Research review

Plant growth forms: an ecological and evolutionary perspective

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Summary

Trees, shrubs, lianas and herbs have widely different mechanical architectures, which can also vary phenotypically with the environment. This review investigates how environmental effects, particularly mechanical perturbation, can influence biomechanical development in self-supporting and climbing growth forms. The bifacial vascular cambium is discussed in terms of its significance to growth form variation, ecology and evolution among extant plants, and during its appearance and early evolution. A key aspect of this developmental innovation concerned its potential for architectural and mechanical variation in response to environmental effects as well as optimizing hydraulic supply before the appearance of laminate leaves. Growth form diversity and its importance to past and present ecosystems are discussed in relation to both evolutionary constraints and ecological factors such as climatic change and atmospheric CO_2 concentrations. We discuss how widely ranging growth forms such as climbers show a large range of developmental and phenotypic variation that has much to offer in understanding how the environment can modify plant development, particularly in terms of the bifacial vascular cambium. The broad approach we propose would benefit a wide range of studies from research into wood development to long-term ecological censuses of today's potentially changing ecosystems.

Introduction

Some of the main aims of recent evolutionary developmental research have been to discover the genetic and functional organization of the stem, leaf, root and reproductive organs of plants. While increasing efforts are made to understand the development of these organs in model organisms and now a greater variety of plants, few studies have focused on their ecological development and fewer still on how the entire growth form of plants might be altered by the genome and modified by the environment. The extension of evolutionary developmental studies to include the effects of ecology on developmental variation is nowhere more applicable than for understanding growth form diversity of plants.

In this review we discuss how ecology and environment can modify the overall growth forms of plants with particular reference to the mechanical constraints of stems and branches during development and growth. We discuss the main differences

between self-supporting plants and climbers, how such forms vary with the environment and how phylogenetic constraints can influence different developmental patterns. We briefly summarize recent hypotheses on the evolution of some major innovations in plants – secondary growth and the appearance of leaves – and broadly discuss how these were affected by environmental change and, indeed, how they themselves changed the environment. We argue that growth form diversity is an obvious but possibly understudied aspect at opposite extremes of biological research, from censoring natural habitats to choice of model organisms in molecular research. We argue here that growth form eco-devo and evolution is, however, a major factor underpinning ecosystem structure and diversity.

Growth Form Variation: Ecological and Evolutionary Contexts

What ecological conditions favour the tree habit and how do trees vary in different conditions? How do climbing plants differ from trees or shrubs? Can some species grow as shrubs or trees as well as climbers? What ecological effects might mediate these changes? How, and to what extent, is plasticity of growth form governed by phylogenetic constraints? When and how did the vascular cambium evolve and why did it become a key innovation for seed plants and their putative ancestors? The evolution of growth forms since the early terrestrial radiations is a complex history of innovation, complexification, simplification, conservatism, radiation and extinction. Trees, shrubs, climbers and herbs have different ecological preferences and different mechanical attributes. Are certain types of growth form highly constrained and immovable in evolutionary terms? Are some plant groups more 'flexible' in their capacity to evolve widely differing growth forms and is this capacity related to the evolutionary age or complexity of the group? What are the evolutionary developmental processes (e.g. heterochrony, heterotopy and homeosis) and what are the ecological factors that coerce to either canalise or facilitate growth form variation and evolution?

Mechanical architectures of growth forms

Size, height, and the stiffness or flexibility of plant stems are all determined by anatomical development and mechanical properties of their tissues. Trees, shrubs, herbs, vines, lianas, root climbers, epiphytes and hemiepiphytes all have contrasting developmental patterns of the stem and overall mechanical architectures. Biomechanical analyses can determine the stiffness or flexibility of a plant from its base to its apex and from older to younger stages of growth. Mechanical properties can then be correlated with anatomical development and used to pinpoint the developmental processes providing stiffness or flexibility over the plant body. Observations of these changes provide potent tools for determining: (1) phenotypic variation

of species during ontogeny and responses to ecological factors such as light or wind; (2) variations between widely or closely related plants and the developmental traits between putative ancestral and descendant states. In 1999 we provided a synthesis of how this approach is applied to growth forms from trees and shrubs to climbing forms (Speck & Rowe, 1999).

Self-supporting growth forms

All growth forms are essentially 'ecological' in design. There is a wide range of adaptive constraints influencing the mechanical architectures of growth forms but in this review we focus our attention on self-supporting and climbing growth forms. A self-supporting organization must physically support its own static weight and resist higher forces and dynamic loadings from a range of natural factors, particularly high winds. Older, basal parts of the plant body are relatively stiff whereas younger apical axes, as well as leaves and petioles are often more compliant and bend and twist in high winds, reducing drag and potentially destructive loading by wind. From a developmental point of view, this adaptive strategy is complex. Single species show ranges of variation during ontogeny and under different ecological conditions. Recent studies have shown such mechanical variation for mosses (Biehle *et al.*, 1998; Ross *et al.*, 1998), pteridophytes (Niklas, 1990), gymnosperm (Brüchert *et al.*, 2000) and angiosperm trees (Speck & Rowe, 1999) and herbs (Crook & Ennos, 1996).

The notion of 'safety factors' plays a role in many biological systems (Wainwright *et al.*, 1976; Niklas, 1998), particularly in terms of self-supporting plants. Trees and shrubs can vary in overall size, branching and mechanical properties with respect to the wind. Low safety factors with slender, tall stems are observed in sheltered conditions. The same species growing in open conditions exposed to the wind will have a shorter, stouter morphology. Changes in geometry and mechanical properties also occur during ontogeny; young individuals can show relatively low safety factors and mature or aged individuals high ones.

From a mechanical perspective, wind is a critical factor in constraining size, shape and retaining an upright growth form (Ennos, 1997). Responses to physical perturbation are known as thigmomorphogenetic reactions and overall morphological responses have been known for many years (Jaffe, 1973; Telewski & Jaffe, 1986). Responses to mechanical perturbation are now known to at least partly involve *TCH* (touch) genes (Braam & Davis, 1990; Braam, 1992). Recent experiments on ethylene-insensitive mutants of *Arabidopsis* suggest that the phytohormone ethylene is not necessarily required for responses to mechanical stimulation; interestingly, at least one touch gene, *TCH4* is initiated by a range of ecologically important stimuli, including mechanical perturbation, darkness, heat and cold shock (Iliev *et al.*, 2002). While increasing studies are concentrating on thigmomorphogenesis in *Arabidopsis* (Pigliucci, 2002) as well as trees (Pruyn *et al.*, 2000), the

signalling and transduction pathways remain incompletely understood (Johnson *et al.*, 1998; Jaffe *et al.*, 2002).

Plants have probably been buffeted by wind since the earliest radiations of land plants, an influence that increased as plants evolved higher growth forms. As an ecological factor it must have shaped the underlying genetic and developmental trajectories formed during this period when the major clades were accumulating genetic, physiological and structural innovations (Bateman *et al.*, 1998). The view that early plant evolution was marked by strong selective pressure for increasing height, light capture and efficient propagule dispersal, should take into account the effect of wind into the equation (Niklas & Speck, 2001).

Self-supporting architectures are mechanically optimized from the base to the apex of the plant (Niklas, 1999; Speck & Rowe, 1999); they can also show geometric and mechanical changes in exceptionally sheltered conditions. In understory niches of tropical forests, young trees and saplings often reach a point of instability and lean against surrounding trees. A simple interpretation is that competition for light is so fierce that self-supporting architectures are pushed to the upper limits and sometimes beyond their critical buckling length in the need to reach light. Such examples are seen commonly where clearing has removed neighbouring trees and exposed formerly sheltered plants to wind (Fig. 1a). Simply put, many plants, if they are not mechanically perturbed will produce less sturdy mechanical architectures and sometimes growth forms that are no longer self-supporting. This can apply to both large woody growth forms (trees) and to herbs, which can show extreme ecophenotypic variation between sheltered and mechanically perturbed sites.

Climbers

Many dicotyledonous woody lianas show entirely different mechanical architectures compared with self-supporting plants (Fig. 1b). The mature or aged liana can have utterly different mechanical properties from that of a self-supporting plant, reflecting profound differences in ecological function (Gartner, 1991b; Putz & Holbrook, 1991; Speck & Rowe, 1999). These differences have been studied increasingly at an ecological level over recent years (for a general review see Schnitzer & Bongers, 2002). In many lianas, young, distal parts of the plant are composed of relatively stiff tissues and act as 'searchers' spanning gaps between host supports (Rowe & Speck, 1996; Speck & Rowe, 1999). A great many different lianoid species also show a juvenile phase of growth where the young plant is self-supporting before locating a host support (Caballé, 1998). In tropical rainforest understory vegetation, such stems are difficult to distinguish from young self-supporting species. This early growth can represent a 'waiting phase' before appropriate environmental cues, such as light availability or proximity to a support, after which the self-supporting architecture can drastically change. Alternatively when lianoid

species grow in open conditions, some species do not develop a climbing phase (Hegarty, 1991; Gallenmüller *et al.*, 2004) and may die back after a given time; others will, nevertheless, begin to climb and scramble on themselves or anything nearby.

The transition to a climbing mechanical architecture can show profound and abrupt changes in secondary cambial development, particularly among twining lianas. The well-known lianoid species of *Bauhinia* (monkey ladder) can show a well-developed self-supporting phase (Fig. 1c) with a cylinder of dense, stiff wood (Fig. 1d) and heights of up to 2–3 m (Speck & Rowe, 1999; Hoffman *et al.*, 2002). At the onset of climbing, cambial growth is highly modified (Fig. 1e) producing a ribbon-like stem with highly compliant wood. Plants climb via tendrils and woody, hook-like leaf bases. Later development can involve further anomalous cambial activity and huge flexible 'trunks' which can literally swing freely from the canopy of their self-supporting hosts (Fig. 2a). Can the lianoid species *Bauhinia guyanensis* produce a large-bodied tree under certain ecological conditions? The answer is no. Whatever the internal developmental constraints during the ontogenetic trajectory, the self-supporting phase is confined to the 'juvenile phase', which may be expressed for a considerable time before attachment to a support.

Other species of *Bauhinia* do grow as trees. We have observed at least one species in south-east Asia that, having reached a tree-sized self-supporting morphology, will extend branches into the surrounding canopy, which are supported on branches of self-supporting neighbours (Fig. 2b). While not showing the same ribbon-like form, the response to neighbouring support is not consistent with the 'crown shyness' (Putz *et al.*, 1984) commonly seen in mature trees, which often maintain discrete gaps around the branches and canopies of neighbouring dominant trees (Fig. 2c). In *Bauhinia* and possibly many other clades of plants there is an underlying tendency to produce non-self-supporting traits that goes beyond the kind of thigmomorphogenetic reaction shown in Fig. 1a. Are the reactions controlling 'safety factors', the type of thigmomorphogenetic reaction described above, and this tendency or 'prepatterning' in many groups of angiosperms towards lianescence somehow linked?

Shrubs and climbers in the same species

The most detailed study to date of self-supporting and lianoid growth in a single species, by Barbara Gartner, indicated that *Toxicodendron diversilobum* (western poison oak) can grow to maturity as shrubs in the absence of supports and as large-bodied climbers (Gartner, 1991a,b). The plant can grow as modest-sized shrubs (up to 3.8–4 m high, usually up to 2 m, 15–20 cm in diameter) or as climbers (up to over 30 m high, usually 3–10 m high and up to 15 cm diameter). Supported stems show marginally lower values of material stiffness than unsupported stems and do not produce the highly compliant
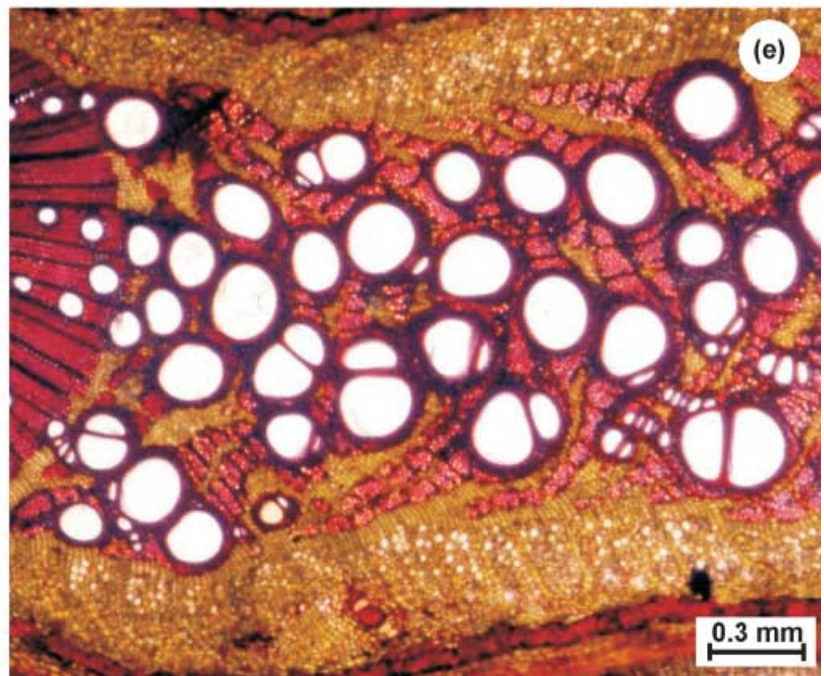
Fig. 2 (a) *Bauhinia guianensis*, mature lianoid form suspended from the host canopy. This mechanical architecture is completely different from the tree nearby – although the trunk diameters are comparable – and differs completely from the juvenile self-supporting phase (Fig. 1c). (b) Unidentified 'tree' species of *Bauhinia*, Yunnan Province, South China. The self-supporting trunk on the left (arrow) produces long slender branches, which straddle the branches of neighbouring trees (arrows left). (c) Many self-supporting trees maintain discrete gaps between their neighbours. This general tendency is fundamentally different from the situation seen in (b) and the overall strategy of climbers (arrows, note invasion by a climber).

Fig. 1 (a) Cleared margin of tropical rain forest, French Guyana, South America. Young trees in centre are unstable and not fully self-supporting after removal of surrounding vegetation. (b) Complete mechanical failure of host tree and survival of the liana summarizes the extreme mechanical and ecological differences between trees and specialized climbers. Although approximately two-thirds of the liana has parted (white arrow), about one-third of the stem is intact (black arrow) maintaining renewed growth further along the stem. (c–e) The liana *Bauhinia guianensis*. (c) Self-supporting phase in understorey vegetation; many lianas adopt this growth form during a juvenile phase and resemble young stages of self-supporting species. It can correspond to a 'waiting' phase and can be interrupted by a range of environmental cues including light and the proximity of mechanical supports. (d) Cross-section of stem showing shift from dense stiff wood (left) to localized development of highly compliant wood. (e) Cross-section of ribbon-like cambial activity with large diameter vessels and less dense fibres providing high compliancy and high hydraulic conductance.

secondary growth of many woody lianas. The difference in material stiffness between shrub and climber could be accounted for by relatively modest changes in wood-fibre wall thickness (Gartner, 1991b). The overall mechanical difference between shrub and climber concerned the wider diameters of stems in self-supporting forms.

These growth forms are not as widely different – in terms of mechanical properties – as between a tree and highly compliant liana (Speck & Rowe, 1999). Interestingly, both show decreasing material stiffness during ontogeny from small diameter to larger diameter stems (Gartner, 1991b), suggesting that the underlying developmental plan is possibly more that of a 'climber' than 'self-supporter'. In the case of poison oak and perhaps other plants like it, ecological conditions, namely the occurrence of substantial host supports, can markedly influence the type of growth form. In the examples above, cambial activity and its response to the environment play a key role in adjusting size and mechanical properties of different growth forms. In the following sections we discuss the evolutionary appearance and ecological implications of this innovation.

The Appearance and Consequences of the Cambium

The size and overall growth form of a species represents a critical interface with the environment and selection. This is largely confirmed by the observation that survival of potentially lethal environmental perturbation or climatic change can depend on body size (McKinney, 2001); at the risk of over generalization – big organisms die, small organisms live. We argue elsewhere (Rowe, 2000; Rowe & Speck, 2003) that the bifacial vascular cambium represented a key innovation in lignophytes and established a developmental template for plants to modify hydraulic and mechanical attributes as well as size and range of growth form. We also proposed that the combination of both secondary xylem and phloem was more adaptable than the almost entirely unifacial meristems in stems of extinct tree-sized lycopsids and sphenopsids and some other groups in the fossil record. Furthermore we suggested that the ability to change size and shape of the growth form via cambial activity offered better chances for later seed plant clades to survive periods of ecological perturbation.

Recent biomechanical models of phylogenetically basal lignophytes with a bifacial cambium from the Middle Devonian (*c.* 360 million years ago (Myr)) indicate that relatively young stages of growth were self-supporting, but that oldest stages were not optimized for a self-supporting growth habit (Rowe & Speck, 2003; Speck & Rowe, 2003), principally because of the wide thickness of soft bark-like secondary tissue around the outside of the wood cylinder. Thus, the oldest stages of growth were relatively flexible and would not have supported the weight of tall, branched stems. However, this

architectural constraint is not inconsistent with a perennial, and larger-bodied procumbent stem system, which would have, hydraulically and mechanically supported younger upright axes. This mechanical strategy is observed among woody plants growing in unstable ecological conditions (Isnard *et al.*, 2003). It favours survival in disturbed sites, producing upright shoots over a wide area and avoiding or traversing inhospitable microhabitats. The biomechanical models of early lignophytes (Rowe & Speck, 2003; Speck & Rowe, 2003) therefore suggest that the initial advantage of the bifacial vascular cambium was more probably one of potential plasticity of growth variation, above that provided by a mechanical architecture, constrained by primary growth and dominated by the outer fibrous hypodermis alone. Such growth forms could have occupied space without the physiological cost of an extensive self-supporting structure. Overall, the evidence suggests that the appearance of the bifacial vascular cambium did not initially confer the ability to produce large-bodied plants with high self-supporting stems. Greater height and size would have required the addition of further novelties with a mechanically optimized ratio of wood to compliant periderm, the presence of leaves and a more indeterminate growth pattern. The appearance of the bifacial cambium in earliest lignophytes can be viewed as a 'nascent innovation' that, after accommodating further added novelties, represented a key innovation, which permitted wide morphological and architectural diversifications. Later evolutionary patterns involving the cambium in lignophytes are a complex history of complexification (e.g. appearance of vessels and libriform fibres in angiosperms) as well as reduction (e.g. loss of the vascular cambium in monocotyledons). These had far-reaching effects on subsequent growth form plasticity and ecological preference within different clades: the paucity of growth form diversity in extant gymnosperms (with the exception of the Gnetales) and extreme growth form diversity in angiosperms.

Profound alterations in growth form such as transitions to climbers or herbs can canalise subsequent evolution, setting different limits on growth-form plasticity in different clades and species. A pine tree cannot grow as a highly compliant liana whatever the ecological circumstances; the poison oak can grow as fairly modest-sized shrubs and up to 30-m high climbers – albeit not highly compliant specialized ones; a lianoid species of *Bauhinia* can grow as an upright sapling in sapling-dominated forest understory but eventually swings freely from the canopy as an adult. From a mechanical perspective these constraints result principally from phylogenetic constraints centred on wood development.

Phylogenetic studies exploring growth form evolution in plants are few and far between both at the macro and micro evolutionary scale (Funk, 1982; Bateman *et al.*, 1992; Bateman, 1994; Böhle *et al.*, 1996; Civeyrel & Rowe, 2001; Speck *et al.*, 2003). Recent studies suggest a complex evolution of growth forms within the Aristolochiaceae (Speck *et al.*, 2003);

the basal taxa, *Asarum* and *Saruma* are herbs, whereas the genus *Thottea*, which is sister to *Aristolochia* s.l., is a small-bodied shrub. Most species of *Aristolochia* s.l. are lianoid with herbs appearing in the mostly lianoid *Aristolochia* s.st. and *Howardia*. Three rare, woody shrub-like species, as well as lianas, occur in *Isotrema*, which, interestingly is sister group to another occurrence of a diminutive herb. While woody shrub-like forms are rare in the group, the prevalence of lianas and herbs suggest an underlying development constraint, which does not readily accommodate self-supporting woody architectures. In the young searcher phases of the climbers tested, stiffness is imparted via an outer ring of thick-walled hypodermal tissue (Fig. 3d), possibly reflecting that of putative ancestral herbs (Speck *et al.*, 2003). The wood produced is of a single highly compliant type: once secondary growth has ruptured the outer wall of stiff material (Fig. 3e), the stiffness of the stem is irreversibly reduced. This does have ecological implications on the physical distance and longevity of the 'searching' phase and quite possibly constrains the 'type' of climbing behaviour.

In other groups, such as the trees, shrubs and lianas of *Strychnos* (Loganiaceae), the architecture is predominantly woody. Climbers show an initial stiff searcher phase, which can extend from one host plant to another over a matter of metres (Fig. 3a) and is characterized by a cylinder of dense, stiff wood (Fig. 3b). When a support is secured via the woody hooks on apical branches, a second type of compliant wood is produced (Fig. 3c). This development can vary the amount and degree of dense or compliant wood, probably related to the degree of support from neighbouring plants. The type of mechanical architecture might also be coupled with different modes of attachment to the host vegetation such as by anchoring wide-angled branches or placing hooks, as in *Strychnos*, into the surrounding vegetation. Different lianoid species can therefore inherit different types of mechanical architecture, which can directly influence the ecology and thus plasticity of their climbing strategy and overall growth form.

Wood, Leaves and Atmosphere: Functional Links and Ecological Feedback Loops

Plants can respond to lower atmospheric ρCO_2 by phenotypically increasing stomatal densities of leaves and thus increasing net diffusion of CO_2 into the leaf. Recent studies have documented this general tendency from: (1) experimental studies of living plants growing under differing CO_2 levels; (2) analyses of historic herbarium material and sub-fossil leaf material that can be correlated with anthropogenic/industrial aged changes in atmospheric CO_2 recorded from ice cores (Woodward, 1987), and analyses of fossil stomatal densities from older geological sediments in Mesozoic and Palaeozoic plants, which can be compared with estimates of ancient atmospheric CO_2 content based on geochemical analyses and computer modelling of global carbon cycling (McElwain, 1998; McElwain

et al., 1999). A number of difficulties are centred on the interpretation and significance of these changes particularly when applied to stomatal changes in deep time (Royer, 2001). They include the type of stomatal parameter quantified for fossil leaves combined with the effect of local fluctuations of CO_2-levels, the variation of stomatal numbers on sun and shade leaves of the same organism (Poole & Kürschner, 1999), the sensitivity of stomatal density (number of stomata per mm^2 on the leaf surface) as opposed to stomatal index (the number of stomata in reference to the number of leaf epidermal cells), the relative sensitivity of stomatal parameters with other environmental effects such as light intensity, temperature and humidity, and the relative sensitivity and variation observed between changes in stomatal parameters by different phenotypes and genotypes (Royer, 2001; Beerling & Royer, 2002; Woodward *et al.*, 2002).

Despite the uncertainties surrounding the actual cause, effect and variation underlying stomatal parameters, early land plants in the Silurian to Middle Devonian lack laminate foliage and recent studies indicate that these have low stomatal densities, coinciding with relatively high atmospheric CO_2 concentrations. Laminate leaves are generally perceived to have appeared rather 'late' in plant evolution and recent observers have linked their appearance with lowered atmospheric ρCO_2 towards the Late Devonian *c.* 360 Myr (Beerling *et al.*, 2001; Osborne *et al.*, 2003). These authors propose that archaic land plants were constrained from developing laminate leaves in the early Devonian because high ρCO_2 precluded high stomatal densities and sufficient cooling via transpiration to dissipate heat from solar radiation and avoid lethal overheating of the laminate leaf (Beerling *et al.*, 2001). By the late Devonian and Early Carboniferous, ρCO_2 had dropped by 90%, and planate leaves were a more common though by no means exclusive component of terrestrial plants. The authors suggest that lower ρCO_2 elicited a response to higher stomatal densities, permitting the evolution of laminate foliage after enhancing stomatal conductance and cooling. If true, this scenario is an interesting case where phenotypic plasticity in relation to a specific environmental factor – stomatal densities in relation to ρCO_2 – could have played a role in unlocking a developmental constraint for a major innovation.

The 'delay' in laminate leaf evolution could have also resulted from the fact that requisite hydraulic traits are highly integrated with many other aspects of the plant's physiology and morphology: from water uptake in the root, water storage, water conduction and safety factors in terms of hydraulic stress/failure and trade-offs with mechanical functioning (Rowe & Speck, 2003). This is contrary to the view that the evolution of the leaf lamina might have been 'developmentally simple' (Kenrick, 2001; Osborne *et al.*, 2003). Increasing hydraulic conductance would have been a requisite upgrade in complexity to accommodate lamina evolution and would have required significant alteration of the hydraulic and
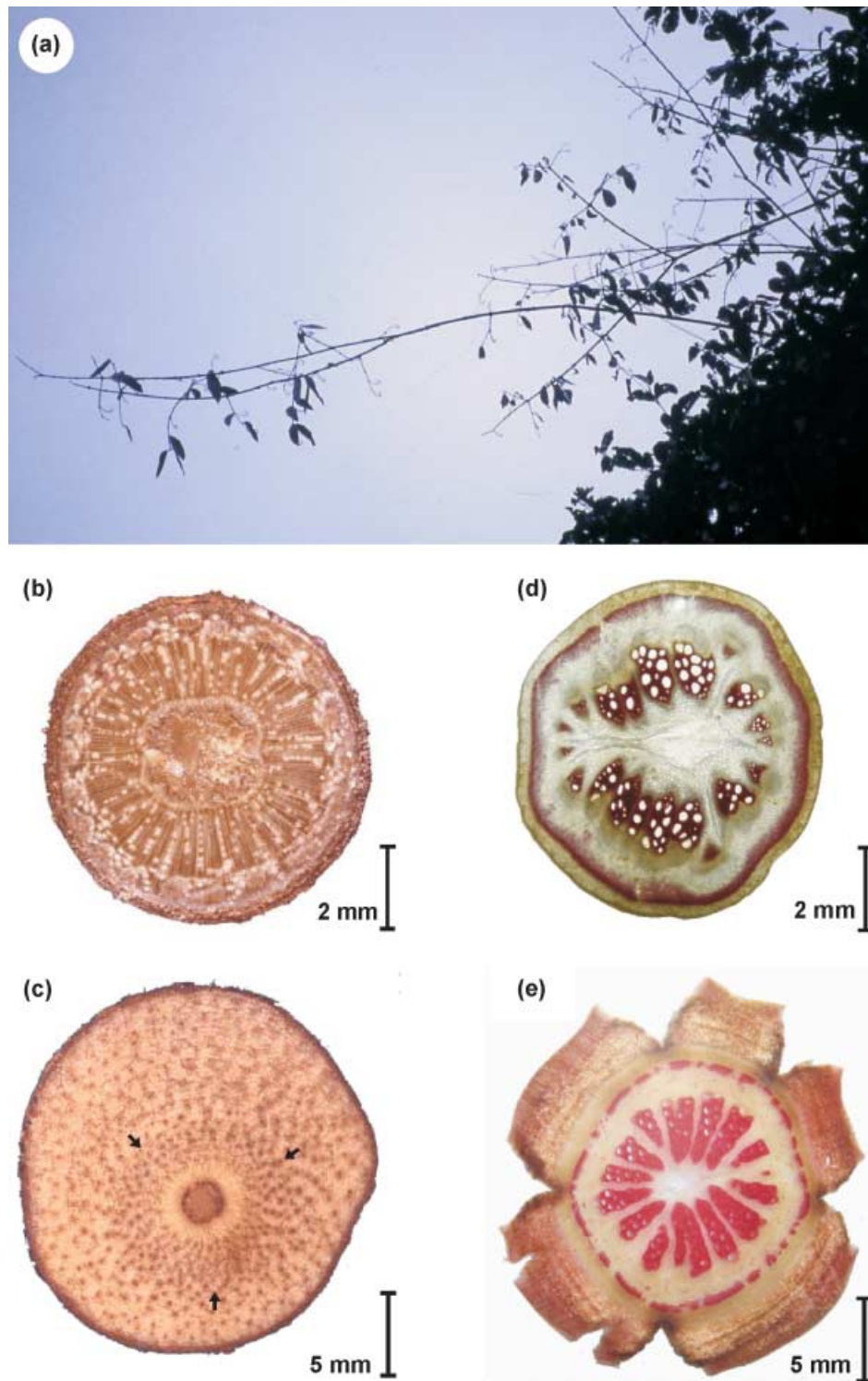
Fig. 3 (a) Searcher morphology of the woody liana *Strychnos*, young branches can extend 3–4 m to locate new supports; attachment is provided by tendril-like hooks from modified axillary shoots. (b–d) The type of climbing architecture and its ecological variation can depend on the ancestral development and mechanical architecture. (b) Lianas of the predominantly woody genus *Strychnos* comprise a juvenile phase with dense juvenile wood. (c) A second, less dense and more compliant wood is produced during the adult climbing phase (arrows). Basal members of the Aristolochiaceae are small-bodied perennial herbs (*Asarum*, *Saruma*), which are self-supporting or procumbent. Herbaceous traits potentially constrained subsequent shrub-like and lianoid mechanical architectures. (d) In young 'searchers' of *Aristolochia brasiliensis*, a ring of outer lignified fibres provides stiffness and the early formed wood cylinder is highly compliant. (e) Further development of the cambium ruptures the outer fibre ring and the transition from relative high stiffness to compliance is irreversible.

mechanical architecture of possibly the entire plant body. The most important innovation, which succeeded in doing this, in addition to enlarging primary xylem conduit diameter, was probably the appearance of wood – which brings us back to the cambium and growth forms.

Secondary growth of xylem occurred in at least five lineages by the end of the Devonian during the crucial period leading to the establishment of laminate foliage. In the lignophyte lineage, the appearance of the cambium in the middle Devonian before the appearance of laminate leaves in the group represents an important preaptation for the appearance of leaves and large self-supporting trees of all other gymnosperms and angiosperms. Whatever the exact combination of ecological factors linking the evolution of secondary growth and leaves, the two innovations marked major turning points in how plants would be able to respond to the environment and indeed change it. Observers, in reference to evolutionary innovations (Cronk *et al.*, 2002) as well as palaeontologists (Algeo & Scheckler, 1998) have remarked on the importance these have had in actually changing the ecology of the planet: turning the land green, forming soils, fixing carbon, sequestering carbon, increasing clastic weathering, and altering atmospheric ρCO_2. Interestingly, some of these effects initiated by increasing growth form size towards the middle Devonian, reduced atmospheric ρCO_2, and might actually have actually initiated the appearance of leaves. A two phase feedback loop whereby: (1) increasing growth form size and complexity in the lower to Middle Devonian led to increased sequestering of carbon, soil formation, clastic erosion and lowered atmospheric ρCO_2: (2) lowered ρCO_2 possibly released a phenotypic constraint from low to high stomatal densities, thus providing the requisite preaptation for lamina-cooling and leaf evolution. In the seed plant lineage, the bifacial cambium was already in place for potentially modulating the mechanics and hydraulics necessary for leafy growth forms.

Growth Forms, Ecosystems and Responses to Environmental Change

Climbers can show markedly increased rates of photosynthesis (Greaves & Buwalda, 1996) and higher biomass (Granados & Korner, 2002) when grown in elevated atmospheric ρCO_2. Recent studies based on long-term censused tropical forest sites report an increase in abundance and dominance of lianas, especially in the neotropics (Phillips *et al.*, 2002; Wright *et al.*, 2004; but see Caballé & Martin, 2001) for the paleotropics of West Africa. Increases in liana abundance have been discussed with reference to the fact that climbers respond particularly quickly to elevated CO_2 levels as well as forest disturbance. Either or both of these factors could explain increases in liana abundance. What is of great interest is whether the increase of lianas does either locally or more generally raise atmospheric ρCO_2 either by increased turnover – sequestering more biomass

into leaves relative to wood – or by slowing wood growth and increasing mortality rates of self-supporting plants. Of further interest is whether this causes a positive feedback loop (Phillips *et al.*, 2002) where increased lianoid growth would elevate atmospheric ρCO_2 and thus further increase lianoid growth to the detriment of trees. Whatever the reality in this complex issue – most commentators state that more information is required – changes in ecological composition in tropical forests do appear to affect varying growth responses to the environment. A key factor being different environmental effects on different growth forms.

Growth form diversity has been, until relatively recently, an arguably understudied aspect of land plant biodiversity and evolution. Especially so compared with recent emphasis on systematic diversity via nucleotides of genes that are not implicated in growth form development and differentiation. However, phylogenetic studies are essential for placing patterns of growth form in an evolutionary context. Genomic studies on the secondary vascular cambium have been relatively slow to develop compared with those based on primary meristems, leaves and floral development for a variety of reasons (Chaffey, 2002). While studies on model organisms such as *Arabidopsis* are providing a way forward for how growth forms might respond differently to the environment, much of the development crucial for growth form variation arguably concerns the vascular cambium. Although *Arabidopsis* can produce a limited amount of wood in the hypocotyl (Chaffey *et al.*, 2001), and may be useful for some aspects of wood development (Bhalerao *et al.*, 2003), it is limited for exploring changes in cambial activity of large-bodied woody plants with long life trajectories and wide ranges of wood development variation (Cseke & Podila, 2004). Genomic studies on woody plants are now providing more insight on developmental variations during wood formation (Hertzberg *et al.*, 2001) and comparative genomics of wood-forming tissues in pine and *Arabidopsis* (Kirst *et al.*, 2003). The latter suggests a high similarity of long-chain sequences related to wood development between *Populus* and *Arabidopsis*, suggesting long-term conservation of coding sequences since the estimated last common ancestor of *c.* 300 Myr. The plant fossil record can go some way to substantiate such inferences, if not by molecular evidence, then by exquisitely preserved cellular preservation of tissue development. Figure 4a illustrates the detailed organization of the cambial tissue preserved in a *c.* 340 Myr old seed plant with many of the cell types and differentiating zones present in gymnosperms and angiosperms today.

Observers of evolutionary developmental approaches have encouraged more research into phylogentically distanced organisms in order to understand key evolutionary processes and innovations (Cronk, 2001). A similar suggestion can be voiced for genomic investigations of widely ranging growth forms, particularly the differing wood types between young and old development. Such changes are implicit to many self-supporting and climbing woody plants.
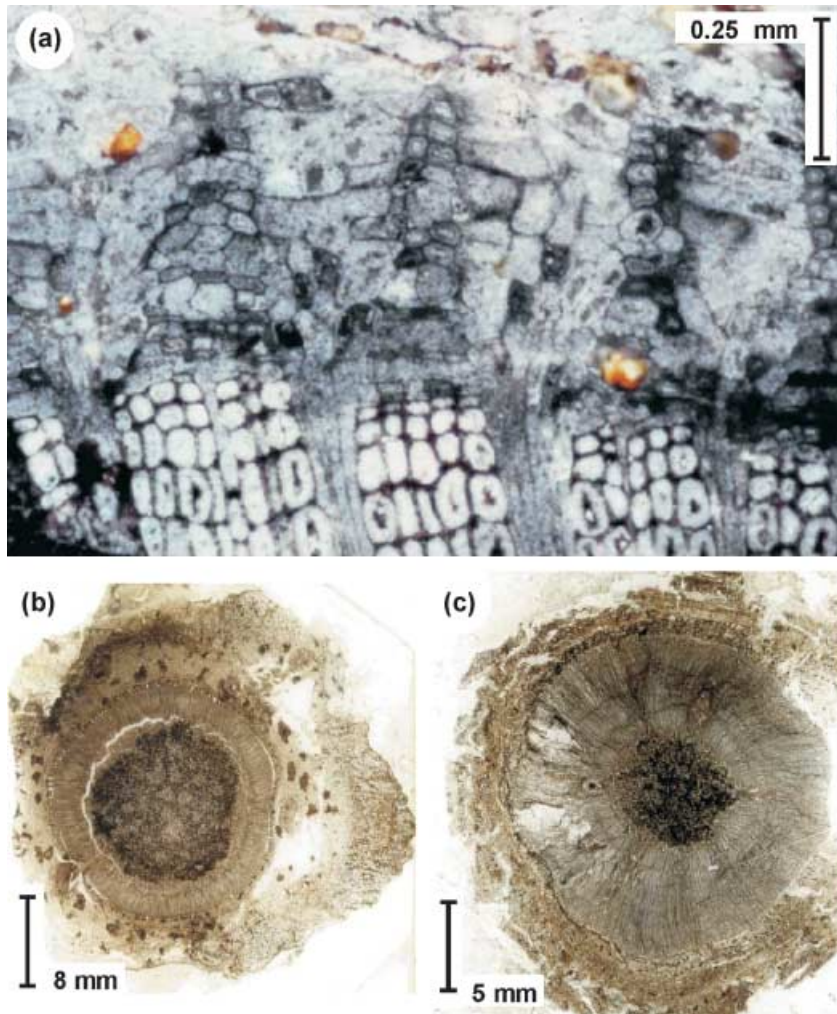
Fig. 4 (a) A 340-million-yr-old fossil of the bifacial vascular cambium of an early seed plant showing developmental features involving at least eight tissue types, with stages of differentiation. From above to below: Secondary phloem rays, secondary phloem sieve cells, secondary phloem fibres, differentiating secondary phloem, cambial initials, differentiating tracheids, wood rays, fully differentiated tracheids. Such material, while not offering molecular comparisons with genomic research does offer a substantial chance to date and compare detailed developmental trajectories at the cellular level. (b,c) Young (b) and older stage (c) of the leafy, self-supporting, tree of the early seed plant *Pitus dayi* see (Speck & Rowe, 1994); the transition from a compliant early stage (little wood, attached leaf bases and much primary cortex) is followed by a mechanically stiffer stem of wood and periderm. The primary key innovation, the bifacial vascular cambium has been augmented by further adaptive novelties including laminate foliage, leaf abscission, entire periderm development and indeterminate growth, establishing the developmental template in seed plants for ecological and morphological flexibility, survival and dominance.

The genomic and environmental controls of these transitions are of great interest for both ecology and evolution. Heterochronic mechanisms are increasingly being seen as important for evolutionary change in plants (Kellogg, 2002). We suspect that evolutionary transitions involving heterochronic modification of the developmental plan can have a significant effect on the resulting mechanical architecture. Lianas can range from saplings to highly flexible, suspended trunks. Retention of juvenile characteristics (stiff juvenile wood) into maturity could result in a self-supporting plant, whereas rapid expression of adult characters (compliant wood) would result in high flexibility from an early age with little or no self-supporting phase and possibly an entirely different growth form. Such scenarios are at least partly consistent with recent discussions on saltational evolutionary change in plants through mutations of key developmental genes (Bateman & DiMichele, 1994, 2002; Bateman, 1994). Some growth forms can show profound morphological changes during the growth trajectory, which could be viewed as a type of age or ontogeny-related phenotypic plasticity. Environmental effects play an important role in modifying these changes. We propose that this kind of phenotypic and evolutionary flexibility centred on the growth form and, in particular, the vascular cambium, at least partly explains the survival of the lignophyte clade across periods of perturbation and extinction, leading to their dominance today.

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