examine variation in IBT and OBT. We also carried out re-fits based on single samples as described for self- and nonself-supporting plants (Table S2).

Bark thickness variation and angiosperm vs gymnosperm phloem cells

To compare TBT between angiosperm vs gymnosperms, we fitted a model predicting $\log_{10}$TBT based on $\log_{10}$SD, the variable 'phloem cell' (with levels 'angiosperm' and 'gymnosperm') and an SD–phloem cell interaction. Equivalent models were fitted for IBT and OBT. Again, we carried out re-fits based on single samples per species (Table S3).

The potential confounding effect of selection favoring thicker inner bark in dry areas

Our predictions involved expectations of thicker or thinner inner bark, mostly considering the characteristics of the phloem. However, inner bark is often predictably thicker in drier areas, probably as a result of selection favoring its water storage capacity (Rosell & Olson, 2014; Rosell, 2016). Such variation could confound the testing of our predictions if selection favoring greater storage and thus thicker inner bark coincides with the directionality of our predictions. To help factor out storage as the main explanation of thicker inner bark in lianas, we examined whether lianas, which are expected to have thicker bark, occurred in drier areas than self-supporting species in our dataset. We observed the opposite trend. Lianas inhabited sites that had higher annual precipitation than sites inhabited by their self-supporting counterparts (see Notes S1; Fig. S4). We also ruled out that species with phloem-bearing bark came from drier places, thus having thicker inner bark reflecting the need for storage. We observed that species with successive cambia tended to inhabit equally dry or even drier sites than species with single cambia, again rejecting the possibility that thicker inner bark of single cambium species was mainly explained by storage needs (Notes S1; Fig. S5). Gymnosperms, predicted to have thicker inner bark than angiosperms, did not differ in the annual precipitation of their sites, or occupied habitats with higher precipitation in the driest period of the year (Notes S1; Fig. S6). These results allowed us to reject the idea that thicker inner bark might reflect storage needs in drier habitats across the groups we compared, indicating that the differences are associated with photosynthate translocation.

Evolutionary lability of bark thickness traits across the woody plants

To examine the evolutionary lability of TBT, IBT and OBT, we built a phylogeny of the 913 species using the Angiosperm Phylogeny Group backbone. We resolved relationships within groups using specialized literature (Fig. S3). Branches were assigned unit length. To assess the evolutionary lability of residuals of thickness traits (once SD had been taken into account), we used the randomization procedure based on phylogenetically independent contrasts and the K statistic of Blomberg *et al.* (2003), as implemented in the R package Picante (Kembel *et al.*, 2010). Given that the final phylogeny had several polytomies, we ran this procedure 1000 times resolving the polytomies randomly. The ranges of P values and the K statistic from these runs are reported.

Results

The 913 sampled species varied widely in stem size. Stems ranged from a few millimeters in diameter to up to 19 cm in lianas, 1.4 m in gymnosperms and 2.4 m in self-supporting angiosperms.

SL ranged from 6 cm to 31.5 m in monocots, 45 m in lianas and 50 m in gymnosperms (Table 2). This wide variation in stem size was mirrored by the wide variation in bark thickness. Thickness ranged from < 1 mm to almost 137 mm for total bark, to 83 mm for inner bark and to 55 mm for outer bark (Table 2), with maximum values observed in *Araucaria araucana*. To examine how variation in bark traits was partitioned across and within species, we carried out a variance components analysis. This analysis showed that variation across species was overwhelmingly larger than that within species (Table S1). For all bark traits, variation across species was > 80%, leaving, at most, 20% of the variation to be accounted for by within-species differences.

Sampling emphasized contrasting vegetations, which translated into contrasting climatic conditions. Annual precipitation ranged from 90 to 4312 mm and mean annual temperature from 1.7 to 27.3°C (Table 1). Sites experienced from 0 to 265 mm of rain in the driest month and to 907 mm in the driest quarter (Table 1).

Bark thickness variation between self- and nonself-supporting plants

All thickness traits scaled similarly with SD across self- and nonself-supporting angiosperms, as indicated by nonsignificant interactions in the model based on species means (Table 3). Lianas had thicker mean total bark (higher intercept) than self-supporting species (Fig. 2a) for a given SD, and congruent with predictions, also thicker inner bark (Fig. 2b). The models for TBT and IBT fitted the data very well, and showed that SD and habit were able to explain 70% and 65% of the variation in the respective thickness trait (Table 3). By contrast, the model for OBT only explained 29% of its variation (Table 3). There was wide and similar dispersion in OBT values for a given SD between habits, and so no difference was detected in mean OBT (Fig. 2c). Fits based on one individual per species were very similar to those using species means, and led to the same conclusions (Table S2). The range of coefficients in the former models overlapped with the 95% confidence intervals of the fits based on species means. Only one difference was detected, which was that 24% of the 1000 fits predicting IBT based on single individuals had a different slope between habits. We examined these fits and, in all cases, IBT for lianas was above that for self-supporting species for SDs > 0.3 cm, and so our inference that lianas have thicker inner bark for a given SD was practically the same using species means or random data of individuals per species.

Bark thickness variation between species with phloem-bearing and phloem-free bark

Angiosperm stem constructions (monocot, single cambium and successive cambia) differed in their TBT–SD scaling slope, that is, the SD–stem construction interaction was statistically significant. The model for TBT fitted the data very well and explained 72% of the variation in this trait. The scaling slopes for monocots and single cambium species were very similar (Table 4), but that for species with successive cambia was much shallower (0.47, Table 4). Although different slopes precluded generalizations regarding TBT across constructions, it was clear that, for SDs larger than 5 cm, species with successive cambia tended to have the thinnest total bark, followed by monocots (Fig. 3a). Single cambium species tended to have the thickest total bark across the angiosperms. Unlike the fit based on species means, in fits based on single individuals, more than half showed no difference in slope across stem constructions (Table S3). Given that slopes in the fit based on species means had a P value of 0.04 (Table 4), it was perhaps not surprising that some of the resamplings would recover no differences in slopes. We checked models based on individuals and observed that, in all cases with equal slopes, the intercept of species with single cambia was the highest, followed by species with successive cambia and monocots. Again, the inferences were not affected using models based on individuals.

Congruent with predictions, inner bark was thicker in species with phloem in their bark (conventional single cambia), and thinner in stems innervated with phloem (monocots and successive cambia; Fig. 3b). Phloem-free barks (monocots and successive cambia) had remarkably similar IBT–SD allometry (Table 4). Despite slope differences, it was clear from Fig. 3b that

Table 2 Total (TBT), inner (IBT) and outer bark thickness (OBT), stem diameter (SD), stem length or height (SL) and sample size (n) across angiosperm habits, angiosperm stem constructions and angiosperm vs gymnosperm phloem cells (only self-supporting species included)

	n	TBT (mm)	IBT (mm)	OBT (mm)	SD (cm)	SL (m)
All species	913	2.8 (0.1–137.3)	2.1 (0.04–82.6)	0.5 (0.02–54.7)	4.7 (0.1–238.7)	4.2 (0.06–50.0)
Habit (angiosperms)						
Nonself-supporting	134	1.7 (0.1–17.5)	1.4 (0.04–16.6)	0.3 (0.04–6.1)	1.5 (0.2–19.0)	6.4 (0.2–45.0)
Self-supporting	712	2.9 (0.2–53.8)	2.3 (0.05–30.6)	0.5 (0.02–41.3)	6.1 (0.1–238.7)	3.8 (0.06–46.8)
Stem construction (angiosperms)						
Monocot	53	1.3 (0.1–27.4)	1.0 (0.1–15.0)	0.3 (0.02–25.4)	3.7 (0.4–238.7)	4.0 (0.5–31.5)
Single cambium	757	2.7 (0.2–53.8)	2.1 (0.04–30.6)	0.5 (0.02–41.3)	4.3 (0.1–210.0)	4.1 (0.1–46.8)
Successive cambia	36	1.7 (0.2–15.0)	1.2 (0.2–4.5)	0.5 (0.05–11.9)	3.4 (0.4–46.7)	3.2 (0.3–45.0)
Phloem cells (self-supporting species)						
Angiosperm	712	2.9 (0.2–53.8)	2.3 (0.05–30.6)	0.5 (0.02–41.3)	6.1 (0.1–238.7)	3.8 (0.06–46.8)
Gymnosperm	67	10.4 (0.6–137.3)	3.9 (0.2–82.6)	4.6 (0.05–54.7)	24.3 (0.3–138.4)	6.8 (0.6–50.0)

Medians are shown with ranges in parentheses.

Table 3 Linear models used to test for differences in mean total (TBT), inner (IBT) and outer bark thickness (OBT) and thickness–stem diameter (SD) scaling across angiosperm habits (self- and nonself-supporting)

	TBT ~ SD + habit	IBT ~ SD + habit	OBT ~ SD + habit
n	846	778	778
R^2_{adj}	0.70	0.65	0.29
Model ANOVA	$F_{2, 843} = 1000$***	$F_{2, 775} = 726.1$***	$F_{1, 776} = 320.2$***
Equality of slopes test	$P = 0.212$	$P = 0.107$	$P = 0.173$
Equality of intercepts test	$P < 0.001$	$P < 0.001$	$P = 0.190$
Nonself-supporting intercept	0.07 (0.02, 0.12)	−0.07 (−0.12, −0.01)	
Self-supporting intercept	−0.05 (−0.10, 0.01)	−0.21 (−0.28, −0.15)	−0.62 (−0.67, −0.56)
Nonself-supporting slope	0.69 (0.66, 0.72)	0.69 (0.65, 0.72)	
Self-supporting slope			0.54 (0.48, 0.59)
Figure	2(a)	2(b)	2(c)

Continuous variables $\log_{10}$ transformed; ***$P < 0.001$. Estimated coefficients are shown with 95% CI in parentheses.

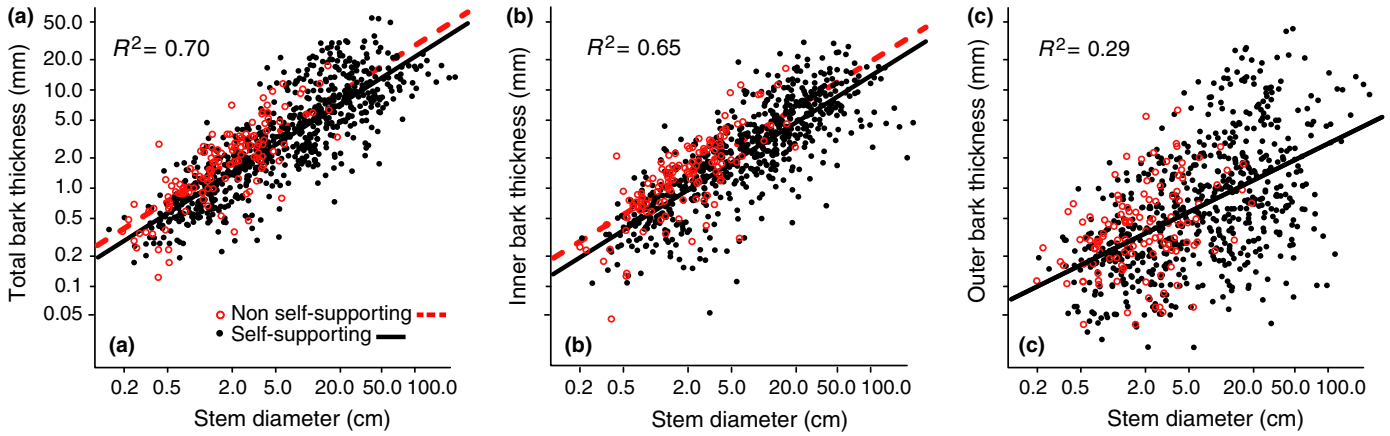

Fig. 2 Bark thickness and plant habit. Variation between nonself- and self-supporting plants in (a) total, (b) inner and (c) outer bark thickness. Nonself-supporting species had thicker total and inner bark, but had outer bark as thick as self-supporting species.

Table 4 Linear models used to test for differences in mean total (TBT), inner (IBT) and outer bark thickness (OBT) and thickness–stem diameter (SD) scaling across angiosperm stem constructions (single cambium, successive cambia and monocots)

	TBT ~ SD × stem construction	IBT ~ SD × stem construction	OBT ~ SD × stem construction
n	846	778	778
R^2_{adj}	0.72	0.67	0.31
Model ANOVA	$F_{5, 840} = 430.1$***	$F_{5, 772} = 312.7$***	$F_{5, 772} = 69.6$***
Equality of slopes test	$P = 0.042$	$P = 0.011$	$P < 0.001$
Single cambia intercept	0.01 (−0.10, 0.11)	−0.16 (−0.28 −0.04)	−0.59 (−0.81, −0.37)
Successive intercept	−0.09 (−0.25, 0.08)	−0.32 (−0.52, −0.13)	−0.45 (−0.80, −0.11)
Monocot intercept	−0.24 (−0.34, −0.15)	−0.31 (−0.43, −0.19)	−0.99 (−1.20, −0.78)
Single cambia slope	0.68 (0.58, 0.77)	0.68 (0.57, 0.79)	0.51 (0.32, 0.71)
Successive slope	0.47 (0.28, 0.65)	0.54 (0.31, 0.77)	0.15 (−0.26, 0.55)
Monocot slope	0.69 (0.60, 0.78)	0.52 (0.41, 0.63)	0.88 (0.69, 1.06)
Figure	3(a)	3(b)	3(c)

Estimated coefficients are shown with 95% CI in parentheses.
Continuous variables $\log_{10}$ transformed; ***, $P < 0.001$.

species with a single vascular cambium had thicker inner bark, supporting the prediction that photosynthate translocation is an important function explaining variation in bark thickness. 30% of the resampling models based on single samples had equal slopes. After checking the intercepts, we found that the ranking of IBT remained unaffected in these models, with species with single cambia having thicker inner bark than species with successive cambia and monocots. These results suggest that our conclusions are robust to the effects of intraspecific variability (Table S3). OBT showed wide dispersion within all angiosperm

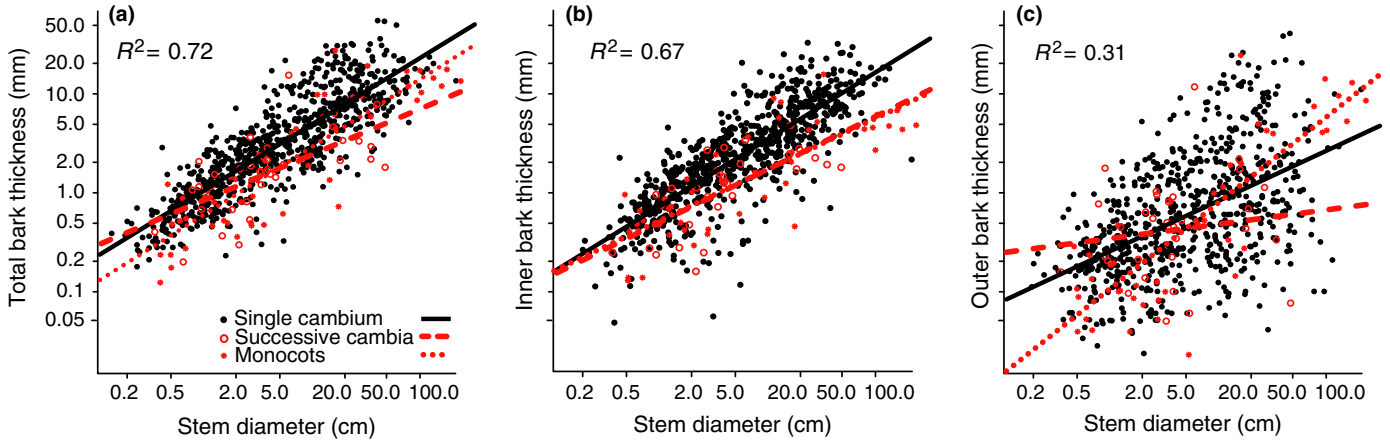

Fig. 3 Bark thickness and stem construction. Variation across species with traditional cambia, successive cambia or monocot construction in (a) total, (b) inner and (c) outer bark thickness. At most stem diameters, monocots and species with successive cambia had markedly thinner inner bark for a given stem diameter than species with normal cambium. No such patterns were observed for outer bark, which varied more markedly.

stem constructions ($R^2 = 0.31$, Table 4), and its scaling with SD was very different between constructions (Fig. 3c).

Bark thickness variation and angiosperm vs gymnosperm phloem cells

Gymnosperms had thicker mean total bark than angiosperms, but a similar TBT–SD scaling slope (Fig. 4a). The model supporting this inference fitted the data well and explained a large percentage of variation in TBT ($R^2 = 0.72$, Table 5). Contradicting the expectations of a greater radial extent of phloem compensating greater resistance in gymnosperms, IBT did not differ between angiosperms and gymnosperms (Fig. 4b). As for outer bark, the model prediction explained only 39% of its thickness variation and suggested a different scaling slope with SD (Fig. 4c). The coefficients of all models based on single samples per species fell within the 95% confidence intervals of coefficients of the model based on species means (Table S4). Given that models based on species means and single samples per species lead to the same conclusions, we make reference to the models based on species means in the Discussion.

Evolutionary lability of bark thickness traits across the woody plants

Most thickness traits were highly evolutionarily labile. When calculated based on residual thickness (once stem size was taken into account), the K statistic for all thickness traits was ≤ 0.58, indicating low or very low phylogenetic signal (Table 6). Congruently, the P values associated with the randomization test based on phylogenetically independent contrasts were, in general, > 0.05, indicating that the phylogenetic signal was not significant (Table 6). The only exception was gymnosperms, for which significant phylogenetic signal was detected, although it was not very high ($K \leq 0.58$, Table 6).

Discussion

Bark thickness variation in woody plants has been studied at global scales in the context of plant size, protection against fire and the storage of water and other compounds (Pausas, 2015; Rosell, 2016). However, it is still unclear how other bark functions might cause variation in the thickness of this complex

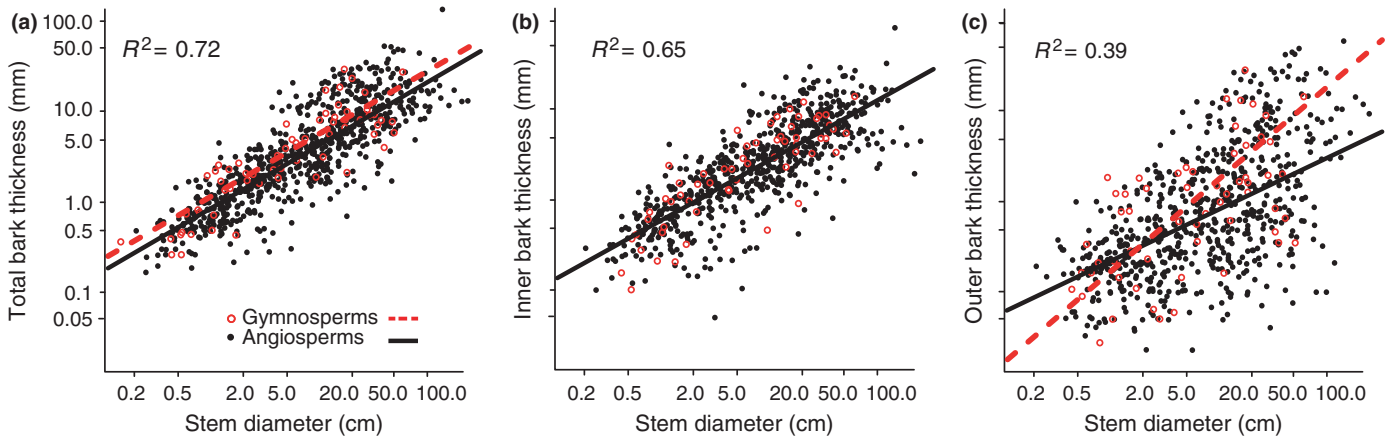

Fig. 4 Bark thickness and angiosperm vs gymnosperm phloem cells. Variation between angiosperm and gymnosperm phloem cells in (a) total, (b) inner and (c) outer bark thickness. Although gymnosperms had thicker total bark, inner bark was as thick as in angiosperms, whereas outer bark scaled differently between angiosperm vs gymnosperm phloem cells.

Table 5 Linear models used to test for differences in mean total (TBT), inner (IBT) and outer bark thickness (OBT) and thickness–stem diameter (SD) scaling across angiosperm vs gymnosperm phloem cells (self-supporting species only)

	TBT ~ SD + phloem cell	IBT ~ SD + phloem cell	OBT ~ SD * phloem cell
n	779	719	719
R^2_{adj}	0.72	0.65	0.39
Model ANOVA	$F_{2, 776} = 1002.0$***	$F_{1, 717} = 1347.0$***	$F_{3, 715} = 152.3$***
Equality of slopes test	$P = 0.216$	$P = 0.338$	$P < 0.001$
Equality of intercepts test	$P < 0.005$	$P = 0.235$	–
Angiosperm intercept	−0.05 (−0.08, −0.01)	−0.20 (−0.24, −0.17)	−0.65 (−0.71, −0.58)
Gymnosperm intercept	0.08 (−0.002, 0.16)		−0.76 (−1.07, −0.44)
Angiosperm slope	0.69 (0.66, 0.72)	0.67 (0.63, 0.70)	0.56 (0.50, 0.63)
Gymnosperm slope			1.00 (0.77, 1.24)
Figure	4(a)	4(b)	4(c)

Estimated coefficients are shown with 95% CI in parentheses.
Continuous variables $\log_{10}$ transformed; ***, $P < 0.001$.

Table 6 Evolutionary lability of residual bark thickness

	Total bark thickness	Inner bark thickness	Outer bark thickness
All species	0.11–0.12 (0.06–0.12)	0.13–0.14 (0.04–0.09)	0.11–0.12 (0.08–0.17)
Habit (angiosperms)			
Nonself-supporting	0.21–0.22 (0.06–0.12)	0.19–0.21 (0.09–0.18)	0.18–0.20 (0.14–0.26)
Self-supporting	0.16–0.17 (0.12–0.19)	0.18–0.20 (0.07–0.13)	0.09–0.10 (0.47–0.61)
Stem construction (angiosperms)			
Single cambium	0.14–0.15 (0.14–0.22)	0.15–0.16 (0.10–0.18)	0.09–0.10 (0.49–0.63)
Successive cambia	0.33–0.36 (0.17–0.29)	0.37–0.40 (0.16–0.26)	0.28–0.36 (0.19–0.41)
Monocots	0.18–0.20 (0.84–0.95)	0.50–0.55 (0.04–0.10)	0.36–0.39 (0.13–0.21)
Phloem cells (self-supporting species)			
Angiosperm	0.12–0.13 (0.21–0.30)	0.13–0.14 (0.17–0.26)	0.09–0.10 (0.48–0.61)
Gymnosperm	0.44 (0.001–0.008)	0.58 (0.001–0.003)	0.32 (0.01–0.05)

Range of the *K* statistic is shown for the 1000 runs with randomly resolved trees, as well as the range of the *P* value of the test with phylogenetically independent contrasts. The phylogenetic tree for gymnosperms was fully resolved.

region of the stem. Although our understanding of the physiology of photosynthate translocation and phloem structure has increased significantly (Thompson & Holbrook, 2003; Mencuccini *et al.*, 2013; Petit & Crivellaro, 2014; Ryan & Asao, 2014; Savage *et al.*, 2016), it has remained unclear whether photosynthate translocation modalities affect bark thickness. Based on the largest available dataset on TBT, IBT and OBT across the seed plants, we show that the climbing vs self-supporting habit and the way in which translocating tissues are deployed in a stem (conventional cambium vs successive cambia and monocots) have a significant effect on bark thickness.

Self- vs nonself-supporting habit and the deployment of photosynthate translocating tissue predicted variation in inner bark thickness

Higher demand for photosynthate translocation for a given SD was associated with thicker inner bark in our dataset, as suggested by nonself-supporting species having thicker inner bark, controlling for stem size. Based on the linear fits in Table 3, stems of 10 cm in diameter would have an inner bark of 4.15 mm if the species is nonself-supporting, or of 2.97 mm if self-supporting. Lianas have higher leaf area and biomass for a given SD than self-supporting plants (Putz, 1983; Niklas, 1994; Ichihashi & Tateno, 2015). Compensating for narrow SD, selection could favor more layers of living phloem in lianas (Ewers & Fisher, 1991), and thus thicker inner bark, in association with higher leaf metabolic demands on a given SD. Despite differences in IBT for a given SD across habits, if metabolic proportionalities drive inner bark amount, it is likely that inner bark volume scales with leaf area similarly in nonself- and self-supporting species. Because inner bark is predictably thicker in lianas, and because this IBT–SD relationship seems likely to be of functional significance, it is hard to entertain notions of this relationship at large as being one driven mainly by passive ontogenetic accumulation and not requiring explanation.

Thicker bark in lianas could be the result of selection favoring resistance to external mechanical damage, given that the slender stems of lianas routinely fall from the canopy, are struck by falling branches and are battered in the wind (Isnard & Feild, 2015). If so, then thicker outer bark, which is not only the outermost protection, but, being dead, is also less metabolically demanding than living inner bark, would be expected in lianas relative to self-supporting plants. Although outer bark can be very thick in lianas (Fig. 1a), nonself-supporting species did not differ from self-supporting species in their OBT for a given diameter (Table 3). Instead, thicker bark in lianas was mainly driven by the inner and mostly living portion. Nor was there any difference

between lianas and self-supporting species in their IBT–SD scaling slope (Fig. 2b). This similarity in slope seems to suggest that the thicker bark of lianas for a given SD is best explained by metabolic differences, perhaps proportionality with leaf area.

The thickness of inner bark is probably associated with traits reflecting metabolic activity, such as leaf area (Jensen *et al.*, 2012; Zhang *et al.*, 2016). Based on our data on self-supporting angiosperms with single cambia, we offer some predictions regarding IBT scaling with leaf area. We calculated the empirical allometric exponent between IBT and wood diameter (0.638, model not shown) and generated a theoretical dataset with wood diameter, IBT and SD. We used this calculated SD to estimate height based on the scaling slope of 0.682 across our data (model not shown). We then estimated the area of the inner bark ring and multiplied it by tree height to estimate the inner bark volume. We then calculated the theoretical leaf area assuming that leaf area scales with SD with a power of 2 (West *et al.*, 1999; Enquist *et al.*, 2009; Simini *et al.*, 2010). These estimates yielded a model in which inner bark volume scaled with leaf area with a slope of 1.177 (not shown), very close to isometry. The inner bark volume is probably underestimated in our calculations, given that we idealized a tree as a non-tapering cylinder with no branching. Precise calculations of bark volume will probably recover scaling exponents closer to one. Isometric scaling has been observed between other pairs of traits involved in plant metabolism, such as biomass and leaf area in small plants (Reich *et al.*, 2006), and biomass and plant respiration (Mori *et al.*, 2010). Likewise, isometry would be expected between the volume of inner bark and leaf area, because they should be mutually coupled in photosynthate production, storage and translocation.

With regard to translocation, variations in patterns of deployment of phloem in the stem seem to have an important effect on the thickness of angiosperm inner bark. In general, phloem-free inner barks were significantly thinner for a given stem size than phloem-bearing inner barks. Across phloem-free barks, there was remarkable similarity in IBT. Both monocots and 'dicots' with successive cambia had very similar fits when IBT was plotted against SD (Fig. 3b, Table 4). Based on these fits, inner bark in a stem of 10 cm in diameter would be twice as thick in a plant with a conventional cambium relative to one with successive cambia or a monocot (3.3 vs 1.6 mm). Phloem-free barks offer important study systems to continue disentangling the effects of the different functions of bark on its thickness, and in understanding why certain bark thickness–SD allometries are observed. Phloem-free barks do not translocate sugars, but still carry out photosynthesis and storage, and provide mechanical support and protection to stems. As a result, phloem-free barks of fire-prone areas could provide information on the minimum bark thicknesses providing protection to vascular bundles (monocots) or successive cambia against different fire regimes. Tree and shrubby species with successive cambia from habitats with frequent fires, such as *Nuytsia floribunda* from Western Australia (Lamont & Downes, 2011), could prove to be key systems. Likewise, phloem-free barks from fire-free localities with different water availabilities could provide information on how storage needs produce variation in IBT and TBT.

In addition to differences in the deployment of translocating tissue in a stem, angiosperm vs gymnosperm phloem cells were expected to have an effect on the thickness of inner bark. However, we found no difference in the inner bark of angiosperms and gymnosperms when stem size was taken into account. Gymnosperms do not seem to compensate the slower flow of their phloem with more tissue (Jensen *et al.*, 2012), if IBT is any guide. This could suggest that this slower flow could be associated with lower photosynthetic capacity (Lusk *et al.*, 2003; Brodribb *et al.*, 2005; Lusk, 2011), or that the presence of additional tissues in angiosperm inner bark in addition to conductive phloem is obscuring the expectation. Testing this latter hypothesis would require detailed anatomical work to quantify the percentage of inner bark devoted to conductive phloem.

Inner and outer bark showed contrasting trends with stem size

Although our hypotheses chiefly concerned IBT, we also examined OBT to examine whether differences in TBT were mainly driven by inner or outer bark. In general, trends for outer bark contrasted markedly with those recovered for inner bark. The thicker total bark of lianas was mainly driven by inner bark, given that, for a given diameter, lianas had thicker inner bark but equivalent outer bark relative to self-supporting species (Fig. 3). By contrast, the thicker total bark of gymnosperms seemed to be mainly driven by outer bark, because inner bark did not differ between gymnosperms and angiosperms (Fig. 4). Thicker outer bark could be the result of selection favoring fire resistance (Graves *et al.*, 2014; Schafer *et al.*, 2015; Rosell, 2016), given that most gymnosperms in our dataset came from fire-prone environments (Cornwell *et al.*, 2015). This highlights the need to include more conifers from fire-free habitats in our dataset (see Richardson *et al.*, 2015). Although OBT scaled with SD, this scaling was not as strong as that observed with the inner living region of bark.

Looser covariation would be expected between OBT, which is dead, and SD. Models based on SD explained < 39% of variation in OBT, compared with 65–67% in IBT (Tables 3–5). Given SD, outer bark varied widely (Figs 2c, 3c, 4c), this variation almost certainly reflecting differing selective scenarios for outer bark. Unlike inner bark, outer bark could be subject to maximum thickness thresholds. For example, photosynthetic activity in bark is severely limited by the thickness of the outer dead layer (Pfanz *et al.*, 2002). An outer bark of 1 mm decreases the probability of observing photosynthetic activity in bark by 50%, and practically no bark carries out photosynthesis if its outer layer is thicker than 4 mm (Rosell *et al.*, 2015). This maximum threshold applies independently of the stem size. Likewise, outer bark would be expected to have a minimum thickness threshold in fire-resistant species of fire-prone areas (Hoffmann *et al.*, 2012).

Bark thickness traits were highly evolutionary labile

Phylogenetic signal was mostly lacking in our dataset, with the exception of the gymnosperms. This result is not surprising given

the marked lability in size, habitat and even habit between closely related species. Most nonself-supporting species in our sampling were closely related to self-supporting species. Likewise, most of the species with successive cambia came from clades with close relatives with single cambia. The only exception was the gymnosperms, with significant, although low ($K \leq 0.58$), phylogenetic signal. This relative predictability given phylogeny seems to parallel the relatively low morphological diversity in the conifers. That said, our sampling was restricted to self-supporting gymnosperms and did not include climbers (in *Ephedra* or *Gnetum*) and included only one with successive cambia (*Welwistschia*).

Conclusion

Increasing evidence points to a diversity of factors beyond fire causing bark thickness variation. Our results suggest that photosynthate translocation is one such factor, especially in inner living bark. Our results highlight bark thickness–SD allometry as a phenomenon requiring explanation, and point to metabolic proportionalities, such as that between phloem volume and leaf area, as possible drivers. Bark thickness variation cannot be attributed to any single function. Instead, translocation demands must interact with the many other functions of bark, such as mechanical support, photosynthesis, storage and protection, to produce thickness variation across species, all in the context of thickness–stem size scaling.

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Author contributions

J.A.R. and M.E.O. planned and designed the research and conducted the fieldwork. J.A.R., M.E.O., T.A. and N.M-M. analyzed the data and wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Barks with successive periderms form a rhytidome, which is made up of the products of different meristems at different stages.

Fig. S2 Bark in woody monocots.

Fig. S3 Phylogeny of the 913 sampled species.

Figs S4–S6 Comparison of precipitation variables across habits, stem constructions and between angiosperms and gymnosperms.

Table S1 Estimates of the variance observed across and within species for total, inner and outer bark thickness

Tables S2–S4 Linear models examining differences in mean total (TBT), inner (IBT) and outer bark thickness (OBT), and thickness–stem diameter (SD) scaling, across angiosperm habits, stem constructions and between angiosperm and gymnosperms based on a random individual per species

Notes S1 Examination of the potential confounding effect of selection favoring thicker inner bark in dry areas.

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