

INVITED REVIEW

Evolution and ecology of plant architecture: integrating insights from the fossil record, extant morphology, developmental genetics and phylogenies

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- **Background** In contrast to most animals, plants have an indeterminate body plan, which allows them to add new body parts during their lifetime. A plant's realized modular construction is the result of exogenous constraints and endogenous processes. This review focuses on endogenous processes that shape plant architectures and their evolution.
- **Scope** The phylogenetic distribution of plant growth forms across the phylogeny implies that body architectures have originated and been lost repeatedly, being shaped by a limited set of genetic pathways. We (1) synthesize concepts of plant architecture, so far captured in 23 models; (2) extend them to the fossil record; (3) summarize what is known about their developmental genetics; (4) use a phylogenetic approach in several groups to infer how plant architecture has changed and by which intermediate steps; and (5) discuss which macroecological factors may constrain the geographic and ecological distribution of plant architectures.
- **Conclusions** Dichotomously branching Paleozoic plants already encompassed a considerable diversity of growth forms, here captured in 12 new architectural models. Plotting the frequency of branching types through time based on an analysis of 58 927 land plant fossils revealed a decrease in dichotomous branching throughout the Devonian and Carboniferous, mirrored by an increase in other branching types including axillary branching. We suggest that the evolution of seed plant megaphyllous leaves enabling axillary branching contributed to the demise of dichotomous architectures. The developmental-genetic bases for key architectural traits underlying sympodial vs. monopodial branching, rhythmic vs. continuous growth, and axillary branching and its localization are becoming well understood, while the molecular basis of dichotomous branching and plagiotropy remains elusive. Three phylogenetic case studies of architecture evolution in conifers, *Aloe* and monocaulous arborescent vascular plants reveal relationships between architectural models and show that some are labile in given groups, whereas others are widely conserved, apparently shaped by ecological factors, such as intercepted sunlight, temperature, humidity and seasonality.

Key words: Architectural models, branching, developmental genetics, dichotomous vs. axillary branching, growth orientation, growth rhythmicity, modularity, morphology, plant architecture, plant evolution, plant fossils, reiteration.

INTRODUCTION

Plant growth forms have long attracted naturalists and botanists, and a series of classification schemes have been published. The first such classification system separated herbs, trees and shrubs, and, among the latter, annuals and perennials. A review by Du Rietz (1931) provides a history of life form classifications from Theophrastus to Raunkiaer (1934; updated by Ellenberg and Mueller-Dombois, 1967). Raunkiaer's life form system, which became the most widely accepted, is based on a plant's adaptations to the dominant climate under which it evolved. In the 1970s, a novel approach emerged – plant architectural analysis – that aimed to discern, by means of morphological observations and sometimes also experimentation, the endogenous processes moulding a plant's growth form (Hallé and Oldeman, 1970; Hallé *et al.*, 1978; Barthélémy and Caraglio, 2007). A handful of morphological characters, such as the position of sexual structures or the orientation of axis

growth (Fig. 1), permitted the recognition of 23 architectural models to which most natural growth forms can be assigned (Hallé and Oldeman, 1970; Hallé *et al.*, 1978; Hallé, 2004). Several important concepts, such as the architectural unit, architectural models and reiteration, arose from the field of architectural analysis (Barthélémy and Caraglio, 2007; Fig. 1) and allow an integrative understanding of whole-plant development. Recently, architectural analysis has been applied to moss gametophytes, revealing the convergence of a diverse array of gametophyte growth forms (Coudert *et al.*, 2017).

Plant architectural analysis was developed for seed plants, especially tropical angiosperms (Hallé and Oldeman, 1970; Hallé *et al.*, 1978), which branch laterally via axillary branching. In contrast, most non-seed plants branch apically via dichotomous branching, suggesting that there is an overlooked diversity of dichotomous architectures. This study aims to bridge this gap by expanding architectural analysis to the full phylogenetic spectrum of fossil plants. Any one plant's

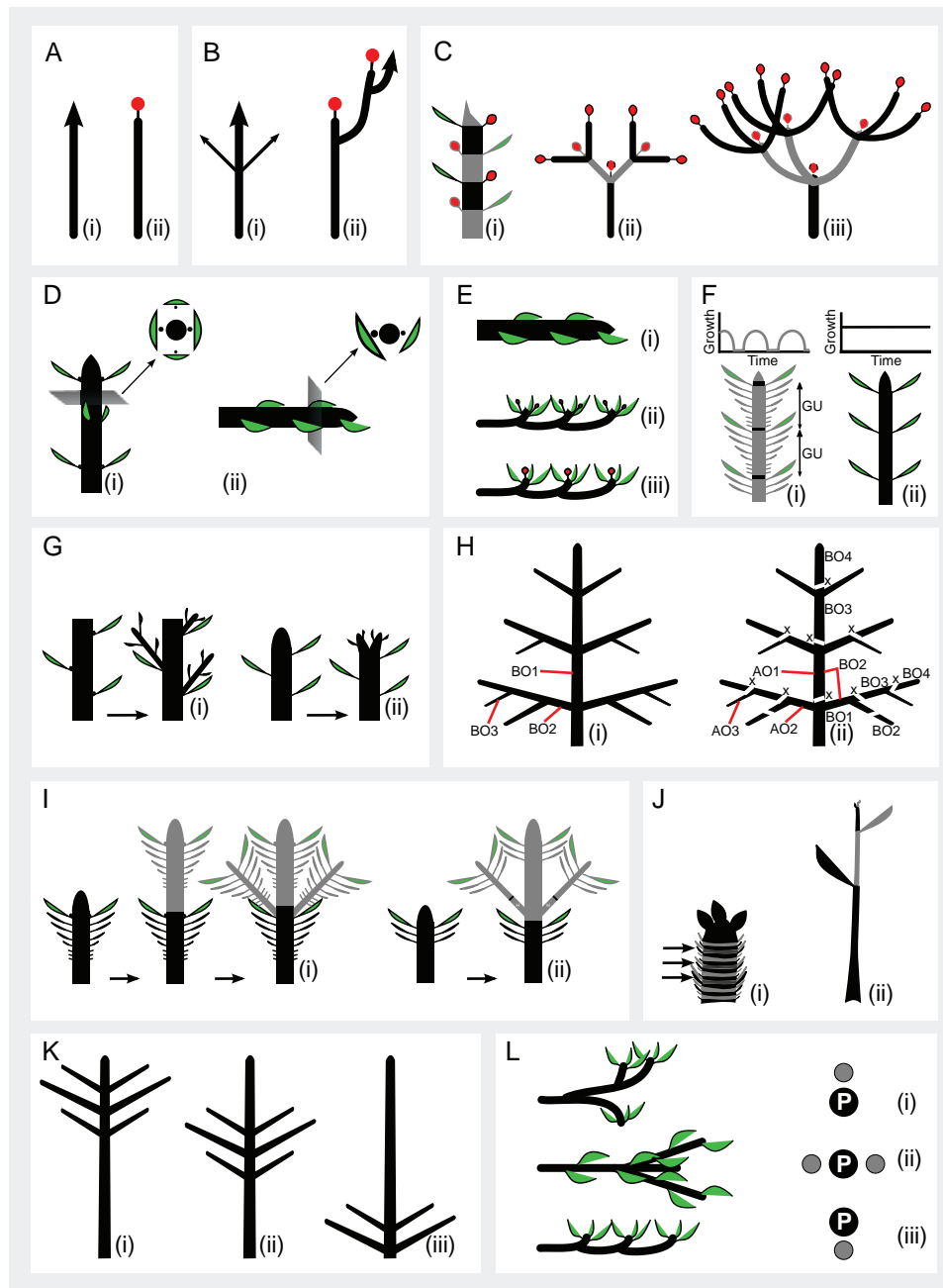


FIG. 1. Main concepts in plant architecture. (A) Growth pattern indeterminate (i) or determinate (ii). (B) Monopodial (i) vs. sympodial (ii) branching. (C) Types of sympodial branching related to the number of relay meristems: monochasium (i), dichasium (ii) and polychasium (iii). (D) Orientation growth of a stem can be orthotropic, when the growth is upright and stem symmetry is typically radial (i), or plagiotropic, when it is horizontal (as a result of endogenous processes, not environmental effects) and often associated with bilateral symmetry (ii). (E) Plagiotropic branches can be monopodial (i) or sympodial, and in this case result from mixed axes with either axillary inflorescences: plagiotropy by apposition (ii) or with terminal inflorescences, implying that each new module is needed to maintain the reproductive and vegetative function: plagiotropy by substitution (iii). (F) Rhythmic growth with periods of endogenous growth cessation (GUs) where the apical meristem rests in a bud (i) vs. continuous growth where there is no endogenous growth cessation (ii). Scale leaf scars show clear growth units (GUs). (G) Branching can be lateral (axillary), as in almost all seed plants (i), or terminal, involving meristem dichotomy as in lycopsids and various extinct plant groups (ii). (H) Examples of monopodial (i) and sympodial (ii) architectural units. Note that the branching order (BO) increases rapidly in the sympodial architectural unit, while the apparent branching order (AO) mirrors the branching order of the monopodial unit. X denotes apex death. (I) In species with rhythmic shoot growth, branching can be delayed (i) when the axillary meristem outgrowth is delayed compared with apical meristem outgrowth, or immediate (ii), when the apical and axillary meristem branch concurrently. Immediate branching is often characterized by extensive primordium neof ormation (Cremer, 1972), and a long first internode in axillary branches termed a hypopodium (H). (J) In species with rhythmic branching, a small number of condensed internodes per GU associated with little intermodal extension defines short shoots (i), which often have specialized functions (e.g. brachyblasts in *Pinus*), as opposed to long shoots (ii). (K) On a vertical axis or GU, the preferential repartition branches can be towards the apex (acrotony) (i), towards the middle (mesotony) (ii) or towards the base (basitony) (iii). (L) On a horizontal stem or growth unit, a sibship shoot can occur in an upper position (epitony) (i), lateral position (ii) or basal position (hypotony) (iii).

modular construction is the result of exogenous constraints and endogenous processes. The focus here is primarily on the endogenous processes that shape plant architecture and its evolution. Macroecological (exogenous) factors that may constrain the distribution of plant architectures are briefly summarized in the final section.

Plant fossils are rarely preserved whole. Most often, only small parts such as seeds or leaves are preserved in locations far apart. The hardest task for palaeobotanists is to link together these disconnected fossils to form a single whole-plant concept, a process called reconstruction (Bateman and Hilton, 2009). Plant reconstruction requires palaeobotanists to find physical connections between plant organs, and has only been achieved for a small sub-set of plant fossils (Stewart and Rothwell, 1993; Taylor et al., 2009). We here expand architectural analysis to some of the best-known, fully reconstructed Palaeozoic plant fossils. The architectural approach is fundamentally distinct from classifications of land plant body plans (e.g. Rothwell, 1995; Tomescu, 2011).

Over the last three decades, major advances have been made in plant developmental genetics, fuelled by the rise of genomics and insights from plant model species amenable to forward and reverse genetics. This has improved our understanding of, amongst other things, the molecular basis of meristem maintenance and leaf and flower development (e.g. Coen and Meyerowitz, 1991; Byrne et al., 2000; Schoof et al., 2000). In parallel, molecular phylogenetics has developed as a powerful tool in evolutionary biology, which led to the successful disentangling of evolutionary relationships in many parts of the tree of life. Despite the fundamental importance of plant architecture, its analysis has attracted relatively little attention from developmental and evolutionary plant biologists. These fields are brought together to answer the following questions. (1) What were the architectures of extinct dichotomously branched plants? (2) What can be learned from developmental genetics that is relevant to plant architecture? (3) How can phylogenies inform our understanding of plant architectural evolution? (4) Which macroecological factors most constrain the distribution of plant architectures?

PLANT ARCHITECTURAL TRAITS AND ARCHITECTURAL MODELS

The architecture of a plant is the result of the spatiotemporal expression of its meristems because meristem hierarchy and fate determine architecture through time. The principal architectural traits and concepts are summarized in Fig. 1. The ‘architectural model’ of a plant encapsulates the different developmental phases on a wider scale. So far, 23 formal models have been proposed that encompass the architectures of most extant seed plants (Hallé and Oldeman, 1970; Hallé et al., 1978; Hallé, 2004). Rather than being strict categories, these models are viewed as the most likely architectures within an architectural continuum. The degree of conformation to the model is species specific, but also depends on environmental variables, such as sunlight (Charles-Dominique et al., 2009, 2012). Variation within each architectural model is encapsulated in the concept of an ‘architectural unit’, which designates the developmental sequence of a plant and is species specific. Each architectural model has a unique combination of (1) growth pattern

[determinate vs. indeterminate (Fig. 1A) and rhythmic vs. continuous growth (Fig. 1F)]; (2) branching pattern [terminal vs. lateral (Fig. 1G), monopodial vs. sympodial branching (Fig. 1B, C), rhythmic vs. continuous or diffuse branching and immediate vs. delayed branching (Fig. 1I)]; (3) axis differentiation [orthotropic, plagiotropic or mixed (Fig. 1D, E)]; and (4) the position of sexual structures [lateral vs. terminal (Fig. 1Eii, Eiii)]. If all these features could combine freely, this would yield a larger array of architectural models than the 23 currently recognized, which may reflect genetic and environmental constraints, as also proposed for inflorescence architecture (Prusinkiewicz et al., 2007). On the other hand, it was suspected from the beginning that additional models might exist, notably in herbs or vines (Hallé et al., 1978), given that the 23 were developed mainly from the study of extant tropical trees.

The simplest plant architecture consists of a single axis (a monocaulum) that terminates in a reproductive structure (Holtum’s model; Fig. 2A). Monocaulous growth can also be indeterminate and then either rhythmic or continuous (Corner’s model; Fig. 2B, C), and a further alteration of monocaulous models involves integrated basal branching (Tomlinson’s model; Fig. 2D, E). Branching can either be immediate, where the plagiotropic modular system is developmentally integrated and typically leads to geometric shoot systems (e.g. those of many Zingiberaceae and Costaceae), or delayed, where the system is more opportunistic and could be interpreted as reiteration (see below) of a monocaulous model (Chomicki, 2013). From the basic monocaulous and determinate Holtum’s model arises a series of architectures with the ability to branch, leading to modular growth. If the growth unit can branch only once, the tree remains monocaulous (Chamberlain’s model; Fig. 2F). Other patterns involve the production of three equal modules below the terminal inflorescence of each unit (Leeuwenberg’s model; Fig. 3A) or two unequal modules (one overtopping the other – Koriba’s model; Fig. 3B). Whereas in Koriba’s model the trunk and branch modules are initially the same and differentiate only by overtopping, they differ from each other in Prévost’s model, which involves determinate trunk modules producing branch modules (Fig. 3C). In contrast, Fagerlind’s model involves a monopodial trunk, sympodial branches that become plagiotropic by substitution (Fig. 1E) and rhythmic branching of the trunk (Fig. 3D); when the branch modules are indeterminate [plagiotropy by apposition (Fig. 1E)], the architecture is assigned to Aubréville’s model (Fig. 4A). Petit’s model is a variant with continuous/diffuse branching, found for instance in several *Piper* species (Fig. 3E). A very distinctive architecture – found in cocoa (Fig. 3F; Nozeran’s model) – involves differentiated trunk and branch modules and a sympodial trunk, where each module produces monopodial, plagiotropic branches. Scaronne’s model involves a monopodial trunk and sympodial branch modules, both orthotropic and branching rhythmically (Fig. 4B), whereas Stone’s model is a variant with continuous/diffuse branching (Fig. 4D). A common set of architectures involves a monopodial trunk with rhythmic branching and plagiotropic growth (Massart’s model; Fig. 4C); continuous/diffuse branching and plagiotropic branches (Roux’s model; Fig. 4E); rhythmic branching and orthotropic branches (Rauh’s model; Fig. 5A); or continuous/diffuse branching and orthotropic branches (Attims’ model; Fig. 5B). Bell’s model lumps together all species with

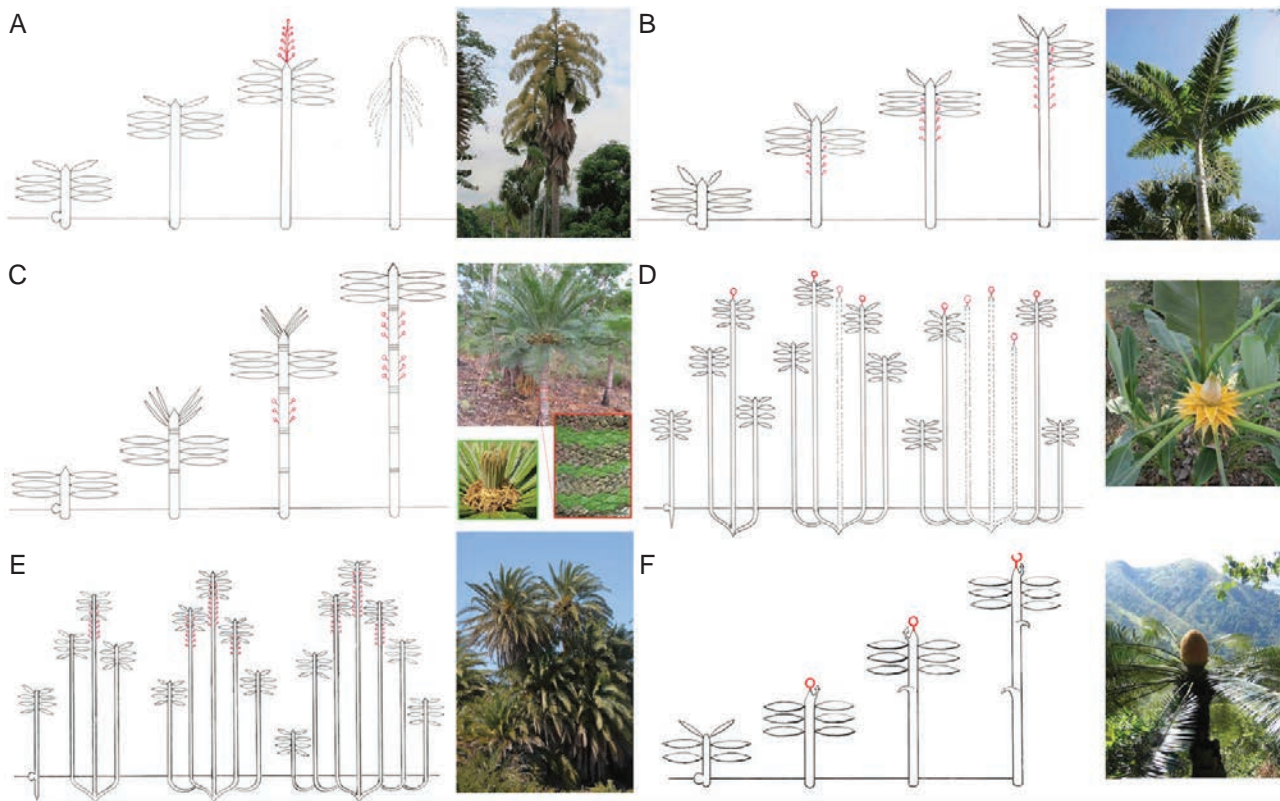


FIG. 2. Architectural models 1. (A) Holtum's model, exemplified by *Corypha umbraculifera*. (B) Corner's model, form with continuous growth, as found in most palm species (here *Veitchia arecina*). (C) Corner's model, form with rhythmic growth, here exemplified by a female *Cycas armstrongii*. (D) Tomlinson's model, form with a terminal inflorescence, here exemplified by *Musella lasiocarpa*. (E) Tomlinson's model, form with a lateral (axillary) inflorescence, here exemplified by *Phoenix theophrastii*. (F) Chamberlain's model, here exemplified by a male *Cycas pectinata*. Photo credit: Wikipedia, except (B), (D) and (E): G. Chomicki. All architectural models were drawn by Yasumin Sophia Lerner.

monopodial (and plagiotropic) stolons or creeping axes, independent of the architecture of the aerial part (Fig. 4F). The final three models involve a mix of orthotropic growth modules with a transition to plagiotropy (Mangenot's model; Fig. 5C), orthotropic growth and bending by gravity (Champagnat's model; Fig. 5D) or mixed orthotropic/plagiotropic axes forming either a monopodium or a sympodium (Troll's model; Fig. 5E, F). Troll's model is the most common in woody flowering plants (Hallé et al., 1978).

THE ORIGIN OF PLANT ARCHITECTURES: TIMELINE FROM THE FOSSIL RECORD

The unbranched, determinate sporophytes of bryophyte-like plants must have given rise to the complex sporophytes of vascular plants (Bower, 1908), and two alternative hypotheses for how this occurred have been formulated: the homologous and the antithetic hypothesis (Pringsheim, 1878; Bower, 1908). The former posits that land plants evolved from ancestors with morphologically equivalent sporophytes and gametophytes, as found in certain algal lineages, and thus that the land plant sporophyte is a physiognomic modification of a pre-existing algal sporophyte (Pringsheim, 1878). In contrast, the antithetic hypothesis postulates that the sporophyte generation arose *de novo* by the intercalation of mitotic divisions after the formation of the zygote by delaying meiosis (Bower, 1908).

Phylogenetic work identified the Charales (Karol et al., 2001), the Coleochaetales (Finet et al., 2010) or, more recently, the Zygnematophyceae (Timme et al., 2012; Wickett et al., 2014) as the green algal sister group of land plants (embryophytes). Because Charales, Coleochaetales, Zygnematophyceae and bryophytes all have gametophyte-dominant life cycles, the homologous theory currently has little support. Molecular work on the moss *Physcomitrella patens* moreover shows that the bryophyte sporophyte has an embryonic vegetative phase (Sakakibara et al., 2008; Mosquna et al., 2009; Okano et al., 2009), suggesting that the first branching event of the sporophyte involved the co-option of this vegetative phase (the so-called 'apical growth hypothesis'), rather than the vegetative phase evolving *de novo* (sterilization or intercalation hypotheses) (reviewed by Tomescu et al., 2014).

The process of dichotomous branching involves the bifurcation of an apical meristem into two meristems, either unequal (Fig. 6A–E) or equal (Fig. 6F–H). Kenrick and Crane (1997) coined the term polysporangiophytes to emphasize that a branched sporophyte (the only way to have several sporangia per sporophyte) is a synapomorphy of all post-bryophyte plants. Dichotomous branching of non-vascular early polysporangiophytes (protracheophytes), such as *Aglaophyton major*, indicates that branching of the sporophyte evolved before its vascularization (Kenrick and Crane, 2001), as early as the Lower Devonian (410 Ma).

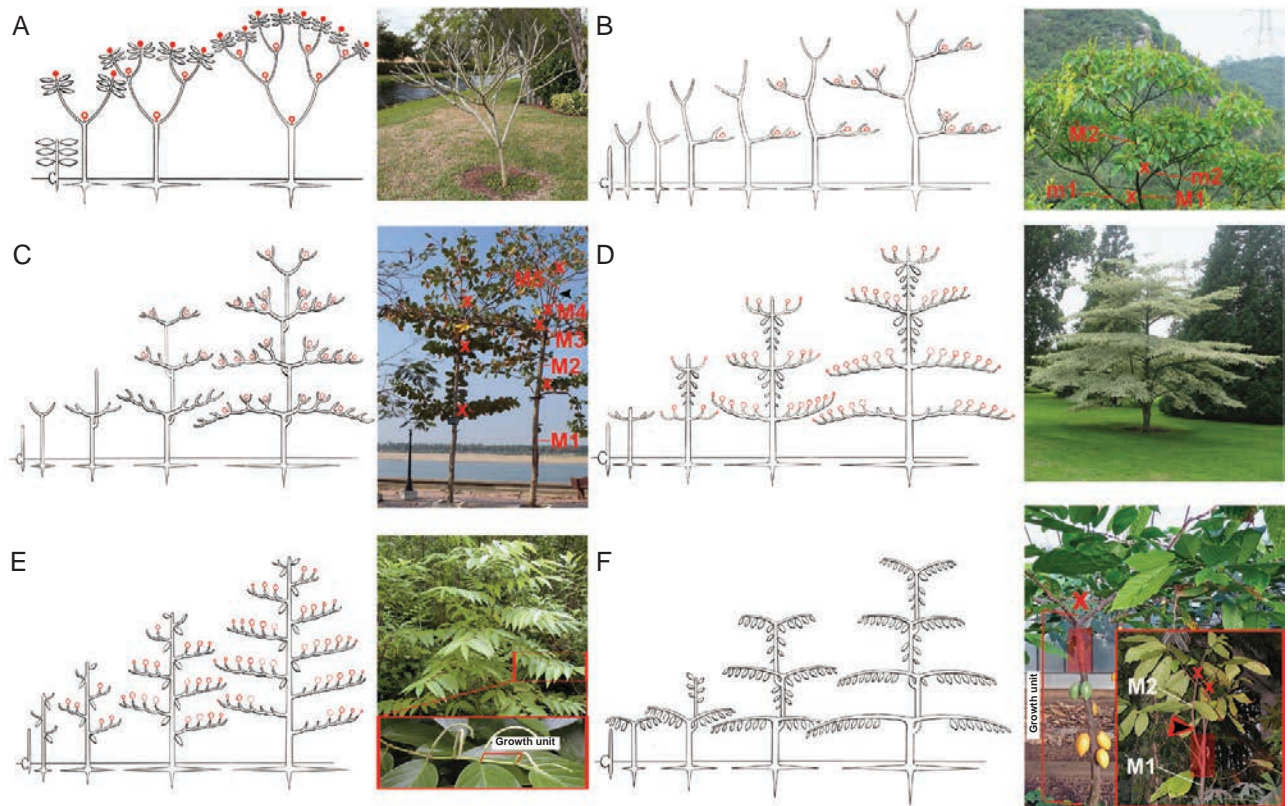


FIG. 3. Architectural models 2. (A) Leeuwenberg's model, exemplified in *Plumeria rubra*. (B) Koriba's model, exemplified in *Sapium discolor*. (C) Prévost model, here exemplified in *Alstonia scholaris*. (D) Fagerlind's model, here exemplified in *Cornus alternifolia*. (E) Petit's model, here exemplified by *Piper aduncum*. (F) Nozeran's model, here exemplified by *Theobroma cacao*. Photo credit: Wikipedia, except (A): G. Chomicki. All architectural models were drawn by Yasumin Sophia Lerner.

Evolution of a diversity of dichotomous architectures in land plants

The definition of architectural models (Hallé and Oldeman, 1970; Hallé et al., 1978; Figs 1–5) and the criteria for architectural analysis and description (Barthélémy and Caraglio, 2007) have been developed based on classical seed plant morphology. As a result, all architectures involving dichotomous branching – a mechanism that is exceedingly rare in extant seed plants – were placed in a single model (Schoute's model; not illustrated). This decision has for long hampered the recognition and understanding of several truly distinct early-evolving architectures. This section (1) demonstrates the diversity of dichotomous architectures in fossil plants and proposes 12 new architectural models (Fig. 7) for these plants; (2) highlights the evolution of architectural traits on a phylogeny of early (fossil) land plants (Fig. 8); and (3) provides a timeline for their evolution (Fig. 9). Because deciphering plant architectures based on fossil evidence is a challenging task, emphasis has been placed on the best-known plant reconstructions, implying that the approach is non-exhaustive. A list of the reconstructed fossils and their architectural model is provided in Table 1.

Earliest branched plants: isotomy, basal anisotomy and mixed axes

The evolution of dichotomous branching in the sporophyte of protracheophytes was the first major event in the evolution

of sporophyte architectures. The earliest branched sporophytes were those of non-vascular polysporangiophytes (protracheophytes), probably a paraphyletic group (Kenrick and Crane, 1997) of small plants, never exceeding 10 cm in height (Stewart and Rothwell, 1993; Taylor et al., 2009). The sporophytes of the protracheophyte *Aglaophyton major*, and probably also the sporophytes of rhyniophytes and zosterophylls, were apparently independent of the gametophyte (Taylor et al., 2005, 2009), but measurements suggest that the sporophyte of *Cooksonia* may have been physiologically dependent on the gametophyte (Boyce, 2008), which is consistent with the discovery of *Cooksonia* sporophytes attached to a potential gametophytic structure (Gerrienne et al., 2006).

Two major architectures can be recognized. The first major growth form found in these early land plants involves an orthotropic, isotomously branching axis with terminal reproductive structures. This type of growth is found in many *Cooksonia* species (e.g. *C. paranensis*, *C. hemispherica*, *C. caledonica* and *C. pertonii*; Edwards and Rodgeron, 1979; Gerrienne et al., 2001, 2006; Genez and Gerrienne, 2001; Taylor et al., 2009). We here term this architecture Edwards' model (Fig. 7A) in honour of the British paleobotanist Dianne Edwards' and her landmark work on *Cooksonia* (Edwards and Davies, 1976; Edwards and Rodgeron, 1979; Edwards and Feehan, 1980; Edwards et al., 1992, 1995). The second involves a prostrate, potentially plagiotropic indeterminate rhizomatous stem that at each dichotomy produces an orthotropic, determinate stem that generally branches a few more

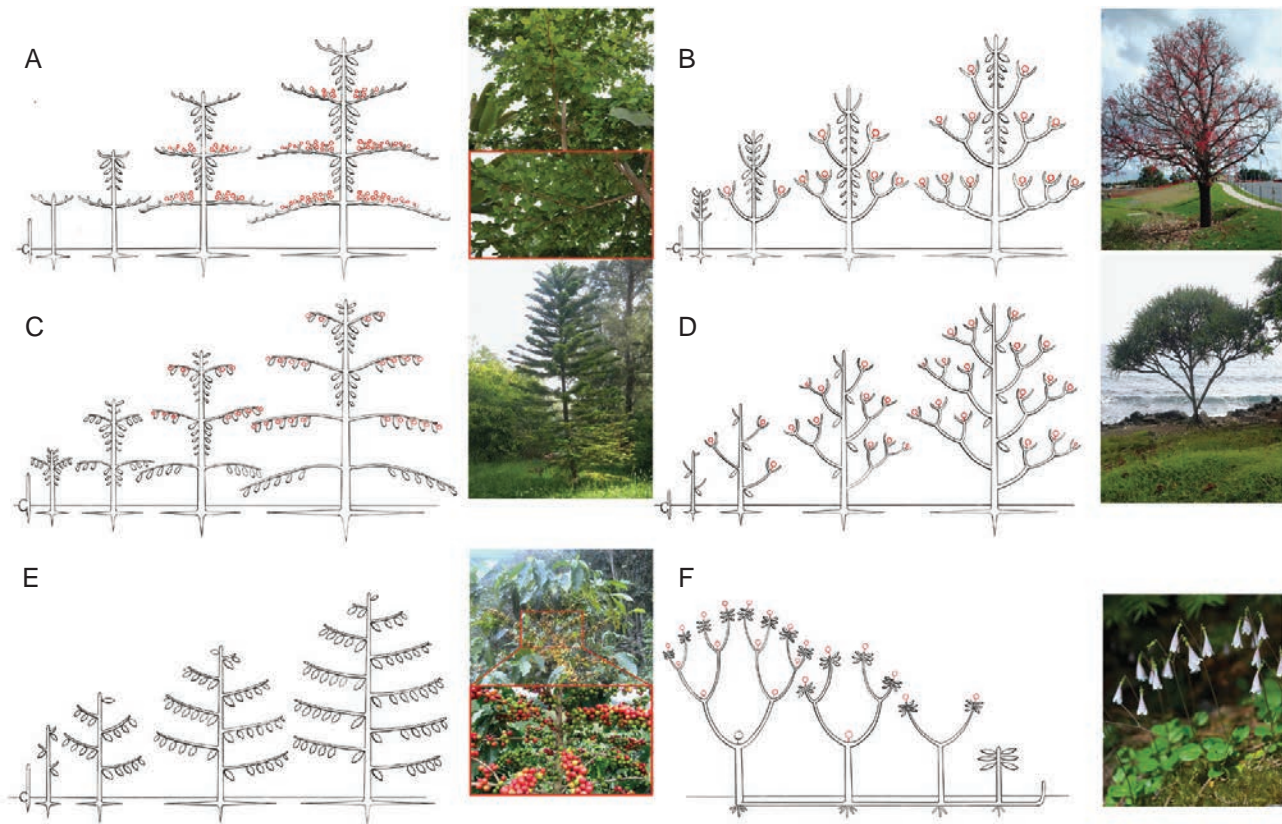


FIG. 4. Architectural models 3. (A) Aubréville's model, here exemplified by *Terminalia catappa*. (B) Scaronne's model, here exemplified by *Brachychiton acerifolius*. (C) Massart's model, here exemplified by *Araucaria heterophylla*. (D) Stone's model, here exemplified by *Pandanus tectorius*. (E) Roux's model, here exemplified by *Coffea arabica*. (F) Bell's model, here exemplified by *Linnaea borealis*. This model is centred on the monopodial plagiotropic shoot system, and the aerial part can take various architectures in different species (Hallé, 2004). Photo credit: Wikipedia, except (A) and (C): G. Chomicki. All architectural models were drawn by Yasumin Sophia Lerner.

times before producing terminal reproductive structures (sporangia in this case). This results in mixed axes, with a prostrate (plagiotropic), indeterminate part and an orthotropic, determinate part. This growth form is characteristic of several Early Devonian plants from the Rhynie chert (*Aglaophyton major*, *Rhynia gwyne-vaughanii* and *Horneophyton ligneri*), although in *H. ligneri*, the prostrate stems are short and thick (termed corms). We here term this type of growth Kidston's model (Fig. 7B) in honour of the Scottish paleobotanist Robert Kidston, for his landmark work on the Rhynie chert flora (Kidston and Lang, 1920a, b, 1921a, b). *Rhynia gwyne-vaughanii* has in addition small projections on the aerial stems, which are interpreted as adventitious branches (Edwards, 1980; Kenrick and Crane, 1997). Dichotomy was unequal (anisotomous) on the prostrate stem (at each meristem division, one shoot generating the upper part and another the prostrate stem), but equal (isotomous) on the aerial stem. Whereas there are no indeterminate axes in Edwards' model and the sporophyte is therefore short lived, it is long lived in Kidston's model and has the potential to create large colonies (Taylor et al., 2009).

Architectural experimentation in the zosterophylls

Among the earliest land plants, the zosterophylls present high levels of taxon diversity and morphological disparity (Kenrick

and Crane, 1997; Cascales-Miñana and Meyer-Berthaud, 2015). All members of this group show a mixture of prostrate and erect axes, with sporangia borne laterally (Jensen and Gensel, 2013). Another interesting feature of the zosterophylls are so-called 'K' branches, with unequal branching of the prostrate axis leading to both erect and root-like axes (Kenrick and Crane, 1997). Some species, such as *Discalis longistipa* and *Zosterophyllum myrtonianum*, had a prostrate axis that dichotomized unequally, as in rhyniophytes, but remained unbranched or branched rarely (for a contrasting interpretation, see Niklas and Banks, 1990). The distal end of the unbranched erect shoot sometimes terminates in a circinate hook. We here refer to this architecture as Kenrick's model (Fig. 7C) in honour of the British paleobotanist Paul Kenrick, whose work has contributed greatly to the understanding of zosterophylls (Kenrick and Edwards, 1988a, b; Kenrick and Crane, 1997). A variation of Kenrick's model is found in *Zosterophyllum shengfengense*, in which the rhizomatous stems branch profusely with very limited elongation, producing determinate orthotropic shoots in a rosette-like configuration, and with root-like axes (Hao et al., 2010).

The members of the zosterophyll order Sawdoniales sensu Kenrick and Crane (1997) are characterized by a more complex aerial system involving both isotomous and pseudomonopodial branching, with a planar disposition of the branches (Kenrick and Crane, 1997a; Jensen and Gensel, 2013). Moreover, the

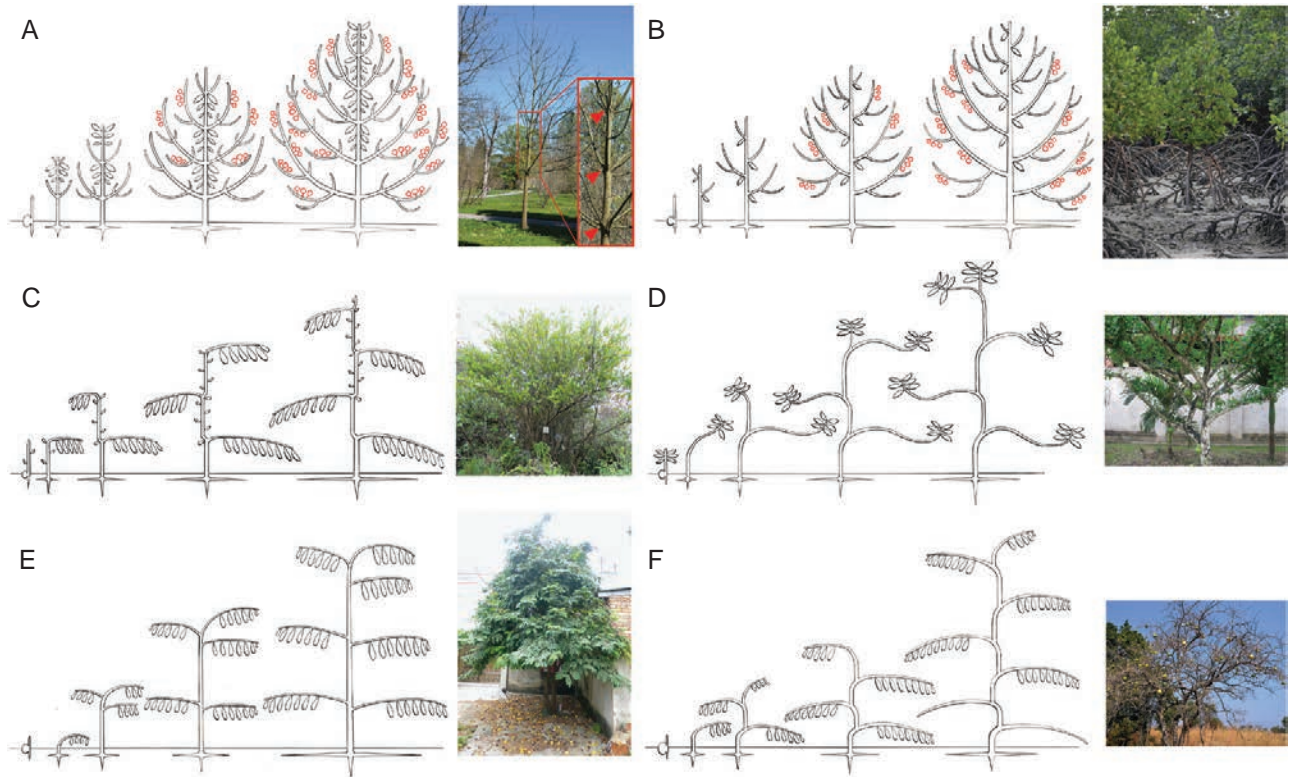


Fig. 5. Architectural models 4. (A) Rauh's model, here exemplified by *Rhus vernicifera*. (B) Attims's model, here exemplified by *Rhizophora mangle*. (C) Mangenot's model, here exemplified by *Eurya japonica*. (D) Champagnat's model, here exemplified by *Crescentia cujete*. (E) Troll's model, monopodial form, here exemplified by *Averrhoa carambola*. (F) Troll's model, sympodial form, here exemplified by *Strychnos spinosa*. Photo credit: Wikipedia, except (A) and (B): G. Chomicki. All architectural models were drawn by Yasumin Sophia Lerner.

Sawdoniales are characterized by so-called subordinate branches (or axillary tubercles), the developmental origin of which is unclear. We refer to the architecture of the Sawdoniales as Hueber's model (Fig. 7D), in honor of Francis M. Hueber, who first identified *Sawdonia* as a unique plant (Hueber, 1971). Hueber's model differs from Kidston's model by the presence of both unequal and equal branching in the aerial axes and in the lateral position of the sporangia. In practice, it may be difficult to distinguish between both models, and variation may be present in some species, meaning that only species with many well-conserved shoot systems can be classified as having only equal dichotomy (Kidston's model) or both equal and unequal (Hueber's model). Outside of the Sawdoniales, a variation of the Hueber model can be found in *Nothia aphylla* from the Rhynie Chert (Kenrick and Crane, 1997; Kerp et al., 2001). In this plant, the aerial branches, which were probably short lived (Kerp et al., 2001; Daviero-Gomez et al., 2005), did not branch in a planar way. The discovery of the zosterophyll genus *Forania* from the Early Devonian of Canada (Jensen and Gensel, 2013), with 20 % of the branching events being isotomous and the remaining 80 % being anisotomous, provides a quantitative analysis of Hueber's model.

Increasing complexity of embryophyte architecture

The sporophytes of protracheophytes, *Cooksonia*, rhyniophytes and some zosterophylls were small (5–15 cm), possibly

due to hydraulic and mechanical constraints (Boyce, 2008). Although unequal dichotomies are present on the prostrate stem of rhyniophytes, they are absent on their orthotropic (aerial) part. Aerial stem anisotomy evolved independently in several lineages, including trimerophytes (e.g. *Renalia hueberi*) and in zosterophylls (Fig. 8). In *R. hueberi*, there are apparently no prostrate axes, and thus the architecture consists of a single orthotropic axis that dichotomizes unequally to produce lateral branches, with the latter then dichotomizing equally (Gensel, 1976). We term this architecture Gensel's model (Fig. 7E) in honour of Patricia G. Gensel, who described the genus *Renalia* and who contributed greatly to our knowledge of early land plants. Another architectural form found in trimerophytes resembles Gensel's model, but involves a prostrate axis, as seen in *Psilophyton crenulatum* (Doran, 1980). We term this architecture Dawson's model (Fig. 7F) in honour of John W. Dawson, who discovered the first trimerophyte species *Psilophyton princeps* and initially thought it possessed prostrate stems (Dawson, 1859) – an interpretation since challenged (Hueber and Banks, 1967). It is difficult to attribute all trimerophyte species to either Gensel's or Dawson's models because few macrofossils present the required connections among branches. The presumed absence of truly indeterminate meristems, judging from the apparent termination of all apices in sporangia or determinate vegetative structures, suggests that the trimerophyte architecture was roughly equivalent to the panicle inflorescence of a flowering plant. The greater

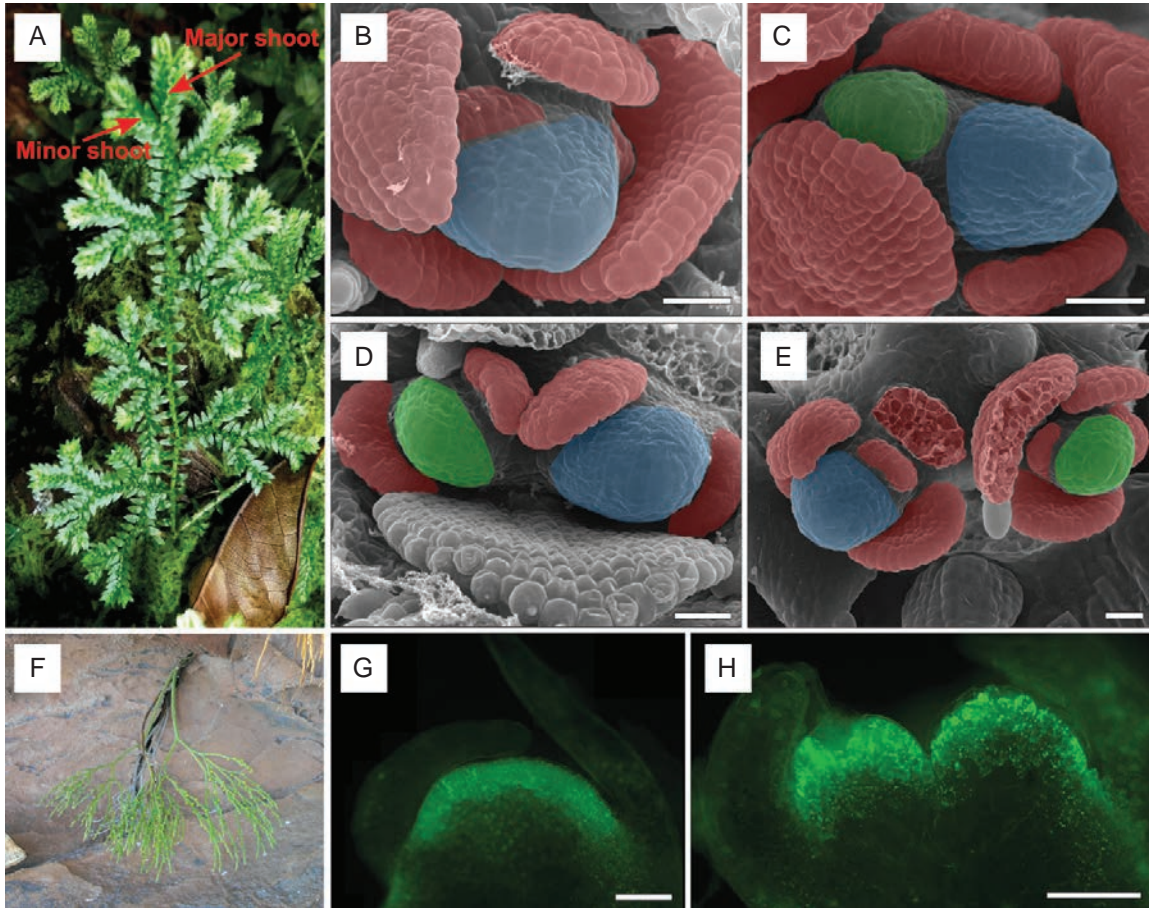


FIG. 6. Types of dichotomic branching. (A–E) Anisotomous (unequal) dichotomy in *Selaginella kraussiana*. (A) Growth habit of *Selaginella kraussiana*, showing the major and minor shoots. (B–E) Scanning electron micrographs showing the steps of unequal dichotomy in *S. kraussiana*. Blue shows the apical meristem of a major shoot, and green the apical meristem of a minor shoot. (F–H) Isotomous (equal) dichotomy in *Psilotum nudum*. (F) Growth habit of *Psilotum nudum*, showing the system of equally branching shoots. (G–H) Fluorescence microscopy images showing the steps of equal dichotomy in *P. nudum*, stained using an aqueous solution of diphenyl boric acid-2-aminoethyl ester (DPBA) (Sheahan and Rechnitz, 1992); green fluorescence shows flavonoid-enhanced fluorescence after DPBA complexation. Photo credit: G. Chomicki except A and F: Wikipedia.

height of trimerophytes compared with the earlier groups, with some taxa such as *Pertica* exceeding 1 m (Kasper and Andrew, 1972), suggests that unequal dichotomy, wherein one of the sister shoots overtops the other to yield seemingly monopodial growth (pseudomonopodial), played an important role in plant size increase towards arborescence.

Lycopsids: lateral sporangia and indeterminacy

The lycopsids are an important group of free-sporing vascular plants that arose from or within zosterophylls (Bateman et al., 1992; Gensel, 1992; Bateman, 1994; Kenrick and Crane, 1997). Lycopsids are remarkable in their diversity of growth forms, ranging from herbaceous to (extinct) arborescent trees of >40 m in height; the latter had a unique photosynthetic pathway (Green, 2010). The Early Devonian Rhynie Chert fossil *Asteroxylon mackei* is generally regarded as one of the earliest unambiguous fossils of the Lycopsida (Kenrick and Crane, 1997); it is the tallest and most complex of the Rhynie Chert plants (Taylor et al., 2009). Its architecture consisted of a

mixed rhizomatous axis from which pseudomonopodial aerial shoots emerged, with all sporangia produced laterally and thus indeterminate growth. We term this architecture Lyon's model (Fig. 7G) in honour of Alexander G. Lyon, who discovered the lateral position of sporangia on *Asteroxylon* (Lyon, 1964), initially described as terminal by Kidston and Lang (1920b). In non-lycopsid species with terminal sporangia, the distinction between Gensel's and Lyon's model can be difficult, and a continuum between these models is likely. *Drepanophycus*, another early lycopsid, differs in that the prostrate part is a true shoot, not a root-like organ. *Drepanophycus* had isotomous or anisotomous branching on its aerial part forming a rhizome (Li et al., 2000), placing it in Huebert's model. The recently described early lycopsid *Sengelia radicans* was a non-self-supporting plant that branched dichotomously via K-branching type and isotomous branching (Matsunaga and Tomescu, 2017). Its architecture differed from Huebert's model in that it was entirely creeping. We classify its growth form as Matsunaga's model (Fig. 7H), in honor of Kelly Matsunaga who provided a very detailed whole-plant concept for *S. radicans*. This architecture may also have occurred in some zosterophylls.

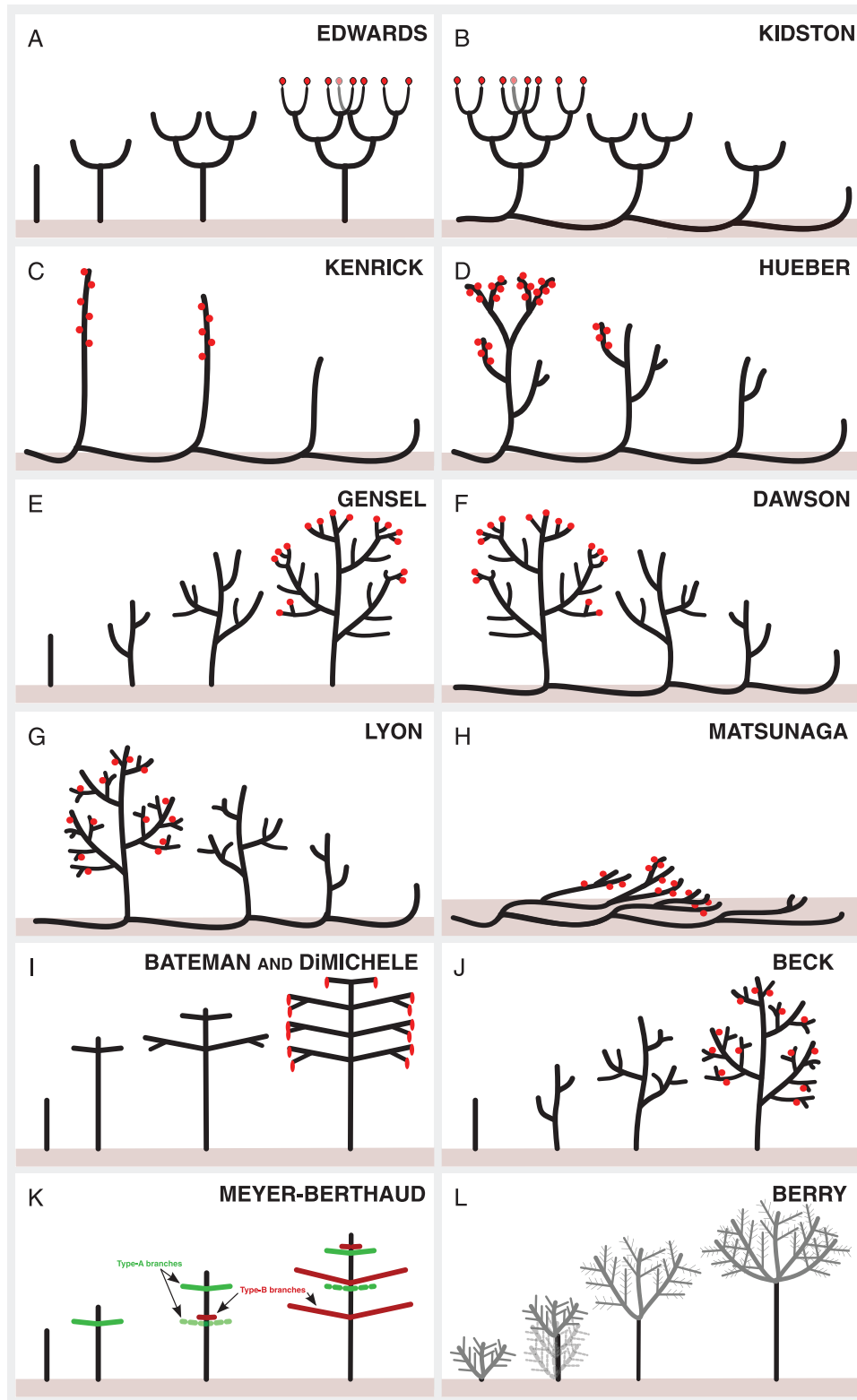


FIG. 7. Twelve new architectural models for dichotomously branched fossil plants. (A) Edwards' model, highlighted in *Cooksonia* species from the Silurian. (B) Kidston's model, featured in several plants of the Rhynie chert such as *Aglaophyton major*. (C) Kenrick's model featured in many zosterophylls, such as *Zosterophyllum myretonianum*. (D) Hueber's model, found in *Sawdonia* for instance. (E) Gensel's model, as in *Renalia hueberi*. (F) Dawson's model occurring in various trimerophyte species such as *Psilophyton crenulatum*. (G) Lyon's model, found in the Rhynie chert lycopsid *Asteroxylon mackei*. (H) Bateman and DiMichele's model, found in several arborescent lycopsids, notably in *Synchysidendron*. (I) Beck's model, found in many aneurophytlean progymnosperms. (J) Matsunaga's model, found in the early lycopsid *Sengalia radicans*. (K) Meyer-Berthaud's model, unique to *Archeopteris*. (L) Berry's model, found in cladoxylophytes such as the 'Gilboa tree' (*Eospermatopteris*).

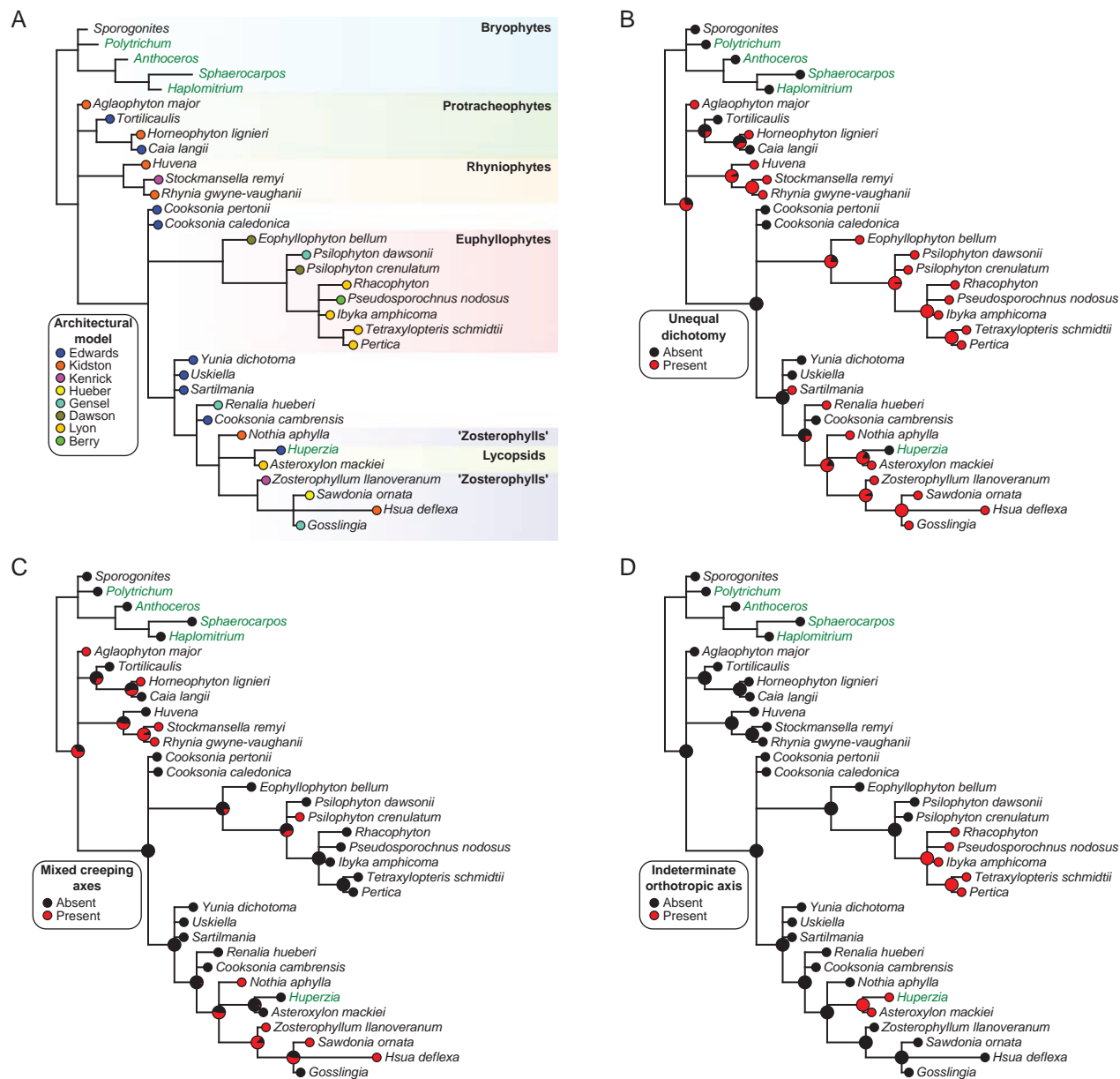


Fig. 8. The evolution of fossil architectures. Architectural traits mapped on a phylogeny inferred from a fossil matrix (Kenrick and Crane, 1997, p. 367), reanalysed using Bayesian inference (see Supplementary Data Materials and Methods). (A) Architectural models mapped on the tree. Ancestral state reconstructions for the occurrence of unequal dichotomy (B), mixed creeping axes (C) and indeterminate orthotropic axes (D).

The arborescent *Lepidodendrales* had a unique architecture that in some aspects of development was analogous to that of palms, especially in the establishment phase, which resembled palms' 'establishment growth' (Bateman, 1994). A distinctive feature of *Lepidodendrales* is the stigmarian shoot-like root system in which the emerged 'roots' were probably photosynthetic (Phillips and DiMichele, 1992). The trunk grew quickly from a single large apical meristem, and trees were monocarpic with all axes being determinate, although the growth rate may have been overestimated (Boyce and DiMichele, 2016). Dichotomy generally occurred in the later phase of development and was unequal, leading to a pseudomonopodial, but poorly branched tree with lateral plagiotropic, deciduous branches, as in

Diaphorodendron, *Synchysidendron* and *Sigillaria* (DiMichele and Bateman, 1992; DiMichele et al., 2013). We term this architecture Bateman and DiMichele's model (Fig. 7I) in honour of Richard M. Bateman and William A. DiMichele, who have contributed extensively to the knowledge of *Lepidodendrales*. Variants exist where the lateral branches are unbranched, as in *Sigillaria*, or where the lateral branches are branched at least once, as in *Diaphorodendron*. Extant lycopsids still exhibit a variety of branching patterns, including many that involve a pseudomonopodial plagiotropic rhizome and diverse orthotropic axes from unbranched–determinate to complex pseudomonopodially branched structures (Øllgaard, 1979), and require further scrutiny.

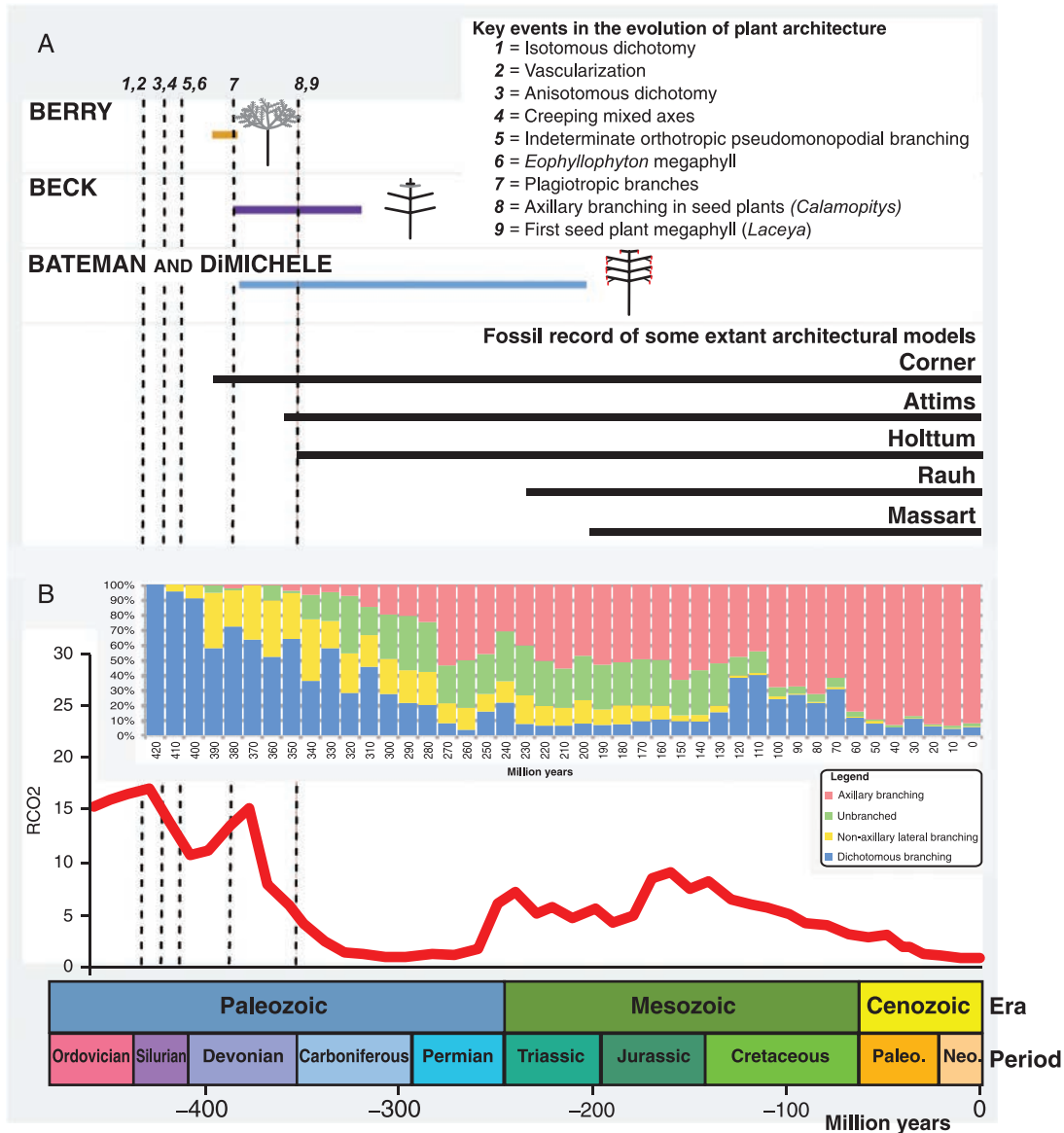


FIG. 9. Timeline of plant architectures and branching mechanisms through time. (A) Timeline for architectural models for which we have sufficient data, including three models that are extinct (for the remaining models for dichotomously-branched plants, further data are needed to assess their geologic time range, and further models may still be present in lycopsids or ferns). Five (out of 23) models for axillary-branched plants are shown, namely Corner's model found in Devonian arborescent ferns and seed ferns; Attim's model found in Cordaitales mangrove-dwelling species, Holttum's model in the lycopsid *Pleuromeia*, and Rauh and Massart's models in conifers. The age range of fossils representing the new dichotomous models or extant architectural models was taken from the paleobiology database (<http://fossilworks.org>). The CO₂ curve was adapted from Berner and Kothavala (2001). (B) Frequency of branching mechanisms through time estimated from 58 927 land plant fossils was taken from the paleobiology database (<https://paleobiodb.org>); see Supplementary Data Materials and Methods for more details.

The evolution of trees with long-lived plagiotropic branches

In modern spermatophyte floras, trees with plagiotropic branches are common. The simplest (monopodial) plagiotropic trees exhibit Massart's or Roux's models, depending on whether branching is continuous or rhythmic (Fig. 4C, E). The first large trees with plagiotropic branches belong to the progymnosperm genus *Archaeopteris*. The discovery that *Archaeopteris* foliage and *Callixylon* wood represent the same plant led to the establishment of the group known as progymnosperms (Beck, 1960a, b). Progymnosperms are characterized by gymnospermous secondary wood and pteridophytic free-sporing reproduction (Beck, 1960b; Beck and

Wight, 1988). Five main groups of progymnosperms are recognized: the leafless Aneurophytales, the megaphyllous Archeopteridales, the Protopytales, the Cecropsidales and the Noeggerathiales (Wang et al., 2017). We focus here specifically on the two first groups, as they are architecturally the best known. Both Aneurophytales and Archeopteridales have an orthotropic first axis (trunk) as part of pseudomonopodial (dichotomous) branching systems. An important architectural distinction between the two groups is that the branches are plagiotropic in at least some species of *Archaeopteris* whereas the whole shoot system is fully orthotropic in aneurophytes (Kenrick and Crane, 1997; Fairon-Demaret and Leponce,

TABLE 1. Examples for the 12 architectural models for dichotomously branching fossil plants proposed in this study

Model	Examples	References
Edwards	<i>Cooksonia banksii</i> , <i>C. caledonica</i> , <i>C. cambrensis</i> , <i>C. crassiparietilis</i> , <i>C. pertonii</i> , <i>C. hemisphaerica</i> , <i>C. paranensis</i> , <i>C. bohemica</i> , <i>Steganotheca striata</i> , <i>Yumia dichotoma</i> , <i>Tortilicaulis transwalliensis</i> , <i>T. offaeus</i> , <i>Caia langii</i>	Edwards (1970); Edwards and Rodgeron (1979); Edwards and Feehan (1980); Fanning <i>et al.</i> (1990); Kenrick and Crane (1997); Gerrienne <i>et al.</i> (2001); Habgood <i>et al.</i> (2002); Gonez and Gerrienne (2010)
Kidston	<i>Horneophyton ligneri</i> , <i>Aglaophyton major</i> , <i>Rhynia gwynne-vaughanii</i> , <i>Huvenia kleui</i> , <i>Huvenia elongata</i> , <i>Hsia deflexa</i> , <i>Ventarura lyonii</i>	Kenrick and Crane (1997); Schultka and Hass (1997); Powell <i>et al.</i> (1999); Wang <i>et al.</i> (2003)
Kenrick	<i>Zosterophyllum myretonianum</i> , <i>Z. shengfengense</i> , <i>Z. xishanense</i> , <i>Z. qujingense</i> , <i>Stockmansella langii</i> , <i>S. remyi</i> , <i>Oxroadia gracilis</i>	Kenrick and Crane (1997); Schultka and Hass (1997); Hao <i>et al.</i> (2007, 2010)
Hueber	<i>Sawdonia ornata</i> , <i>Nothia aphylla</i> , <i>Forania plegiospinosa</i> , <i>Drepanophycus spinaeformis</i>	Kenrick and Crane (1997); Li <i>et al.</i> (2000); Jensen and Gensel (2013)
Gensel	<i>Aarabia brevicaulis</i> , <i>Psilophyton dawsonii</i>	Meyer-Berthaud and Gerrienne (2001); Banks (1980)
Dawson	<i>Eophyllophyton bellum</i> , <i>Psilophyton crenulatum</i>	Hao and Beck (1993); Doran (1980)
Lyon	<i>Asteroxylon mackiei</i>	Lyon (1964)
Matsunaga	<i>Sengelia radicans</i>	Matsunaga and Tomescu (2017)
Beck	<i>Ibyka amphikoma</i> , <i>Tetraxylopteris schmidtii</i> , <i>T. reposana</i> , <i>Pertica quadrifaria</i>	Beck (1957); Hammond and Berry (2005)
Bateman and DiMichele	<i>Synchysidendron</i> , <i>Diaphorodendron</i> , <i>Paralycopodites</i>	Bateman (1994); DiMichele <i>et al.</i> (2013)
Meyer-Berthaud	<i>Archaeopteris</i>	Meyer-Berthaud <i>et al.</i> (2000)
Berry	<i>Eospermatopteris</i> , <i>Pseudosporochnus nodosus</i> , <i>Calamophyton primaevum</i> , <i>Lorophyton goense</i>	Fairon-Demaret and Li (1993); Berry (2000); Berry and Fairon-Demaret (2002); Giesen and Berry (2013)

2001). The aneurophytalean genus *Tetraxylopteris* is characterized by pseudomonopodial branching with a decussate ‘caulotaxy’ of the branches along the stem (Scheckler and Banks, 1971; Beck and Wight, 1988). In contrast, the genus *Triloboxylon* is characterized by helically arranged branches. Some *Rellimia* specimens may have branched by trifurcation or trichotomy (Matten and Schweitzer, 1982). Although a wide range of variation is evident in the architecture of aneurophytalean progymnosperms (see Kenrick and Crane, 1997), we decided to assign them all to Beck’s model, in honor of Charles Beck’s landmark work on the progymnosperms (Fig. 7J). This model is focused on the pseudomonopodial branching, indeterminacy of the first axis and generally the main branches, and orthotropic branches. Although branching in *Archeopteris* was

long thought to be pseudomonopodial (Beck and Wight, 1988; Trivett, 1993), investigation of a young *Archaeopteris erianum* revealed two types of branches (Meyer-Berthaud *et al.*, 2000). The first type (type A) originates in a spiral sequence from presumed pseudomonopodial branching and is thought to be short lived, judging from xylar anatomy. The second type (type B) is thought to be long lived and does not originate in the same spiral sequence as type A branches. This would imply the existence of both dichotomous and lateral branching along the trunk of *Archeopteris*. The integration of the findings by Meyer-Berthaud *et al.* (2000) with the earlier detailed analysis by Trivett (1993) allows us to create Meyer-Berthaud’s model, in honour of the French paleobotanist Brigitte Meyer-Berthaud (Fig. 7K).

Key to the 12 new models for dichotomously branched plants

1a. Basal branching present	2
2a. Prostrate axis leading to aerial axis	3
2b. Prostrate axis producing an exclusively prostrate shoot system	Matsunaga’s model
3a. Aerial axis unbranched	Kenrick’s model
3b. Aerial axis branched	4
4a. Branching of the aerial axes isotomous and anisotomous	Hueber’s model
4b. Branching of the aerial axes isotomous or anisotomous (pseudomonopodial)	5
5a. Branching of the aerial axes isotomous	Kidston’s model
5b. Branching of the aerial axes pseudomonopodial	6
6a. Pseudomonopodial shoot system with lateral sporangia and undeterminate apical meristems	Lyon’s model
6b. Pseudomonopodial shoot system with terminal sporangia and determinate apical meristems	Dawson’s model
7	7
1b. Basal branching absent	Edwards’ model
7a. Branching isotomous	8
7b. Branching non-isotomous	Gensel’s model
8a. All apical meristems determinate, leading to a determinate architecture	9
8b. Apical meristems of the main axis(es) indeterminate, leading to an indeterminate architecture	10
9a. Branches orthotropic	11
10a. First axis (trunk) long lived, but branches shed and clustered at the distal end	Berry’s model
10b. First axis (trunk) long-lived, branches long or short-lived and regularly distributed along the trunk	Beck’s model
9b. Branches plagiotropic	11
11a. Branching pseudomonopodial and not lateral	Bateman and DiMichele’s model
11b. Branching pseudomonopodial and lateral	Meyer-Berthaud’s model

Devonian fern-like plants

Devonian fern-like plants, grouped as cladoxyloids, are a heterogeneous, probably polyphyletic group of free-sporing plants that are thought to include the ancestors of the Filicales. They included tall plants (3–8 m) that formed forests (Stein *et al.*, 2007, 2012), with important genera being *Pseudosporochnus* and *Wattieza*. Both were characterized by an orthotropic, indeterminate trunk branching pseudomonopodially at the distal end (Berry, 2000; Berry and Fairon-Demaret, 2002). The leafless branches clustered at the distal end of the trunk were shed (cladotopsis). Branches were tridimensional, apparently orthotropic, much branched and had pseudomonopodial growth. The first-order branch showed trifurcations that could either represent trichotomies or two successive dichotomies. We term this architecture Berry's model (Fig. 7L) in honour of the British paleobotanist Christopher M. Berry who contributed extensively to the morphological and architectural understanding of cladoxyloids.

Various branching mechanisms in ferns and the unique sphenopsids

The leptosporangiate ferns show a large diversity of branching mechanisms with both isotomous and anisotomous dichotomy, non-axillary lateral branching (as in many extant ferns) and axillary branching (reviewed by Galtier, 1999). The few studies of extant fern architecture suggest that there is an understudied diversity of rhizomatous growth (e.g. Mueller, 1982; Gay, 1991), as suggested for other groups (Chomicki, 2013). Horsetails, both fossil and extant, typically have a rhizome from which emerge orthotropic axes with verticillate branches. This mode of branching is unique and results from endogenous bud formation (Hofmeister, 1862; Stützel and Jaedicke, 2000), similar to lateral roots in seed plants (for reproductive development in *Equisetum*, see also Tomescu *et al.*, 2017). Several *Coenopteris* fossil ferns (e.g. *Ankryopteris* species; Phillips, 1974) evolved axillary branching independently from seed plants. As for the extant lycopsids, the architecture of extant horsetails and ferns is poorly known.

Gymnosperms: evolution of megaphylls and axillary branching, and loss of dichotomous branching

Dichotomous branching is rare in shoot systems of extant gymnosperms, being restricted to cycads (anatomically demonstrated for *Zamia*; Stevenson, 1988). Early seed ferns, including Elkinsiaceae, Calamopityaceae, Buteoxylaceae and Lyginopteridaceae from the Upper Devonian–Lower Carboniferous, are often monoaxial (Galtier, 1999). Branched seed ferns first occurred in the Lower Carboniferous. They had lateral branching, with variable branch position relative to the leaf initially, and rarely axillary (Brenchley, 1913; Delevoryas and Morgan, 1954; Delevoryas, 1955; Long, 1979; Galtier and Scott, 1990; Galtier, 1999). As far as current research indicates, stem dichotomy is absent at least in the early lineages of seed ferns. Megaphylls (true leaves) evolved at least

four times in plants, namely in archaeopteridalean progymnosperms, sphenopsids, ferns and seed plants (Boyce and Knoll, 2002) and possibly up to nine times (Tomescu, 2009). The fossil record provides evidence for a transformational series from a lateral shoot system to megaphylls via overtopping, planation and webbing of an initially simple shoot system such as that of rhyniophytes (telome theory: Zimmermann, 1938, 1952; Kenrick, 2002). Because the closest relatives of the seed plants may be aneurophytlean progymnosperms, it has been suggested that the seed plant megaphyll is the result of the transformation of aneurophytlean lateral branches (Stewart and Rothwell, 1993; Kenrick and Crane, 1997; Galtier, 2010). Galtier (2010, p. 652) adds that 'only very small changes in symmetry and anatomy would be necessary to modify a branch trace of the type found in *Proteokalon* [Aneurophyte] to a petiole trace of the type found in *Laceyia* [pteridosperm]'. In this way, dichotomously branched lateral shoot systems were recruited (and presumably their genetic pathways repurposed; see section on dichotomous branching below) during megaphyll evolution.

The rise and fall of dichotomous plant architectures

Equal dichotomous branching apparently evolved only once (being a synapomorphy of polysporangiophytes; Kenrick and Crane, 1997), prior to the evolution of vasculature. In contrast, unequal dichotomous branching (Fig. 8B) and mixed creeping axes (Fig. 8C) evolved independently in protracheophytes, rhyniophytes, euphylllophytes and lycopsids (including zosterophylls), leading to the convergence of early land plant architectures (Fig. 8A). The evolution of indeterminate orthotropic axes proceeded independently in lycopsids and euphylllophytes (Fig. 8D), in both groups contributing to the evolution of arborescence (cf. the section 'Lycopsids: lateral sporangia and indeterminacy').

Many dichotomous architectures arose during the late Silurian/Early Devonian (see paragraphs above and Fig. 9A). Plotting the frequency of branching types through time based on an analysis of 58 927 land plant fossils revealed the rarification of dichotomous branching, decreasing throughout the Devonian and Carboniferous, mirrored by an increase in other branching types including axillary branching (Fig. 9B). This reflects notably the diversification of non-dichotomously branched groups, particularly sphenopsids, early seed plants and Archeopteridales (the latter had both dichotomous and lateral branching). Additionally, the transition from dichotomous to axillary branching in seed plants may have played a key role in the frequency changes in branching types in land flora. This might have involved three aspects. First, the evolution of the seed plant megaphyll 'recruited' lateral dichotomous branching systems into leaves (Zimmermann, 1938, 1952) and, as a result, the first megaphyll-bearing seed plants were monoaxial (Galtier, 1999). The second possible cause relates to allometry. Corner (1949) predicted that bigger leaves lead to bigger axes and less branching, and the large size of early seed plant megaphylls may have restricted branching because of this allometric principle. The third cause could have been the emergence and rise of axillary branching, which can only occur in species with megaphylls. Species with axillary branching may have outcompeted dichotomously

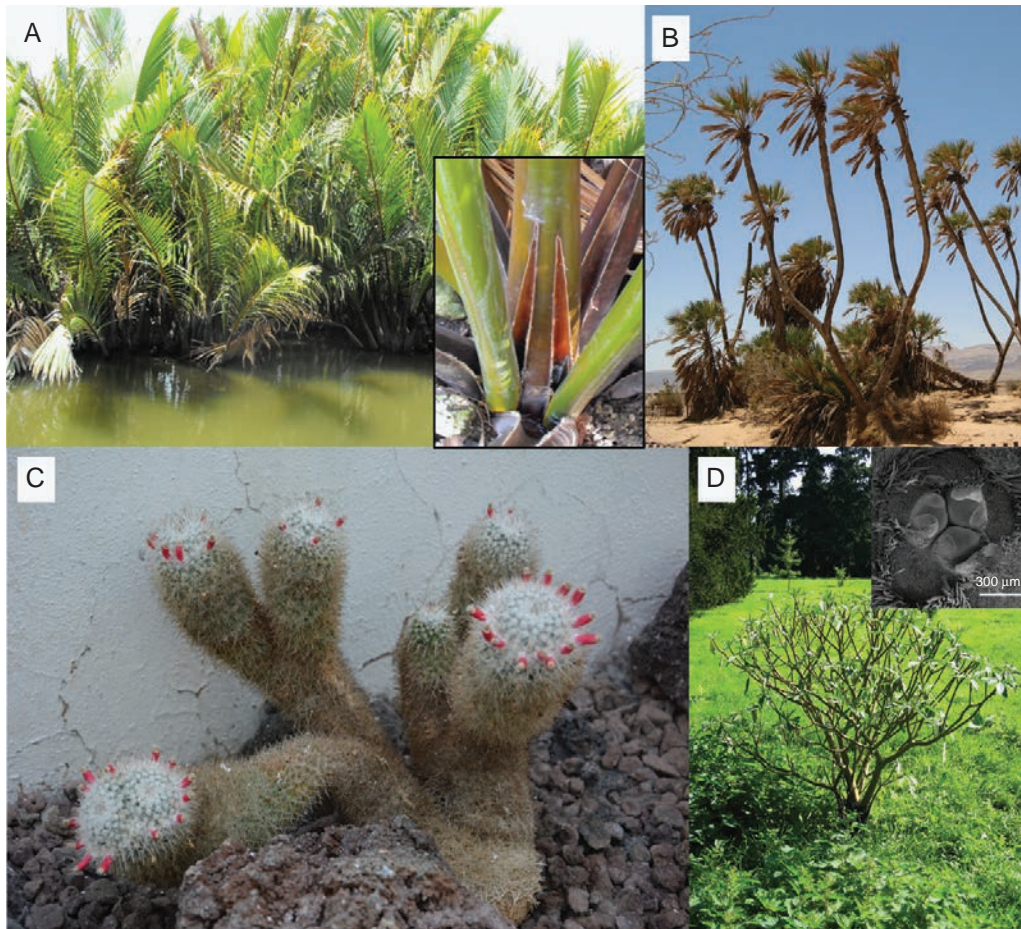


FIG. 10. Dichotomous branching in angiosperms. (A) *Nypa fruticans*. Inset shows a dichotomizing shoot, with one leaf base enclosing the two sister shoots. (B) *Hyphaene thebaica*. (C) *Mammillaria* sp. (D) *Edgeworthia chrysantha*, the only trichotomous angiosperm (Iwamoto *et al.*, 2005). The inset shows a scanning electron micrograph of a trichotomizing meristem (courtesy of Akitoshi Iwamoto). Photo credit: G. Chomicki: A, C; A. Iwamoto: D inset; Wikipedia: B, D.

branching architectures because axillary branching is a much more ‘controllable’ process (only a sub-set of the axillary meristems grow out), allowing growth cessation in adverse seasons, a phenomenon harder to control in dichotomously branching species. The change from predominantly dichotomously branched floras to largely axillary branching floras followed major geochemical changes during the Paleozoic, especially a drop in the atmosphere’s CO_2 concentration. The evolution of megaphyll leaves may have been constrained for >45 million years because planated leaves would have overheated in the CO_2 -rich atmosphere of the late Silurian/Early Devonian (Beerling *et al.*, 2001). The 90 % drop in CO_2 concentration at the end of the Paleozoic, allowing the rise of megaphyll leaves in the land flora, may thus have played a role in the fall of dichotomous architectures, by permitting the evolution of axillary branching that outcompeted dichotomously branched plants.

Dichotomy in angiosperms, a possible escape when axillary branching is restricted

Like other seed plants, angiosperms branch in the axil of their leaves, but there are about 20 exceptions where dichotomous

branching evolved secondarily, notably in palms (Fig. 10A, B) and cacti (Boke *et al.*, 1976; Fig. 10C; Table 2), or even trichotomy in one case (Fig. 10D; Iwamoto *et al.*, 2005). In angiosperms, true dichotomy can easily be confounded with early axillary branching, sub-apical branching or axillary branching followed by meristem abscission or parenchymatization (Hallé *et al.*, 1978; Barthélémy and Caraglio, 2007; Bell, 2008). For these reasons, dichotomy in angiosperms has long been doubted until an extensive anatomical study of the monocot vine *Flagellaria indica* provided an unequivocal demonstration (Tomlinson and Posluszny, 1977a, b). The occurrence of angiosperm dichotomy (Fig. 8) is interesting in that it occurs in groups with little axillary branching potential. Arborescent monocots constitute 65 % of dichotomous angiosperms (Table 2), probably because of a monocot’s restricted axillary branching capabilities due to the absence of a cambium and thus of ‘outer’ vascular bundles facilitating the insertion of axillary buds in the vascular system (Zimmermann and Tomlinson, 1974). In Cactaceae, another group where dichotomous branching is present, large shoots with huge apical meristems (Mauseth, 2004) may restrict axillary branching. Thus, it is posited that dichotomy in angiosperms may represent an escape from (vegetative) axillary branching restriction.

TABLE 2. *Dichotomously branching angiosperms*

Species	Family	Major group	Type of evidence	Type of dichotomy	References
<i>Flagellaria indica</i> L.	Flagellariaceae	Monocots	M, A	Unequal dichotomy	Tomlinson and Posluzni (1977a, b)
<i>Allagoptera arenaria</i> Kuntze	Arecaceae	Monocots	M, A	?	Tomlinson (1967); Hallé et al. (1978); Hallé (2004)
<i>Nypa fruticans</i> Wurbm.	Arecaceae	Monocots	M, A	Equal dichotomy	Tomlinson (1971)
<i>Dypsis utilis</i> (Jum.) Beentje & J. Dransf.	Arecaceae	Monocots	M	Equal dichotomy	Hallé (2004)
<i>Chamaedorea cataractarum</i> Mart.	Arecaceae	Monocots	M, A	?	Fisher (1974)
<i>Syagrus cocoides</i> Mart.	Arecaceae	Monocots	M	?	Pinheiro et al. (1996)
<i>Nannorrhops ritchiana</i> (Griff.) Aitch.	Arecaceae	Monocots	M, A	Unequal dichotomy?	Tomlinson and Moore (1968); Hallé et al. (1978)
<i>Hyphaene thebaica</i> (L.) Mart.	Arecaceae	Monocots	M	?	Schoute (1909); Hallé et al. (1978); Hallé (2004)
<i>Hyphaene ventricosa</i> Kirk.	Arecaceae	Monocots	M	?	Hallé et al. (1978); Lewalle (1968); Hallé (2004)
<i>Hyphaene coriacea</i> Gaertn.	Arecaceae	Monocots	M	?	Hallé et al. (1978)
<i>Eugeissona tristis</i> Griff.	Arecaceae	Monocots	M, A	?	Fisher et al. (1989)
<i>Eugeissona insignis</i> Becc.	Arecaceae	Monocots	M, A	?	Fisher et al. (1989)
<i>Strelitzia reginae</i> Aiton	Strelitziaceae	Monocots	M, A	?	Fisher (1976)
<i>Mammillaria parkinsonii</i> Ehrenberg	Cactaceae	Eudicots	M, A	Equal dichotomy	Boke (1976)
<i>Mammillaria perbella</i> Hildm.	Cactaceae	Eudicots	M, A	Equal dichotomy	Craig (1945); Boke (1976)
<i>Mammillaria karwinskiana</i> Mart. (= <i>M. confusa</i>)	Cactaceae	Eudicots	M	Equal dichotomy	Craig (1945)
<i>Mammillaria rosensis</i> R. T. Craig	Cactaceae	Eudicots	M	Equal dichotomy	Craig (1945)
<i>Mammillaria auriareoli</i> Tiegel	Cactaceae	Eudicots	M	Equal dichotomy	Craig (1945)
<i>Asclepias syriaca</i> L.	Apocynaceae	Eudicots	M, A	Unequal dichotomy	Nolan (1969)
<i>Edgeworthia chrysantha</i> Sieb. & Zucc.	Thymeleaceae	Eudicots	M, A	Equal trichotomy	Iwamoto et al. (2005)

For the type of evidence, M refers to macromorphological observation, A to anatomical studies.

THE MOLECULAR BASIS OF ARCHITECTURAL TRAITS

This section provides a review of key aspects of plant developmental genetics, aiming to illuminate the molecular genetic basis of plant architecture and formulate testable hypotheses regarding mechanisms regulating the diversity of plant architectures in the global flora.

Dichotomous branching

Dichotomy involves the bifurcation of a shoot apical meristem (SAM) into two independent meristems, either symmetric or asymmetric (Fig. 6). This implies that stem cells need to split into two populations. Microsurgical bisection of an angiosperm apical meristem leads to the formation of two sister meristems just as if they had dichotomized (Pilkington, 1929; Steeves and Sussex, 1989). Analyses of clonal shoot sections in *Selaginella kraussiana* have further shown that dichotomous branching involves two steps (Harrison et al., 2007). First, the number of stem cells increases. This is followed by asymmetric cell divisions of these stem cells, with the central cells (so-called merophyte cells) losing their stem cell potential, whereas the cells at the flanks retain it. The increase in stem cell number, followed by asymmetric divisions, mediates dichotomous branching by isolating two stem cell populations (Harrison et al., 2007).

In angiosperms, class I KNOX (Knotted-like Homeobox) genes play a key role in the maintenance of meristem indeterminacy, while ARP (*Asymmetric Leaves 1*, *Rough Sheath 2*, *Phantastica*) genes are expressed in leaf primordia to downregulate KNOX,

promoting leaf determinacy (Timmermans et al., 1999; Tsiantis et al., 1999; Byrne et al., 2000). In *Selaginella*, an ARP gene is expressed not only in leaf primordia, as is the case in seed plants, but also in the meristem, suggesting a potential role in dichotomy by suppressing cell proliferation and thus promoting isolation of the two stem cell populations (Harrison et al., 2005). That the pathway controlling leaf determinacy in seed plants first functioned in dichotomous branching makes sense because seed plant megaphyll leaves arose from the transformation of a lateral shoot system (Zimmermann, 1952; Boyce and Knoll, 2002). Teratological mosses with branched sporangia have been found in extant species (Stefureac, 1947; Demaret, 1950; Watson, 1950). In the moss model *P. patens*, mutation in genes encoding the transcription factor LFY/FLO (Tanahashi et al., 2005), the RNA-binding protein TEL1 (Vivancos et al., 2012), the auxin efflux transporter PINB (Bennett et al., 2014a) or the transcription factor TCP5 (Ortiz-Ramírez et al., 2016) can result in the formation of sporophytes with a double sporangium, while mutations in the polycomb repressive complex 2 protein CLF result in the development of sporophyte-like dichotomous branches in the gametophyte (Okano et al., 2009). Altogether, this supports the presence in bryophytes of the toolkit for dichotomous branching, although the developmental basis for the mutants remains unclear (Harrison, 2017). The independent evolution of dichotomous branching in at least 20 angiosperm species (Table 2; Fig. 10) involves meristems of structures very different from those of bryophytes and lycopsids and thus might involve different genetic mechanisms from those that operated in early polysporangiophytes. The elucidation of the molecular basis of dichotomous sporophyte branching will depend on the

development of efficient forward and reverse genetics methods in lycopsids.

The molecular basis of axillary meristem formation

The molecular basis of axillary meristem initiation has been elucidated over the past two decades (Schumacher et al., 1999;

Schmitz et al., 2002; Greb et al., 2003; Keller et al., 2006; Müller et al., 2006; Raman et al., 2008; Fig. 11). Mutants unable to produce vegetative axillary meristems have been identified in tomato [*Lateral suppressor (Ls)*; Schumacher et al., 1999] and arabidopsis (*LAS*; Greb et al., 2003). *LATERAL SUPPRESSOR* is a putative GRAS family transcription factor gene (Greb et al., 2003). Arabidopsis *las-4* mutants lack branching in the rosette but not in the inflorescence, indicating that branching is *LAS*

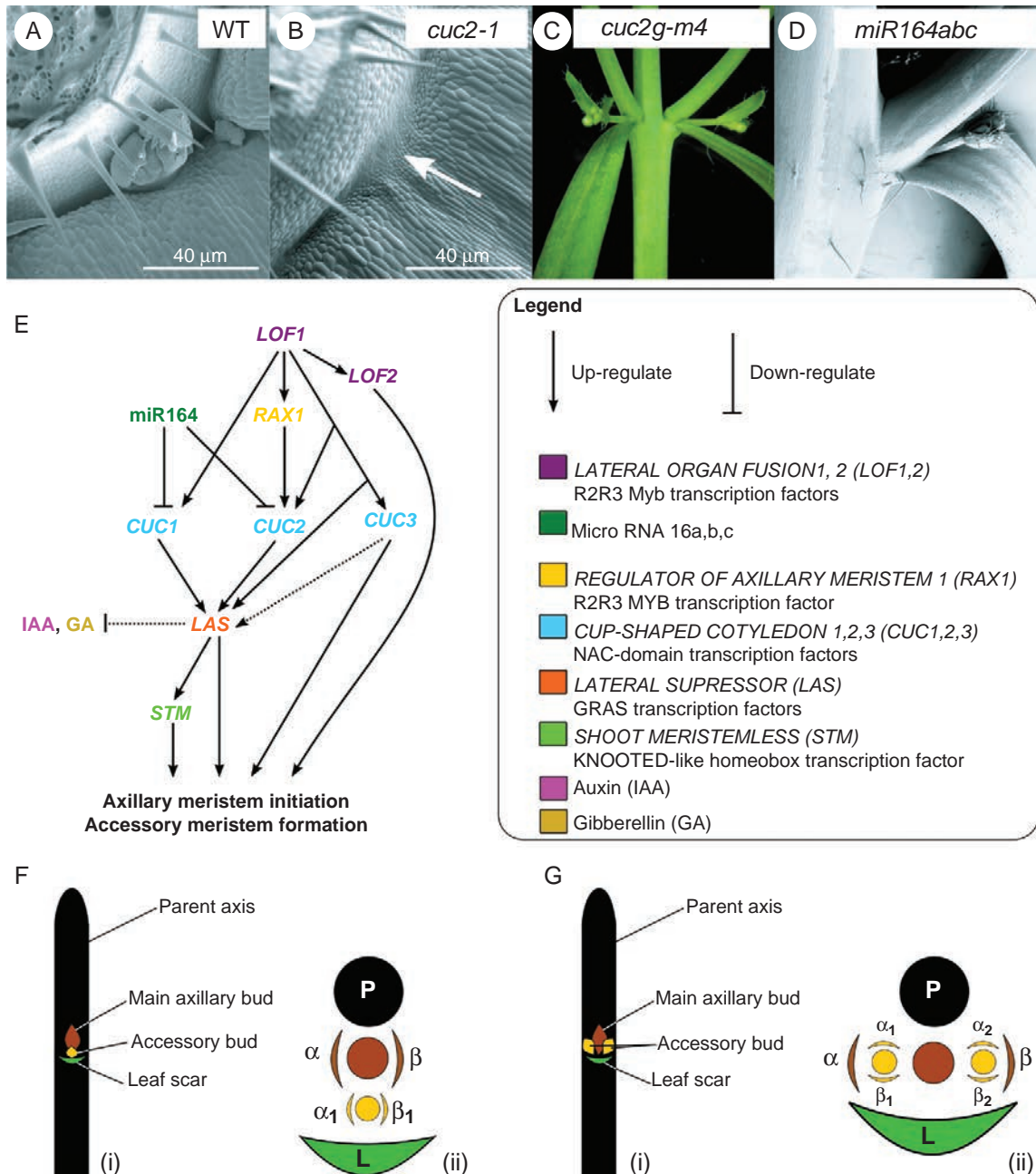


FIG. 11. The genetic basis of axillary meristem and accessory formation. (A) A wild-type (WT) *Arabidopsis thaliana* leaf axil with a normally developing axillary meristem. (B) The mutant *cuc2-2* lacks axillary meristems in rosette leaves. (C) A transgenic line harbouring a *miR164*-resistant version of *CUC2* (*CUC2g-m4*) develops accessory meristems. (D) The triple mutant *miR164abc* similarly develops accessory meristems. (E) Genetic network controlling axillary meristem and accessory meristem formation. (F and G) The two types of accessory bud complexes. (F) Primary bud complex, where the accessory bud results from formation of an independent axillary meristem. (G) Secondary bud complex, where the accessory buds result from branching of the primary axillary bud.

dependent during the vegetative phase but *LAS* independent during the reproductive phase (Greb *et al.*, 2003; Müller *et al.*, 2006).

Axillary meristems could originate either as cell groups detached from the apical meristem but retaining their meristematic identity (Steeves and Sussex, 1989; Long and Barton, 2000) or originate *de novo* from partially or fully differentiated cells (Snow and Snow, 1942; McConnell and Barton, 1998). That *LAS* is expressed only in axillary meristems is consistent with *de novo* axillary meristem formation. The alternative ‘detached’ scenario of axillary meristem formation would be consistent with a *LAS*-independent pathway (Greb *et al.*, 2003). Other genes, expressed in either the apical meristem [*SHOOT MERISTEMLESS (STM)*] or the leaf adaxial side [*REVOLUTA (REV)*], are also expressed in vegetative axillary meristems, providing support for both models of axillary meristem formation (McConnell and Barton, 1998; Greb *et al.*, 2003). Interestingly, cell lineage analysis has shown that the axillary meristem of maize is clonally linked with the leaf above it and its internode, but not with the subtending leaf (and internode) as in arabidopsis (Johri and Coe, 1983; McDaniel and Poethig, 1988), suggesting that vegetative axillary meristem development could be fundamentally distinct from that of reproductive meristems.

The *LAS* expression domain is tightly controlled by a genetic network wherein *CUP-SHAPED COTYLEDON1 (CUC1)* and *CUC2* induce *LAS* expression (Raman *et al.*, 2008), and both *CUC1* and *CUC2* are downregulated by the microRNA family miR164 (*MIR164A*, *MIR164B* and *MIR164C* genes) (Laufs *et al.*, 2004; Schwab *et al.*, 2005; Raman *et al.*, 2008; Fig. 11A–E), altogether controlling the boundaries of axillary meristem formation. Another player in the network is *RAX1*, which upregulates *CUC2* (Keller *et al.*, 2006). *CUC3* promotes axillary meristem formation either via *LAS* or via a *LAS*-independent pathway (Vroemen *et al.*, 2003; Raman *et al.*, 2008). These interactions are summarized in Fig. 11E.

Accessory axillary meristems

The number of axillary meristems is the first limitation to the number of branches a plant can produce and is itself dependent on the number of leaf axils (and hence of phyllotaxy) and on the presence of accessory (or supernumerary) meristems. Accessory axillary meristems can be inserted in vertical or horizontal succession (Barthélémy and Caraglio, 2007; Fig. 11F, G) and often have different fates. Accessory meristems can either become floral meristems or remain dormant as reserve meristems with the same morphogenetic potential as the non-accessory meristem or with the morphogenetic potential of the trunk. A particularly interesting example is found in coffee (*Coffea arabica*; Fig. 3F), in which axillary meristems of the first axis (trunk) develop immediately into plagiotropic shoots while accessory meristems remain dormant as a reserve and have the morphogenetic potential to develop into delayed orthotropic shoots (Varossieau, 1940; Moens, 1963).

From a developmental perspective, an important distinction is that between primary and secondary bud complexes. Primary bud complexes consist of buds in the same leaf axil and are generally initiated in a horizontal sequence either acropetally or basipetally. Secondary bud complexes result from the axillary

branching of the primary axillary bud and are essentially a condensed (short) shoot (Hallé *et al.*, 1978). The development of primary bud complexes involves the sequential formation of axillary meristems, which requires several axillary stem cell niches. Its genetic basis has been uncovered in *A. thaliana*. In this species, the number of axillary meristems is controlled by the expression level of *CUC1* and *CUC2* genes and regulated by microRNA miR164 genes (Raman *et al.*, 2008). *miR164* mutants or transgenic lines of arabidopsis harbouring miR164-resistant versions of *CUC1* and *CUC2* develop accessory buds (Raman *et al.*, 2008; Fig. 11C, D). Interestingly, mutants in distinct miR164 genes form accessory meristems in different, partially overlapping positions: mutants in *miR164A* and *miR164B* genes formed accessory buds in the rosette leaves, while mutants in the *miR164C* gene had supernumerary buds in the inflorescence leaves (Raman *et al.*, 2008). Accessory meristems in the rosette and inflorescence were both organized in a basipetal sequence, meaning below the first axillary meristem. This contrasts with the mangrove tree *Rhizophora mangle*, where accessory meristems develop on vegetative branches or inflorescences but are organized in an acropetal sequence in the first case (above the first axillary meristem) and basipetally in the latter case (below the first axillary meristem; Hallé *et al.*, 1978).

The genetic basis of secondary bud complexes remains unknown. Because any secondary bud complex results from branching of the primary axillary meristem, it relies upon immediate branching (Fig. 11) and thus requires a weak apical dominance from the primary axillary meristem.

The control of axillary branching in time and space

In most plant species, only a small fraction of axillary meristems develop into branches, the others remaining dormant. The study of axillary meristem outgrowth started with the historic experiments of Skoog and Thimann (1933). These experiments showed that removing the apical meristem leads to the activation of the buds below, indicating that the apex exerts an inhibitory force – a phenomenon termed apical dominance. Application of auxin on a decapitated stem maintains bud inhibition, indicating that auxin is the inhibitory substance produced by the shoot apex. Conversely, application of cytokinin on a dormant bud activates it (Skoog and Thimann, 1933; Thimann and Skoog, 1934), but even if cytokinin is required for escaping apical dominance, it is not needed to promote bud release following decapitation (Müller *et al.*, 2015). Application of auxin transport inhibitors in the middle of a shoot results in outgrowth of the axillary buds below, indicating that basipetal auxin transport is necessary for apical dominance (Thimann and Skoog, 1933). However, auxin does not enter the bud (Morris, 1977; Booker *et al.*, 2003), suggesting an indirect effect of auxin on axillary meristem repression. Sachs (1981, 1991) proposed the ‘canalization hypothesis’ (Fig. 12A), a competition-based model put forward to explain the differentiation of vascular strands connecting auxin sources to auxin sinks. The basic idea is that auxin self-organizes its transport: when flowing through tissues, auxin upregulates and polarizes its own transport, leading to a canalized flux away from the auxin source (Sachs, 1981, 1991; Bennett *et al.*, 2014b; Fig. 12A). Later work showed the capacity of buds to export their own auxin and that buds

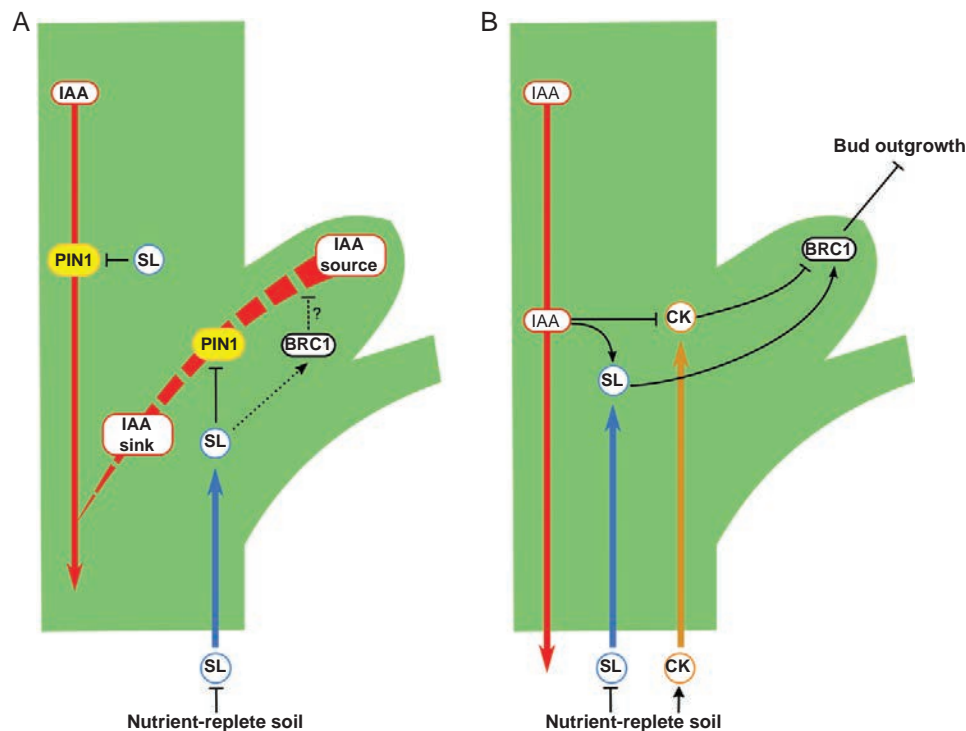


FIG. 12. Two contrasting views of the molecular control of axillary branching in time and space by auxin, cytokinin, strigolactone and the transcription factor BRC1. (A) Canalization model. (B) Direct action model. Adapted from Waters *et al.* (2017).

compete with the SAM and with other buds for auxin export, implying that the stem has a limited capacity for auxin transport (Li and Bangerth, 1999; Bennett *et al.*, 2006) and providing some experimental support for Sachs's canalization hypothesis. Interestingly, modelling suggests that competition between buds may occur before polar auxin transport (PAT) saturation (Prusinkiewicz *et al.*, 2009).

However, many open questions remain, partly because directly measuring auxin concentration in individual cells is not yet possible (Bennett *et al.*, 2014b). Besides the main basipetal, unidirectional PAT stream, another transport pathway, termed connective auxin transport, can allow bud–bud communication (Bennett *et al.*, 2016) and thus potentially play a role in the dominance of branches. Release from apical dominance also leads to an increase in sucrose accumulation in axillary buds, repressing *BRANCHED1* (*BRC1*) and leading to bud release (Mason *et al.*, 2014), suggesting that apical dominance may involve redundant pathways.

In the past decade, mutant phenotypes with affected shoot branching have been found in *Arabidopsis* (*max*) (Stirnberg *et al.*, 2002, 2007; Booker *et al.*, 2004), *pea* (*rms*) (Beveridge *et al.*, 2000) and *Petunia* (*dad*) (Napoli, 1996; Snowden and Napoli, 2003), which led to the elucidation of the strigolactone signalling pathway, a third key determinant of shoot branching together with auxin and cytokinin (McSteen and Leyser, 2005; Domagalska and Leyser, 2011). Strigolactone is a small molecule that acts as ligand of the protein D14, which associates with MAX2 [part of an SCF-type4 ubiquitin ligase (E3); Stirnberg *et al.*, 2007; Yao *et al.*, 2016] and SMXL proteins, such as D53 (Jiang *et al.*, 2013; Zhou *et al.*, 2013). Recruitment of SCF to MAX2 leads to the ubiquitin tagging and degradation

of D53 proteins by the proteasome (Jiang *et al.*, 2013; Zhou *et al.*, 2013; Wang *et al.*, 2015). It is well established that strigolactone signalling negatively regulates branching (Gomez-Roldan *et al.*, 2008; reviewed by Domagalska and Leyser, 2011; Waters *et al.*, 2017), although the exact mechanisms remain unclear. Two non-exclusive models have been put forward (Waters *et al.*, 2017; Fig. 12). The 'direct action' model (Fig. 12B) suggests that strigolactone is a secondary messenger of auxin, implying that auxin upregulates strigolactone signalling and that strigolactone directly targets transcription factors involved in branching – for instance, by upregulating the negative regulator of shoot branching BRC1 (Aguilar-Martínez *et al.*, 2007; Braun *et al.*, 2012; Dun *et al.*, 2012). In contrast, the 'canalization model' (Fig. 12A), which expands Sachs's canalization hypothesis, posits that the capacity of a bud to grow depends on its ability to export auxin and that strigolactone mainly acts via downregulating PAT (PIN1), thereby reducing the auxin sink and therefore increasing the competition between buds so that fewer can grow (Crawford *et al.*, 2010; Shinohara *et al.*, 2013). Strigolactone probably regulates branching in both models (Fig. 12).

The regulation of shoot branching has a massive influence on plant architecture. The TCP transcription factor *TEOSINTE-BRANCHED1* (*TBI*) controls shifts from the highly branched ancestral maize architecture to the monocaulous architecture of cultivated maize (Doebley *et al.*, 1995). Species-specific differences in the level of branching could arise due to variation in the biosynthesis, transport and signalling of auxin, cytokinin or strigolactones or any of their targets (e.g. *TBI*). Systematic shoot overtopping, observed in some architectural models, such as Koriba's model (Fig. 3B), or, conversely, equal growth

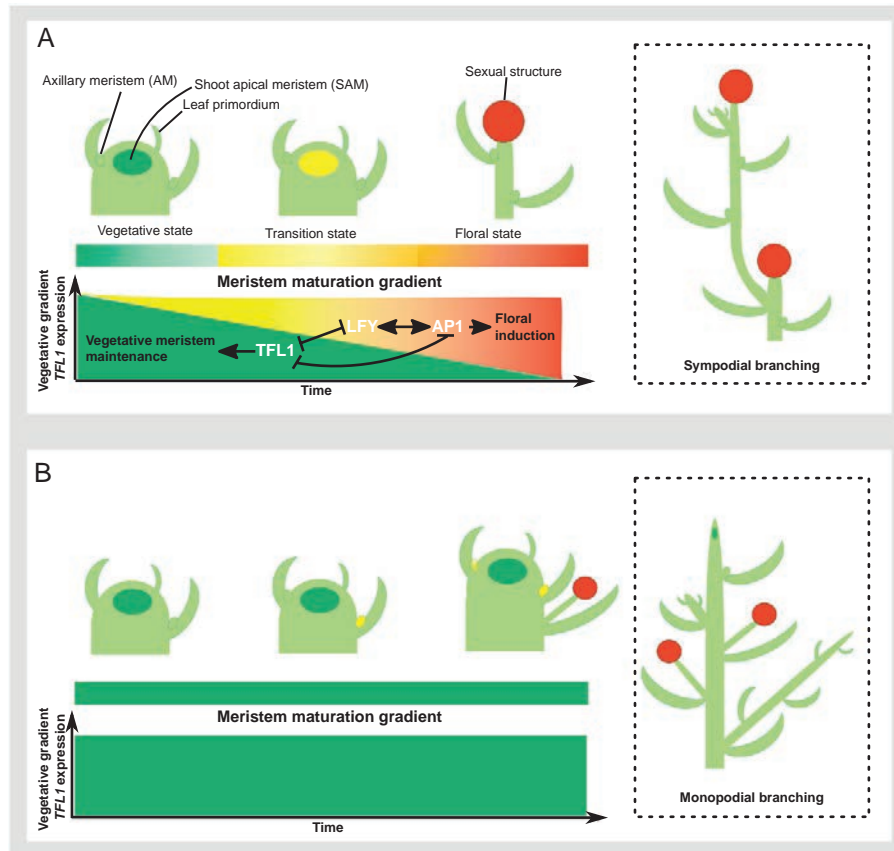


FIG. 13. Genetic basis of sympodial branching. (A) Meristem transition in sympodial shoots. (B) Meristem status in monopodial shoots.

among shoots as observed in Leeuwenberg's model (Fig. 3A), probably results from variation in PAT.

Plagiotropic growth is still poorly understood

Plagiotropic growth is an intrinsic physiological shoot property that results in near-horizontal growth orientation, generally associated with a dorsiventral symmetry (Massart, 1924; Hallé *et al.*, 1978; Barthélémy and Caraglio, 2007; Fig. 1E). Experimental evidence suggests that plagiotropy is dependent on a signal sent by the SAM (Leakey, 1990; Veierskov *et al.*, 2007), with two possibilities being distinguished based on whether the signal is required continuously or only initially as an inducer. The two possibilities are easily distinguished by decapitation experiments or cuttings: decapitation releases the plagiotropy in the first case, but not in the second. In this latter case, potted cuttings from a plagiotropic branch (e.g. of *Coffea* or *Araucaria heterophylla*) will regenerate another plagiotropic branch, not the entire architecture of the plant. Leakey (1990) noted that in most cases plagiotropy is linked to immediate branching (axillary branching simultaneous to apical growth; manifestation of weak apical dominance; Fig. 11). Matching this, Fletcher and Mader (2007) found that plagiotropic shoots have low auxin/cytokinin ratios. The finding of higher auxin transport capacity during the expansion growth

of *Abies nordmanniana* plagiotropic shoots suggests that auxin could be partly responsible for horizontal growth and that the mechanisms controlling branch bud positioning and horizontal growth probably are distinct (Veierskov *et al.*, 2007). However, although SAM-maintained plagiotropy could depend on auxin, non-SAM-maintained plagiotropy as observed in *Coffea* or *Araucaria* probably is dependent on a signal that enters the early axillary meristem produced by the SAM (Leakey, 1990). This signal could be a long-distance-transported mRNA, encoding developmental transcription factors.

Sympodial branching

The construction of an axis can occur from a single indeterminate meristem, resulting in a monopodium, or via successive determinate meristems, resulting in a sympodium (Fig. 1B, C). Monopodial vs. sympodial growth can occur in the whole plant or be restricted to certain axis orders, such as the main branches or the trunk (Figs 2–5). Sympodial branching involves two processes: determinate growth and the capability of a replacement meristem to grow (Fig. 13). Determinate growth can occur due to meristem abscission or death, or transformation of the SAM into a specialized structure, generally an inflorescence or flower but in some cases parenchymatous cells ('parenchymatization'), tendrils or spines. The number of

'relay' meristems is generally fixed, resulting in mono-, di- or polychasia (Fig. 1C).

The outgrowth of the uppermost axillary meristem(s) is promoted by the release of apical dominance resulting from the death of the meristem that interrupts basipetal auxin transport. The gene *TERMINAL FLOWER1* (*TFL1*) conveys shoot identity (Alvarez *et al.*, 1992) by counteracting the floral inductor genes *LEAFY* (*LFY*) and *APETALA1* (*API*) (Liljegren *et al.*, 1999; Fig. 13). Upstream of *TFL1*, two complexes of proteins, AGL24–SOC1 and FT–FD, play important roles in floral induction by activating *LFY* and *API*, respectively (Abe *et al.*, 2005; Lee *et al.*, 2008; Liu *et al.*, 2008, 2009). Overexpression of *TFL1* in arabidopsis leads to the prolongation of vegetative growth and extensive monopodial branching (Liljegren *et al.*, 1999). In contrast, species that branch sympodially, such as tomato (*Solanum lycopersicum*) and pepper (*Capsicum annuum*; both Solanaceae), lack *TFL1* expression in the SAM [orthologues called *SELF-PRUNING* (*SP*) and *FASCICULATE*, respectively], and these genes are instead expressed only in axillary meristems (Pnueli *et al.*, 1998; Thouet *et al.*, 2008; Eitzur *et al.*, 2009). Tomato plants with mutations in the gene *SINGLE FLOWER TRUSS* (*SFT*), a precursor of the florigen FT, that counteracts the vegetative maintenance gene *SP*, show monopodial branching (Shalit *et al.*, 2009), indicating that this gene is essential in the control of sympodial branching. Although the expression of the vegetative maintenance gene *TFL1* provides a simple explanation for the genetic basis of sympodial vs. monopodial growth, it does not explain how distinct sympodial architectures are generated.

Computer simulations integrating gene function and selection show that variation in the rate of meristem maturation from the vegetative to the reproductive state, modelled as the expression of the vegetative-promoting gene *TFL1* and the reproductive-promoting gene *LEAFY* (*LFY*), is sufficient to generate the array of inflorescence architectures found in nature (Prusinkiewicz *et al.*, 2007). Experimental work in tomato has also shown that transcriptomes of distinct meristems indeed present a gradient of vegetative and reproductive genes, corresponding to a 'meristem maturation clock' of which the homeobox transcription factor gene *COMPOUND INFLORESCENCE* (*S*) is a key component (Park *et al.*, 2012). Therefore, it appears that such a gradient of meristem maturation, reflecting the expression ratio of vegetative vs. reproductive genes, could provide an explanation for the array of sympodial growths forms found in nature. *TFL1* is conserved in all angiosperms and in many gymnosperm species (Liu *et al.*, 2016), suggesting that its key role in vegetative meristem determinacy could also be conserved widely across seed plants.

Rhythmic vs. continuous growth and branching

Rhythmic growth requires shoots with periodic growth cessation during which the apical meristem is protected in a bud, as opposed to continuous growth, a process whereby a shoot grows without endogenous periodicity (Hallé and Martin, 1968; Hallé *et al.*, 1978). Seasonal and endogenous growth cessation are distinguished, and we here focus on the former, in the light of recent molecular work. Morphologically, rhythmic growth is identified by a segmentation of the axis, whereby each segment is referred to as a growth unit (Barthélémy and Caraglio, 2007;

Fig. 1F). A species can add either one growth unit per growing season or several, a phenomenon referred to as polycyclism (Barthélémy and Caraglio, 2007). Rhythmic growth should not be confounded with rhythmic branching, which refers to axes that branch periodically. Morphologically, this phenomenon is often reflected by branches inserted in tiers on an axis, and so is easily recognizable along the trunk (Hallé *et al.*, 1978; Barthélémy and Caraglio, 2007; Fig. 5A).

The understanding of the molecular basis of growth rhythmicity has benefitted greatly from the development of poplar (*Populus tremula* × *tremuloides*) as an efficient and transformable genetic model. Böhlenius *et al.* (2006) showed that in poplar, growth cessation is controlled by the CONSTANS–FLOWERING LOCUS T (CO–FT) regulatory module, a gene promoting flowering in long days in the annual *A. thaliana* (Koorneef *et al.*, 1991). In poplar, there are two copies of *FT*: *FT1*, involved principally in flowering time, and *FT2* which mainly controls endogenous growth cessation (but is also involved in flowering; Hsu *et al.*, 2011). Overexpression of *FT2* leads to more active growth and absence of growth cessation even under short-day conditions, whereas knocking down *FT2* using RNA interference (RNAi) leads to less vegetative growth and growth cessation, even under long-day conditions (Hsu *et al.*, 2011). *FT2* acts by co-ordinating a regulatory network controlling growth cessation (Hsu *et al.*, 2011), but rhythmic growth is also controlled by the regulation of plasmodesmata (Paul *et al.*, 2014; Fig. 14). Short days downregulate the growth-promoting *FT2*, and subsequently leaf production shifts to scale leaf production, which sets bud formation, but is not solely responsible for dormancy as growth can resume (if the plant is placed in long days) within 2 weeks after *FT2* downregulation (Ruonala *et al.*, 2008).

Changes in the regulation of other important genes are also correlated with dormancy, notably downregulation of *CENLI* (the orthologue of the arabidopsis vegetative maintenance gene *TFL1*) and upregulation of Dormancy-associated MADS-box genes (*DAM*) (Paul *et al.*, 2014; Fig. 14). Importantly, short days induce a group of GH17-related proteins that increase the activity of 1,3 β-glucanase, leading to the production of callose complexes (called dormancy sphincter complexes) that are deposited in plasmodesmata, thus preventing cell signalling between the apical meristem and the rib meristem (Rinne *et al.*, 2011; Paul *et al.*, 2014). Release from dormancy occurs via chilling [or gibberellins (GAs)] and involves the induction of *FT1* in the dormant bud and the expression of GA-inducible GH17 enzyme genes (1,3 β-glucanases) that hydrolyse callose and re-open plasmodesmata (Rinne *et al.*, 2011). However, chilling does not directly lead to the resumption of growth, but rather shifts the bud from dormancy to a quiescent state with a high freezing tolerance from which growth can resume when the temperature increases (Paul *et al.*, 2014; Fig. 14).

The poplar *FT1* and *FT2* paralogs are unique because they derive from a whole-genome doubling event in *Populus* (Liu *et al.*, 2016). However, phylogenetic analyses have shown that FT-like genes are present in all sampled seed plants, varying from a single copy in papaya or cocoa to 15 in maize (Liu *et al.*, 2016). Recent studies show that FT-like genes are a key component of growth rhythmicity in conifers (Kalgren *et al.*, 2013; Avia *et al.*, 2014). Whether the involvement of FT-like genes in the control of growth rhythmicity is universal remains

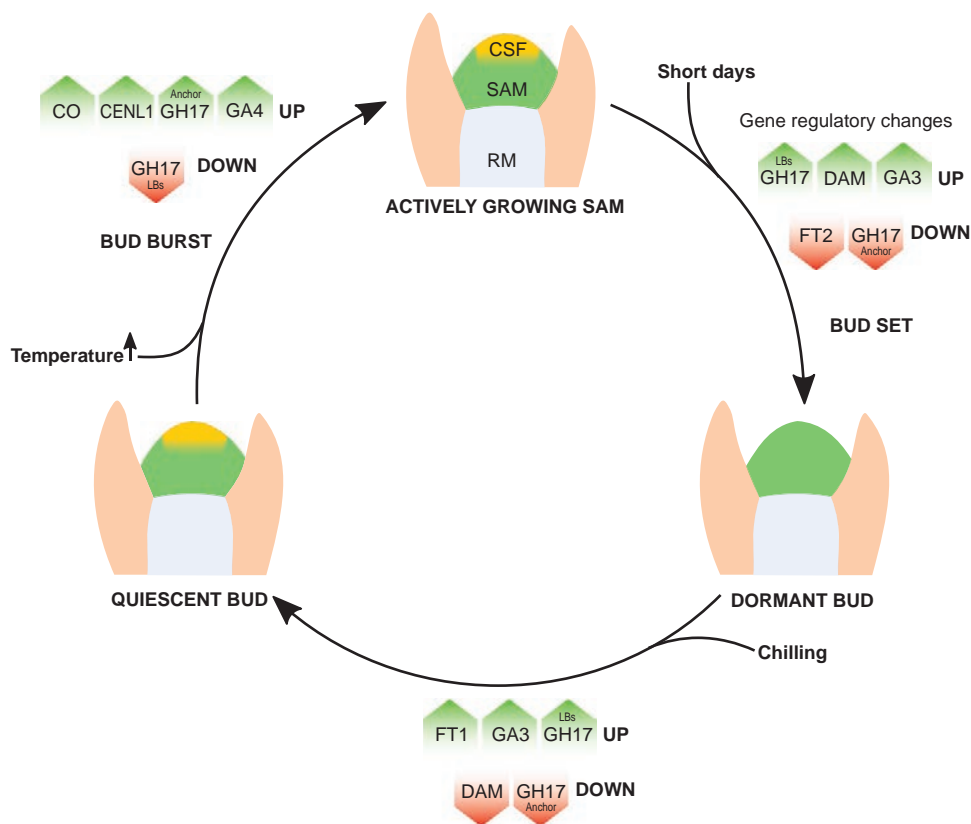


FIG. 14. Genetic basis of rhythmic growth and dormancy cycling in buds. In long days, meristem growth plus a central symplasmic field (CSF) allow cell signaling between the apical and rib meristems. Short days induce a drop of *FT2* expression, which promotes growth cessation, and the expression of various genes is remodelled (most importantly *GH17* family genes), leading to the synthesis of callose, and the obstruction of plasmodesmata and thus the isolation of the apical and rib meristems. Chilling promotes *FT1* expression inside the bud and causes (other) *GH17* family genes to hydrolyse the callose plugs, but in this quiescent state, the bud is inactive and highly frost resistant. Increased temperatures can lead to resumed growth following the expression of growth genes such as *FT2* and *CEN1* (in poplar; *TFL1* orthologue of arabidopsis). Figure adapted from Paul *et al.* (2014).

unknown, but their presence across seed plants makes them good candidates. Important questions include whether shifts to continuous growth as found in many tropical plants (such as palms) could be mediated by relaxed selection on *FT*-like gene promoters and how different environmental cues, such as day-length, temperature, humidity or the perception of variation in sunset or sunrise time, are integrated in the control of growth rhythmicity.

Phyllotaxy

Phyllotaxy, the geometric arrangement of the lateral organs on shoots and flowers, is a fundamental process in plant development that results from an iteration of primordium initiation at the SAM. Phyllotaxy plays an important role in plant architecture by determining the position of axillary meristems around an axis (Fig. 15A–G). The geometry of phyllotaxy has fascinated scientists and non-scientists for centuries, and in some species with a spiral phyllotaxy it has been shown to fit the Fibonacci series in which primordia arise at $137^{\circ}30'28''$ from each other (Mitchison, 1977; Steeves and Sussex, 1989). Hofmeister (1868) apparently was the first to notice that in most phyllotatic systems, leaf primordia appear as far as possible

from each other. This property, referred to as Hofmeister's rule, was further explored by Snow and Snow (1933), who showed that the ablation or isolation of a leaf primordium from the meristem results in a displacement of the next primordium, leading them to deduce that each primordium exerts an 'inhibition field' in which no other primordia can arise. It has been shown that PAT is largely responsible for the inhibition fields and thereby controls phyllotaxy in angiosperms (Fig. 15H–J). Mutation of the arabidopsis *PIN1* gene, which codes for an auxin transport efflux protein, leads to a naked apex in *A. thaliana*, and when wild-type arabidopsis is cultivated on medium containing auxin transport inhibitors, such plants show the same phenotype as the *pin1* mutant (Okada *et al.*, 1991). Furthermore, application of the cell wall-loosening protein expansin on localized sites of the tomato SAM is sufficient to trigger primordium formation and can alter phyllotaxy (Fleming *et al.*, 1997). Likewise, expansins are upregulated in early developing primordia and trigger their initiation, thereby acting as downstream effectors of auxin action (Reinhardt *et al.*, 1998, 2000). Therefore, a model of phyllotaxy based on PAT has been developed (Reinhardt *et al.*, 2003). Spiral phyllotaxy also requires proper expression of the boundary gene *CUC2*, and its downregulation by miR164 (Peaucelle *et al.*, 2007) to delineate leaf primordia boundaries. Failure to control *CUC2* (in lines where *CUC2*

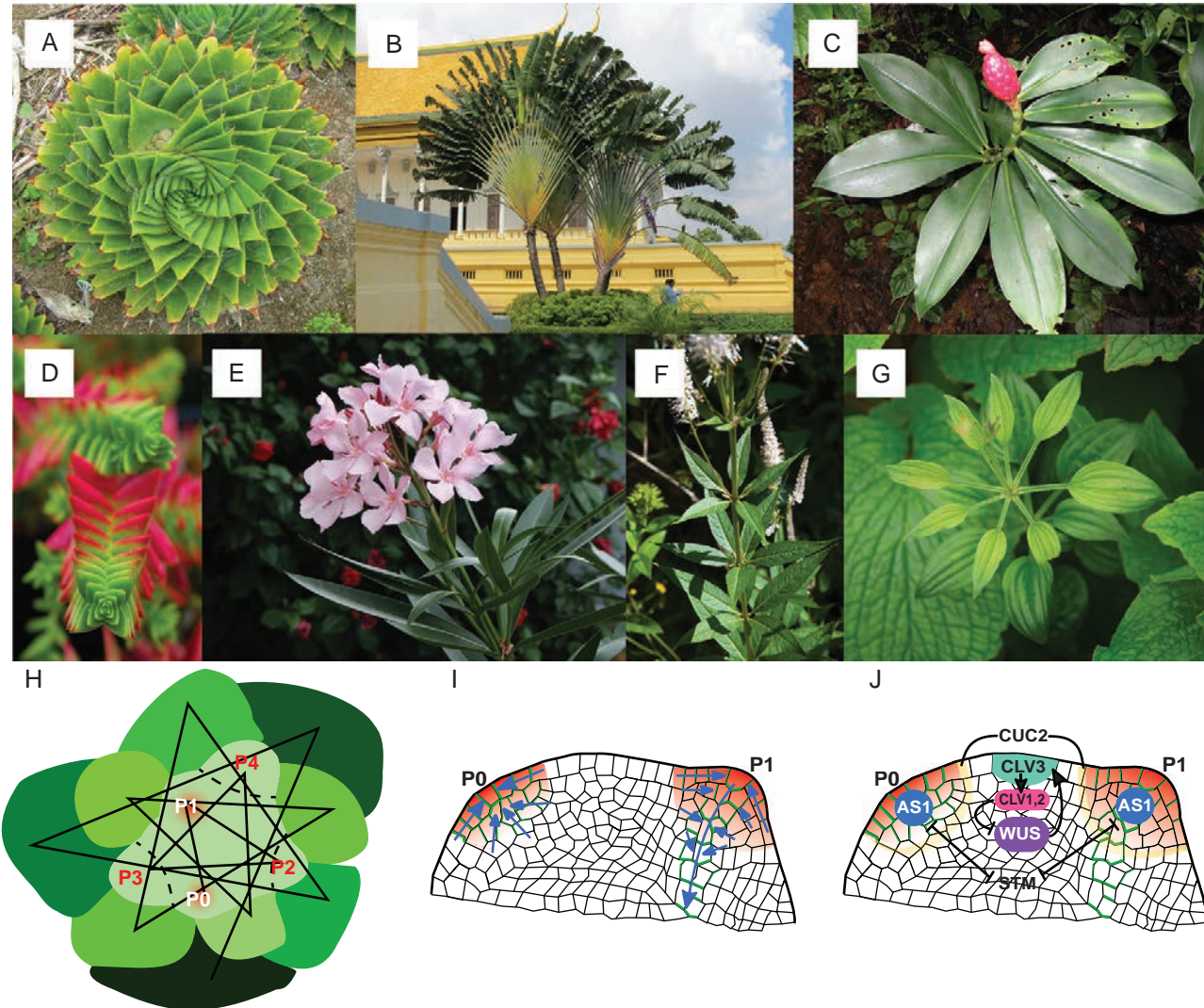


FIG. 15. The control of phyllotaxy. (A–C) Phyllotaxies with a single leaf per node. (A) Spiral phyllotaxy in *Aloe polyphylla*. (B) Distichous phyllotaxy in *Ravenala madagascariensis*. (C) Monostichous phyllotaxy in *Costus* sp. (D–G) Phyllotaxies with 2-many leaves per node. (D) Decussate phyllotaxy in *Crassula capitella*. (E) Tristichous phyllotaxy in *Nerium oleander*. (F) Five-whorled phyllotaxy in *Veronicastrum virginicum*. (G) Eight-whorled phyllotaxy in *Rubia cordifolia*. (H) Spiral phyllotaxy in *Arabidopsis thaliana*, showing the establishment of primordia as far away from each other as possible. (I) The auxin polar transport model of phyllotaxy involves a self-organization leading to auxin maxima arising far away from each, where expansins are activated and anisotropic cell expansion proceeds, leading to primordium growth. (J) In *Arabidopsis thaliana*, successful primordial establishment also depends on the expression of *ARP* genes (here *AS1*) that downregulate the meristematic genes *KNOX* class I (here *STM*), and thus promote leaf determinacy. *CUC2* is a boundary gene, and its correct expression surrounding the primordia is essential for a correct phyllotaxy. Meristematic growth is primarily mediated by the *WUSCHEL/CLAVATA* pathway, wherein the stem cell-produced ligand *CLV3* finds the receptors *CLV1/CLV2*, which activates a pathway downregulating the meristem growth, thus promoting *WUS* which itself upregulates *CLV3*. The scaffold of H, I and J has been adapted from Bennett *et al.* (2014).

is miR164 resistant) leads to a whorled phyllotaxy (Peaucelle *et al.*, 2007). This suggests that variation in the expression of boundary genes could allow shifts from spiral to whorled phyllotaxis. Such shifts are documented in Rubiaceae and other groups. Computer simulations of PAT suggest that most common types of phyllotaxy can arise from the ‘inhibition fields’ model (Smith *et al.*, 2006).

The alternate distichous phyllotaxy of maize involves a homologue of the cytokinin-inducible response regulator gene *ABPHYL1* (Jackson and Hake, 1999; Giulini *et al.*, 2004). *ABPHYL1* encodes a cytokinin-induced two-component response regulator expressed in the SAM (Giulini *et al.*, 2004). The *abphyl1* mutant has an opposite decussate phyllotaxis,

indicating that the presence of functional *ABPHYL1* is required for maize alternate distichous phyllotaxy, and thus down-regulation of *ABPHYL1* could be a potential way to shift to an opposite and decussate phyllotaxy.

REITERATION, LEVELS OF ORGANIZATION AND MORPHOLOGICAL GRADIENTS

Reiteration

While some species conform to one architectural unit throughout their life span, others reproduce their architectural unit, or a part of it, during their development, a process termed reiteration

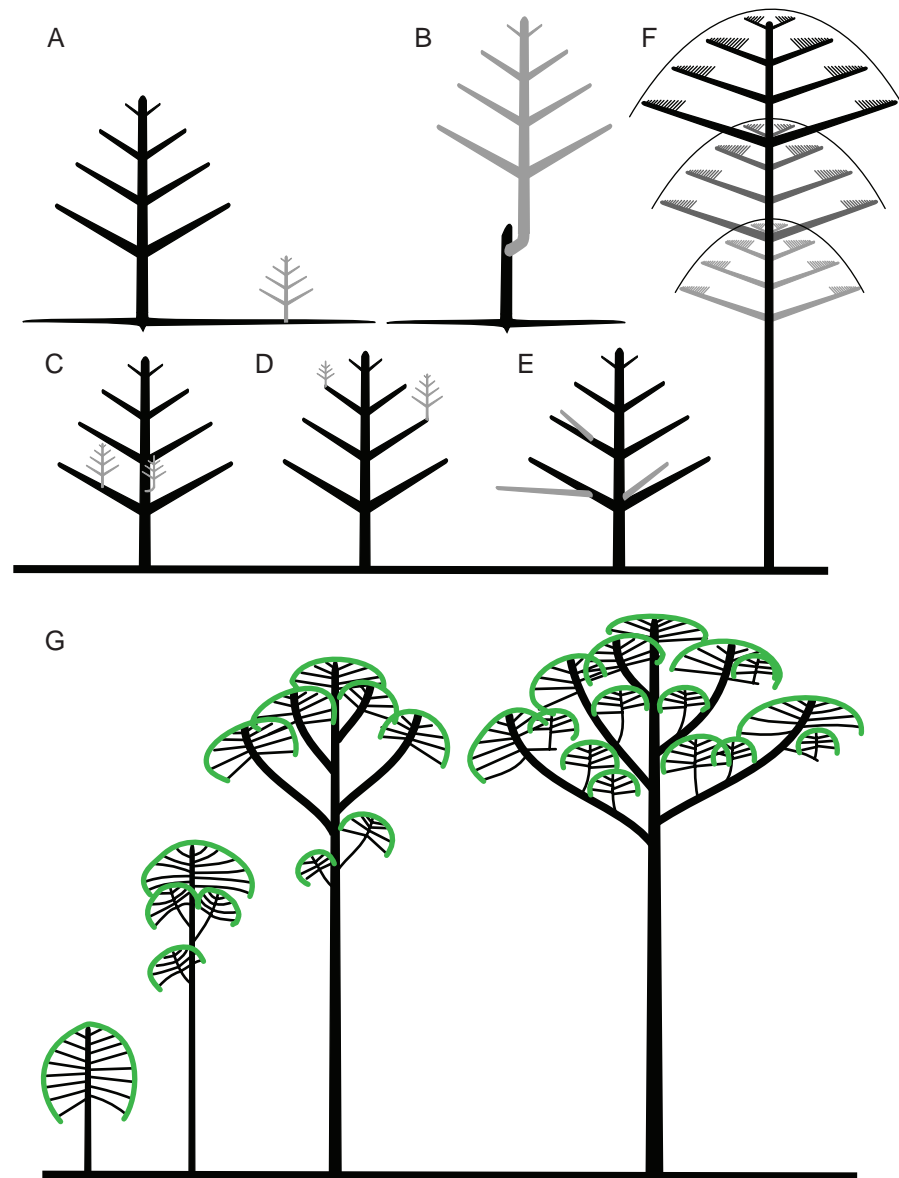


FIG. 16. Reiteration. (A) Basal reiteration (total and delayed) from a root sucker. (B) Traumatic reiteration (total and delayed). (C) Delayed total reiteration occurs by the activation of dormant (often epicormic) buds on the trunk or the main branches. (D) Immediate total reiteration occurs by the re-energization of growing apical meristems, for instance when light or nutrient availability increases. (E) Partial delayed reiteration is important for maintaining crown productivity. (F) ‘Successive nesting crowns’ (partial) reiteration in *Araucaria*. (G) Automatic (or sequential) reiteration is part of the ontogeny of many tropical rain forest trees, here *Shorea stenoptera* (Dipterocarpaceae), adapted from Edelin (1984).

(Oldeman, 1974; Hallé *et al.*, 1978; Fig. 16). Reiteration can occur concurrently with the development of the architectural unit (Fig. 16D), following a shift in the fate of an apical bud (‘immediate reiteration’), or arise from a latent meristem (‘delayed reiteration’; Fig. 16A–C, E, F). In both cases, the reiteration can involve the entire architectural unit (‘complete’ or ‘total’ reiteration; Fig. 16A–C, G) or only part of it (‘partial’ reiteration; Fig. 16E, F). Reiteration can be opportunistic (thus not part of the plant’s architectural genetic programme), for instance in response to a trauma in the case of delayed reiteration (‘traumatic reiteration’) or an increase in light or nutrient resources in the case of immediate reiteration (‘adaptive reiteration’) (Oldeman, 1974; Hallé *et al.*, 1978;

Barthélémy and Caraglio, 2007). However, reiteration can also be part of the developmental sequence of a plant, especially during crown construction in large trees (‘automatic reiteration’: Edelin, 1984; ‘sequential reiteration’: Nicolini, 1997; Fig. 16G). Delayed adaptive reiteration involves the release from dormancy of latent buds, most frequently epicormic buds, and is important for the maintenance of tree crown productivity and tree longevity (Bryan and Lanner, 1981; Lanner, 1996, 2002; Ishii and Ford, 2002). In a 450-year-old *Pseudotsuga menziesii*, shoot clusters on the branches were maximally 24 years old, suggesting a turnover that may help maintain branch photosynthetic productivity (Ishii, 2000). The formation of such branch complexes (partial delayed reiteration) is

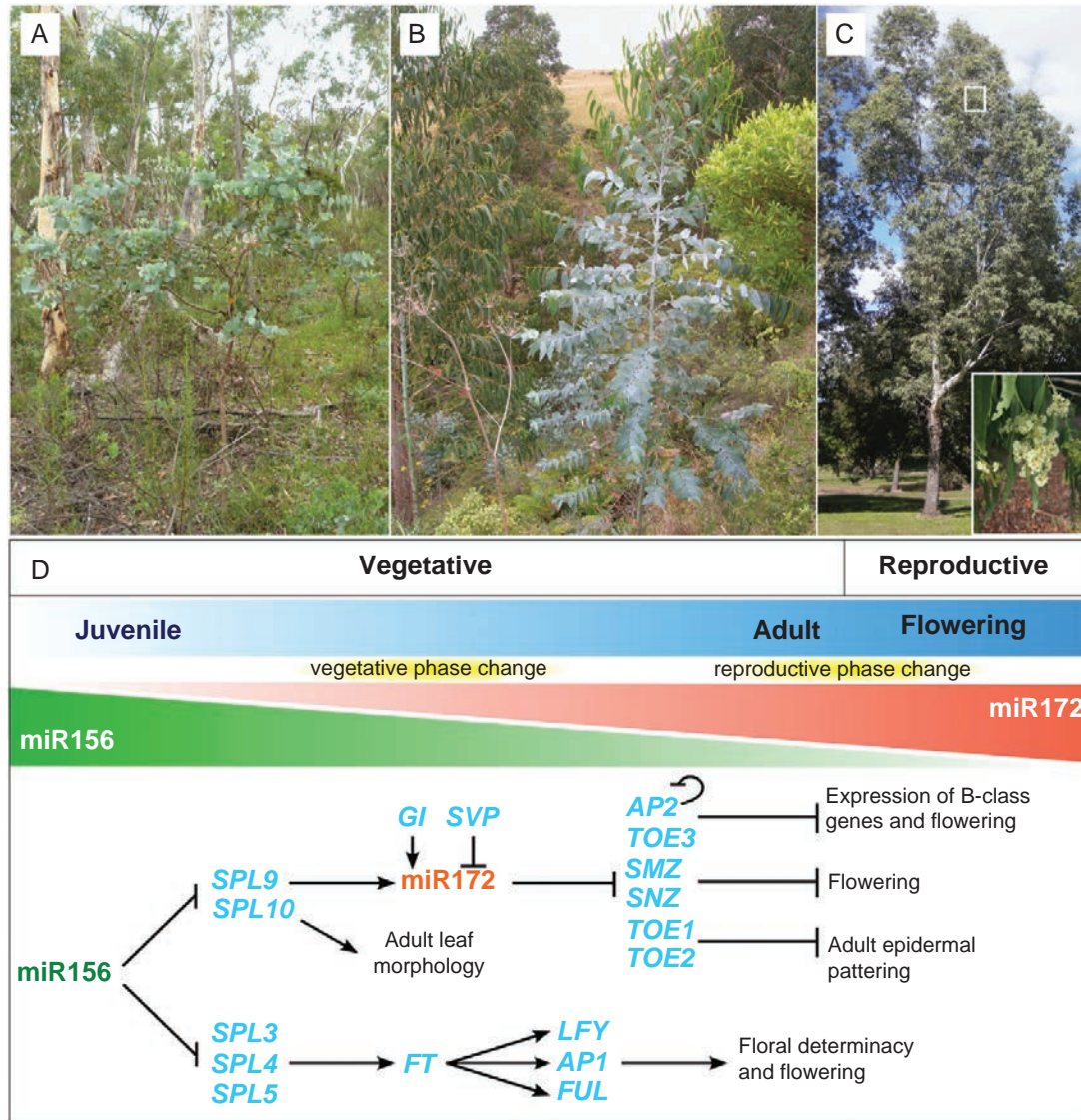


FIG. 17. The genetic control of phase change. (A–C) Example of phase change in *Eucalyptus*. (A) Juvenile phase of *Eucalyptus bridgesiana*, with the characteristic juvenile foliage with an opposite decussate phyllotaxy. (B) Vegetative phase change in *Eucalyptus* sp., with the adult foliate and spiral phyllotaxy at the distal end of the trunk and upper branches. (C) Adult reproductive phase in *Eucalyptus raveretiana*. (D) Genetic network controlling phase change in plants. Photographic credit: Wikipedia.

well known in conifers and has been termed ‘successive series reiteration’ (Edelin, 1977); it has been observed in Pinaceae, Araucariaceae, Podocarpaceae, Taxaceae and Cupressaceae (G. Chomicki, pers. obs.). In *Araucaria*, partial reiteration creates ‘successive nesting crowns’ (Veillon, 1978; Fig. 16F).

The determinants of reiteration

Auxin-mediated apical dominance plays a central role in the maintenance of the hierarchical organization among axes in a plant, and changes in the environment such as nutrient availability directly impact PAT or strigolactone signalling and thus the capacity for branching (Waters et al., 2017; Fig. 12). In old or suppressed trees, decreasing vigour and growth rate of the apical meristems can lead to the loss of apical dominance

(Moorby and Wareing, 1963; Barthélémy et al., 1989), which then can promote reiteration in (1) allowing subordinate axes to become dominant axes (immediate reiteration); or (2) by releasing axillary or epicormic buds from dormancy (delayed reiteration) (Ishii et al., 2007). Epicormic bud release typically occurs in periods of cambial inactivity, suggesting a competitive relationship between epicormic bud production and cambial activity (Bachelard et al., 1969; Nicolini et al., 2001, 2003).

The functional importance of reiteration

Accumulating evidence suggests that reiteration increases tree longevity by delaying tree ageing and enhances tree productivity in old trees. There are four main explanations for how

this may work, though they are not mutually exclusive. Tree ageing could be the result of (1) an increasing respiration-to-photosynthesis ratio with increasing age or decreasing photosynthetic efficiency more generally; (2) hydraulic limitation with increasing tree height and complexity; (3) nutrient limitation; and (4) genetically programmed senescence (Ryan and Yoder, 1997; Ishii *et al.*, 2007). The finding that the ratio of non-photosynthetic tissue over photosynthetic tissue increases with tree age (Yoda *et al.*, 1965) suggests that increased oxygen demand with age would be growth limiting (Westing, 1964; Zimmermann and Brown, 1971; Clark, 1983; Remphrey and Davidson, 1992), although this conclusion is debated (Ryan and Waring, 1992; Ryan *et al.*, 1995) and mechanisms may differ among species. Other work suggests that it is mainly the time-dependent decrease in photosynthetic efficiency that results in ageing (Yoder *et al.*, 1994; Thomas and Winner, 2002). Reiteration within the tree crown could enhance photosynthesis simply by the upright, more exposed position of the younger architectural repeats (reiterates) in the canopy (Schoettle and Smith, 1998; Ishii *et al.*, 2002; 2007).

Hydraulic conductance decreases with increasing tree size, because of increasing length and decreasing xylem conductivity (Tyree and Ewers, 1991; Ryan and Yoder, 1997; Mencuccini, 2002; Phillips *et al.*, 2002). Such a decrease in hydraulic conductance may reduce growth by limiting stomatal conductance and photosynthesis ('hydraulic limitation hypothesis'; Ryan and Yoder, 1997; Ryan *et al.*, 2006) despite mechanisms that partially compensate for a decrease in hydraulic conductance (reviewed by Ishii *et al.*, 2007). Because delayed reiteration occurs on lower branch orders (the trunk or the main branches), it decreases the hydraulic path from roots to leaves and connects young and vigorous parts of the tree directly to main branches with high hydraulic conductivity (Tyree and Ewers, 1991; Kozłowski and Pallardy, 1996; Ishii *et al.*, 2007). Trees also sequester increasing quantities of nutrients as they grow, which could self-limit their growth since woody organs are slow to decompose ('nutrient limitation hypothesis'; Gower *et al.*, 1996). Delayed reiteration might decrease nutrient loss by acting as a nutrient sink that is relocated from senescing parts of the tree (Lockhart *et al.*, 2003; Ishii *et al.*, 2007).

Genetically programmed senescence could decrease the vigour and growth potential of meristems with increasing tree age. The mechanisms are not fully understood but could include the accumulation of DNA methylation (Fraga *et al.*, 2002) and morphological gradients (discussed below). Grafting experiments of shoots from either young trees or old trees onto old crowns showed that young shoots, such as those resulting from reiteration, grow better (Connor and Lanner, 1989; Matsuzaki *et al.*, 2005), suggesting that delayed reiteration can rejuvenate a tree, perhaps because dormant buds kept their initial epigenetic status. Another important aspect of delayed reiteration is that it could rejuvenate the crown simply by developing from meristems with a young 'molecular age' (see above 'Sympodial branching'), as suggested by work on tomato (Park *et al.*, 2012, 2014).

Levels of organization, phase change and sequences of differentiation

Plants are modular organisms that are constructed by the repetition of elementary units nested in one another, the units

being phytomers, growth units, annual shoots, axes, architectural units and whole reiterated organisms (Barthélémy, 1991; Caraglio and Barthélémy, 1997; Barthélémy *et al.*, 1997; Barthélémy and Caraglio, 2007). The structure and status of any repeated unit depends on its topological position and the ontogenetic age of the plant (reviewed by Barthélémy and Caraglio, 2007; previous section). Differences arise through repetition of the elementary units (from phytomers to the architectural unit), either abruptly or continuously, and result in sequences of differentiation.

Phase change refers to the transition among the four ontogenetic phases of plants: seedling, where the primary shoot and root are established; juvenile; adult vegetative phase; and adult reproductive phase (Poethig, 2003, 2010). These phases can be morphologically highly distinct, for instance in *Eucalyptus* where the juvenile to adult phase transition is marked by a change in leaf shape and phyllotaxy (decussate to spiral; Fig. 17A–C). Conserved mechanisms involving microRNAs govern the vegetative to adult phase change in both herbs (arabidopsis, maize) and trees (*Eucalyptus*, *Acacia*, poplar and the vine *Hedera helix*) (Poethig, 2009; Wu *et al.*, 2009; Jung *et al.*, 2011; Wang *et al.*, 2011). During the juvenile phase, miR156 is highly expressed and downregulates activators of floral development, most importantly *SPL* genes (Poethig, 2009; Wu *et al.*, 2009; Jung *et al.*, 2011; Wang *et al.*, 2011; Fig. 17D). The change between the juvenile and the adult phase is mediated by downregulation of *miR156*, which occurs as a time-dependent process and is induced by a leaf-borne signal (Yang *et al.*, 2011). This downregulation occurs via an epigenetic change consisting of an increase in the trimethylation of Lys27 on histone H3 (H3K27me3), which occurs via the binding of a protein complex (Xu *et al.*, 2015). While the decreasing miR156 expression defines a vegetative gradient, another microRNA, miR172, is upregulated and promotes the adult phase and the transition to flowering (Wu *et al.*, 2009; Zhu and Helliwell, 2010). The gradual increase of miR172 expression follows the decrease in miR156 expression, because miR172 is upregulated by *SPL9*, a gene that is downregulated by miR156 (Wu *et al.*, 2009; Zhu and Helliwell, 2010; Fig. 17D). Given that both *miR156* and their *SPL* targets are conserved across land plants (Arazi *et al.*, 2005; Preston and Hileman, 2012), and in light of functional studies in various unrelated angiosperms (cited above), their function in phase change may be widespread.

Other morphological gradients include so-called pauperization, or drift, which is generally a decrease in vigour that occurs in old architectural units. A 'reproductive gradient', such as the one established by miR172, may well play a role in this phenomenon. The notion of 'morphological gradients' also relates to the physiological age of meristems, which does not reflect the elapsed time since a meristem's production, but rather its topological location and the ontogenetic stage attained by the plant (Caraglio and Barthélémy, 2007). An important study characterized the transcriptomes of tomato apices as they gradually transition from vegetative shoot to terminal inflorescences (Park *et al.*, 2012). The authors revealed a gradual, age-dependent change in the expression of thousands of genes, which defines a 'meristem maturation clock' (see also the sections 'Sympodial branching' and 'The functional importance of reiteration'). Modulation of this

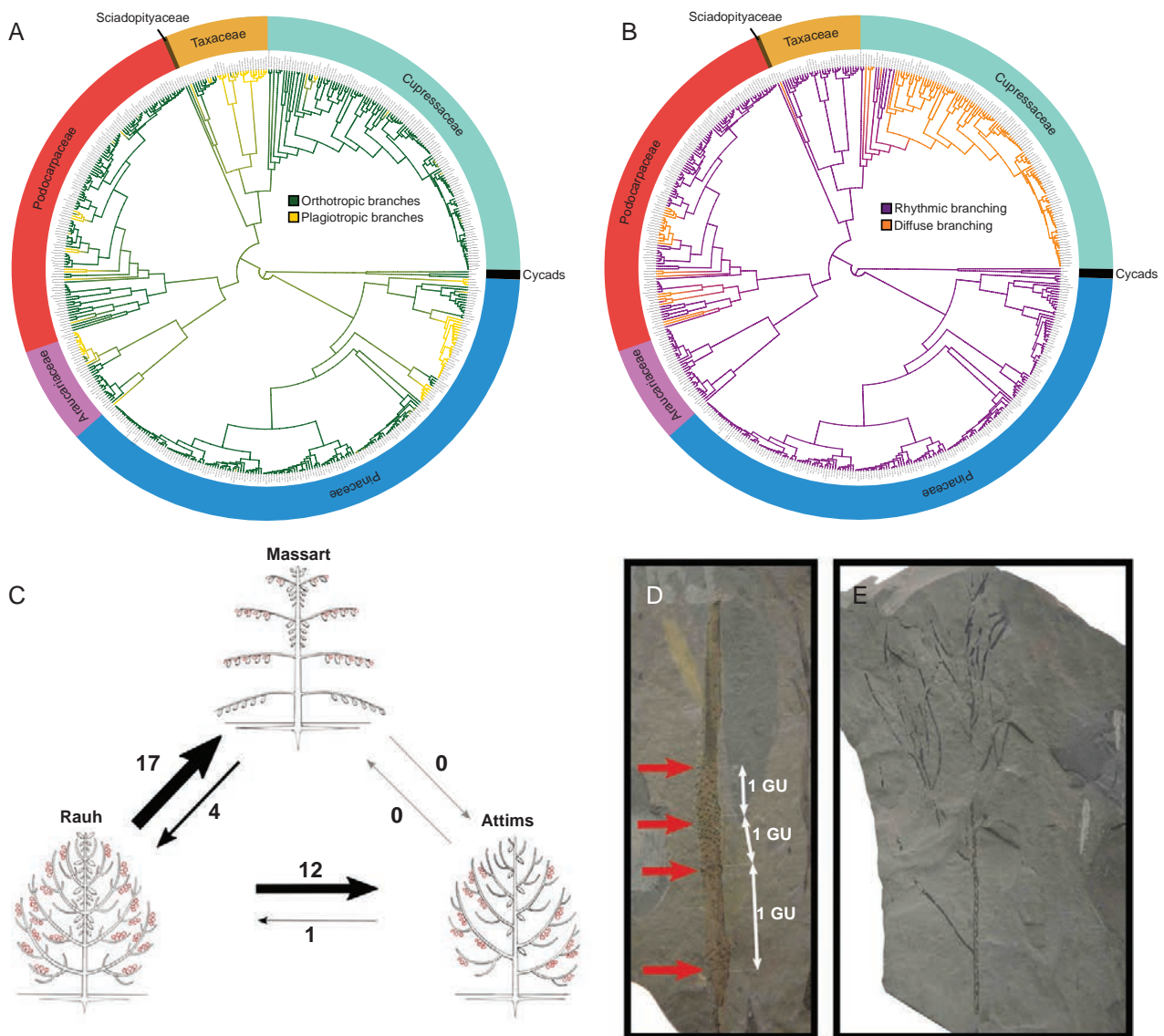


FIG. 18. The evolution of conifer architecture. Stochastic mapping ancestral state reconstruction of (A) branch growth orientation (orthotropic vs. plagiotropic) and (B) rhythmic vs. diffuse (continuous) branching on a phylogeny of approx. 80 % of extant conifers (Leslie *et al.*, 2012, courtesy of Andrew Leslie); see Supplementary Data Materials and Methods for methods. (C) Summary of evolutionary transitions between the three major conifer architectural models (Rauh, Massart and Attimis) inferred from the ancestral state reconstructions. (D) Rhythmic growth in a fossil twig of the Ginkgoales *Schmeissneria* (Jurassic, Pechgraben, Germany). (E) Diffuse branching in the Cretaceous fossil conifer *Sphenolepis kurriana*, a Cupressaceae (formerly Taxodiaceae). See Supplementary Data Materials and Methods. Photographic credit: G. Chomicki, photo taken at the Museum of paleobotany, Córdoba Botanic Garden, Spain.

meristem maturation clock by endogenous processes may be a key determinant of plant architecture. Such modulation could involve lineage-specific components, controlling for the determinacy of architectures (sympodial vs. monopodial branching for example), but could also be responsible for processes such as loss of vigour in the distal part of old architectural units. The potential for such vegetative vs. reproductive gradients to generate an array of distinct architectures is highlighted by a pioneering study that showed through genetic analysis and modelling that the entire array of known inflorescences could be generated by these two opposing gradients (Prusinkiewicz *et al.*, 2007).

THE EVOLUTION OF PLANT ARCHITECTURE

Molecular mechanisms for switching between architectural types

Carroll (2008) formulated a theory of morphological evolution and concluded that most morphological changes occur via mutation in *cis*-acting elements (promoters or enhancers) rather than changes in protein-coding genes. He restricted his examples to animal development, while here the focus is on examples from plant development and on genes that control plant architecture.

Similarly to animal developmental genes, the plant developmental toolkit shows (1) a mosaic pleiotropy, wherein developmental transcription factors are involved in multiple processes

and the patterning of morphological structures, with for instance YABBY genes regulating both leaf polarity and fruit size (Bowman, 2000; Cong *et al.*, 2008); (2) ancestral genetic complexity wherein long-separated taxa share similar developmental toolkits (Floyd and Bowman, 2007); (3) distant orthologues and paralogues that retain equivalent function, as shown for ARP genes in lycopsids and angiosperms (Harrison *et al.*, 2005); (4) morphologically similar structures of independent evolutionary origins that show ‘deep homology’, meaning that they are determined by deeply conserved gene regulatory networks, examples being lycopsid microphylls and seed plant megaphylls, both governed by the KNOX/ARP pathway (Harrison *et al.*, 2005); (5) infrequent duplication of developmental genes, suggesting that duplication is not the main driver of morphological diversity, which is supported by rare duplications before the divergence of all main land plant lineages, for instance in the class III HD Zip transcription factors that are important in leaf polarity determination (Floyd and Bowman, 2007); (6) spatial change in developmental gene expression associated with morphological divergence, as shown for shoot determinacy (Park *et al.*, 2014) or flower symmetry (Luo *et al.*, 1996); (7) *cis*-acting toolkit elements that are large and highly modular (Doebly and Lukens, 1998; Hong *et al.*, 2003); and finally (8) developmental transcription factors, such as *LEAFY* (Winter *et al.*, 2011), that are the ‘hubs’ of large regulatory networks where they target hundreds to thousand of genes.

The role of PAT in generating morphological novelty in land plants has been much debated (Bennett, 2015), but it seems unlikely that shifts in architectural models in seed plants are simply driven by changes in PAT. That said, structurally divergent paralogous lineages of auxin efflux carrier PIN proteins could have contributed to convergent shoot construction in seed plants, fern and lycopsid sporophytes, and bryophyte gametophytes (Bennett *et al.*, 2014c). Concerning architectural shifts in seed plants, they may have been driven by the remodelling of the expression of developmental genes in time and space via mutation in *cis*-regulatory elements of toolkit genes that promote the binding of novel transcriptional factors or that result in the loss of a binding site for a particular transcription factor or, alternatively, the evolution of new *cis*-regulatory elements by the insertion of transposable elements or mutations that affect the strength of the binding of particular transcription factors, similarly to animal morphological evolution (Carroll, 2008).

Phylogeny and the relationships between architectural models

All architectural models are directly or indirectly linked by morpho-anatomical traits (Figs 1–5), ultimately determined by genetic mechanisms (and perhaps also epigenetic mechanisms), as highlighted in the previous sections. Links between models may be identified using ancestral trait reconstruction methods on phylogenies; however, no study has so far performed such analyses on plant architecture. To begin unravelling the evolution of plant architecture, ancestral trait reconstructions were carried out for a few selected groups with diverse architectures and densely sampled phylogenies, namely conifers, *Aloe* and relatives, and monocaulous arborescent vascular plants.

Most conifers conform to three monopodial architectures (Rauh’s model, Massart’s model and Attims’s model; Figs

4, 5) that differ in the orthotropic or plagiotropic orientation of the branches (Fig. 1D) and in whether trunk growth and branching are rhythmic or diffuse (Fig. 1F). Our ancestral state reconstruction of conifer architecture uses a phylogeny sampling 80 % of all extant conifers (Leslie *et al.*, 2012; Fig. 18). The result suggests that Rauh’s model with rhythmic branching and orthotropic branches is ancestral in conifers, with frequent transitions to branch plagiotropy (Massart’s model) or diffuse growth (Attims’s model) and a few reversions to Rauh’s model (Fig. 18A–C). Simultaneous changes were not detected between branch growth orientation and rhythmic branching, and a model of correlated evolution of both traits was strongly rejected (Bayes factor = –188.42, a threshold of just 10 being considered very strong evidence). This suggests that either genetic constraints prevent such a transition or that the resulting architectures are maladapted. The identification of Massart’s model in the early conifer *Thucydia mahoningensis* (Thucydiaceae, Voltziales; Hernandez-Castillo *et al.*, 2003) is consistent with our reconstruction of rhythmic branching as ancestral in conifers, but suggests that the ancestral growth orientation of branches is less clear. The fossil conifer family Cheirolepidiaceae had a habit similar to Cupressaceae, and their unclear position within the conifers (Puttick *et al.*, 2017) might have implied either another event of diffuse branching evolution or diffusely branching conifers.

Species from the succulent genus *Aloe* and related genera (*Aloidendron*, *Gasteria*, *Kumara*, *Haworthia* and *Aloiampelos*) conform to three architectural models: Tomlinson, Corner and Leeuwenberg (Figs 2, 3 and 19A–C). Our ancestral state reconstruction identifies numerous bi-directional transitions between Tomlinson and Corner’s model (Fig. 19D), suggesting that basal stem clustering can easily be gained or lost. We find that Leeuwenberg’s model originates from Tomlinson’s model, not from the monocaulous Corner’s model (Fig. 19D). This suggests that the ability to branch is a pre-requisite for the evolution of Leeuwenberg’s model.

Next a dated phylogeny was used for >20 000 species of vascular plants (Zanne *et al.*, 2014) to map arborescent monocaulous plants, and investigate how many times they evolved (minimally) and whether their ancestors were predominantly woody or herbaceous. Monocaulous plants encompass three architectural models (Fig. 2): Holttum, Corner and Chamberlain. The latter is not properly monocaulous because it consists of modular growth, but a single replacement meristem grows, leading to an apparently single-stemmed tree. Cycads are unusual in that female individuals belong to Corner’s model because the reproductive structures are lateral whereas male individuals conform to Chamberlain’s model because the cones are terminal, and thus a relay meristem continues the growth (Hallé *et al.*, 1978). However, the branching mechanism involved might be dichotomy rather than axillary branching, as suggested by anatomical analyses in *Zamia* (Stevenson, 1988). A total of 118 origins of arborescent monocaulous architectures were found, with 73 for Corner’s model, 22 for Holttum’s model and 23 for Chamberlain’s model (Fig. 20). Of these 118 origins, 40 (34 %) involve the evolution of arborescent monocaulous plants from herbaceous ancestors, including such famous cases of ‘insular woodiness’ as *Echium* and *Espeletia*. This highlights that monocaulous arborescent growth forms are deeply convergent and evolved repeatedly across the plant tree of life. The

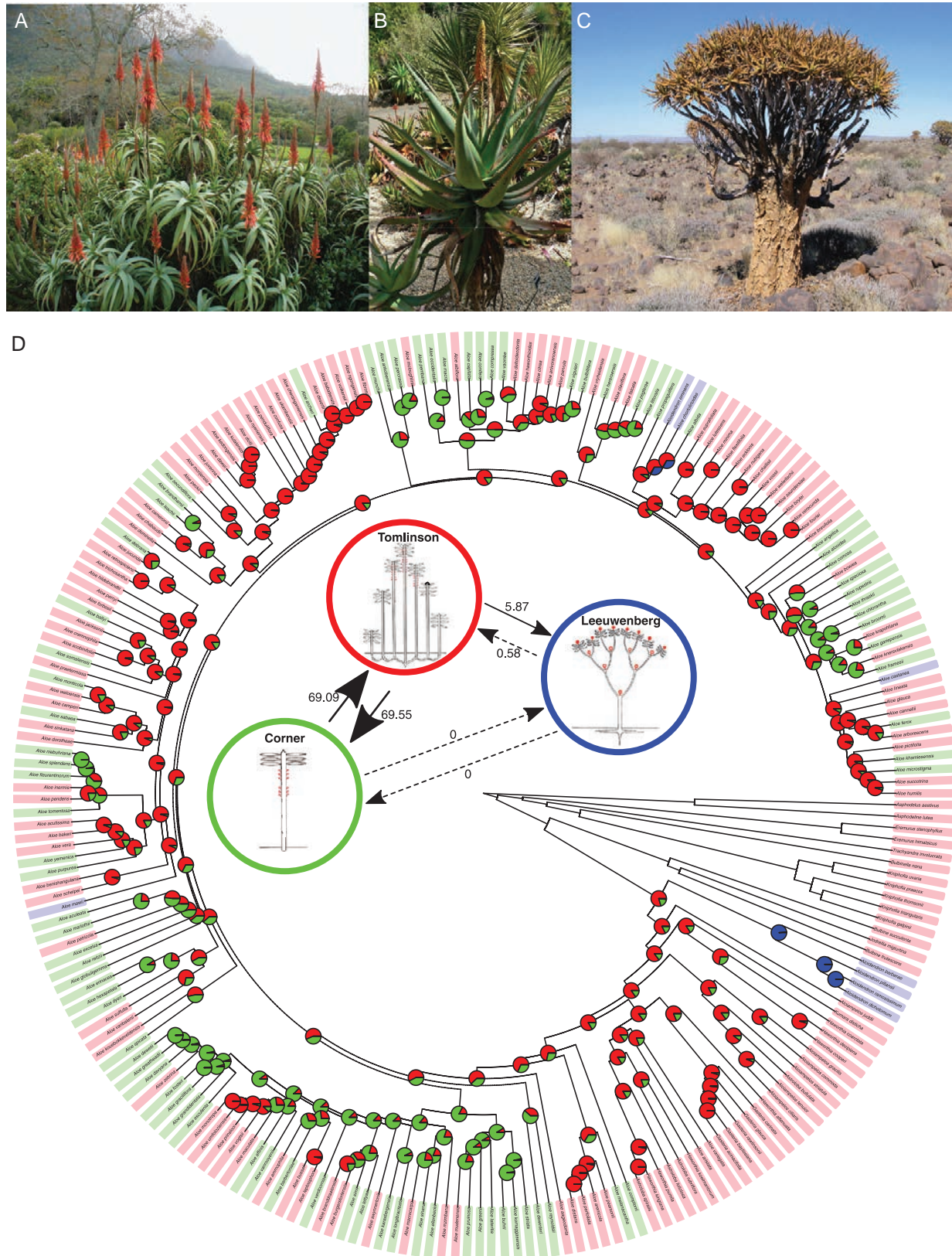


FIG. 19. The evolution of architecture in *Aloe* and related genera, using a phylogeny for 197 species of *Aloe* and relatives (Grace *et al.*, 2015). (A–C) Architectural diversity in *Aloe* and relatives. (A) Tomlinson's model in *Aloe arborescens*, with lateral (axillary) inflorescences. (B) Corner's model in *Aloe africana*. (C) Leeuwenberg's model in *Aloe dichotoma* (*Aloidendron dichotomum*). (D) Stochastic mapping ancestral state reconstruction of the main architectural models found in *Aloe* and relatives (Tomlinson, Corner and Leeuwenberg). See Supplementary Data Materials and Methods. Photographic credit: Wikipedia.

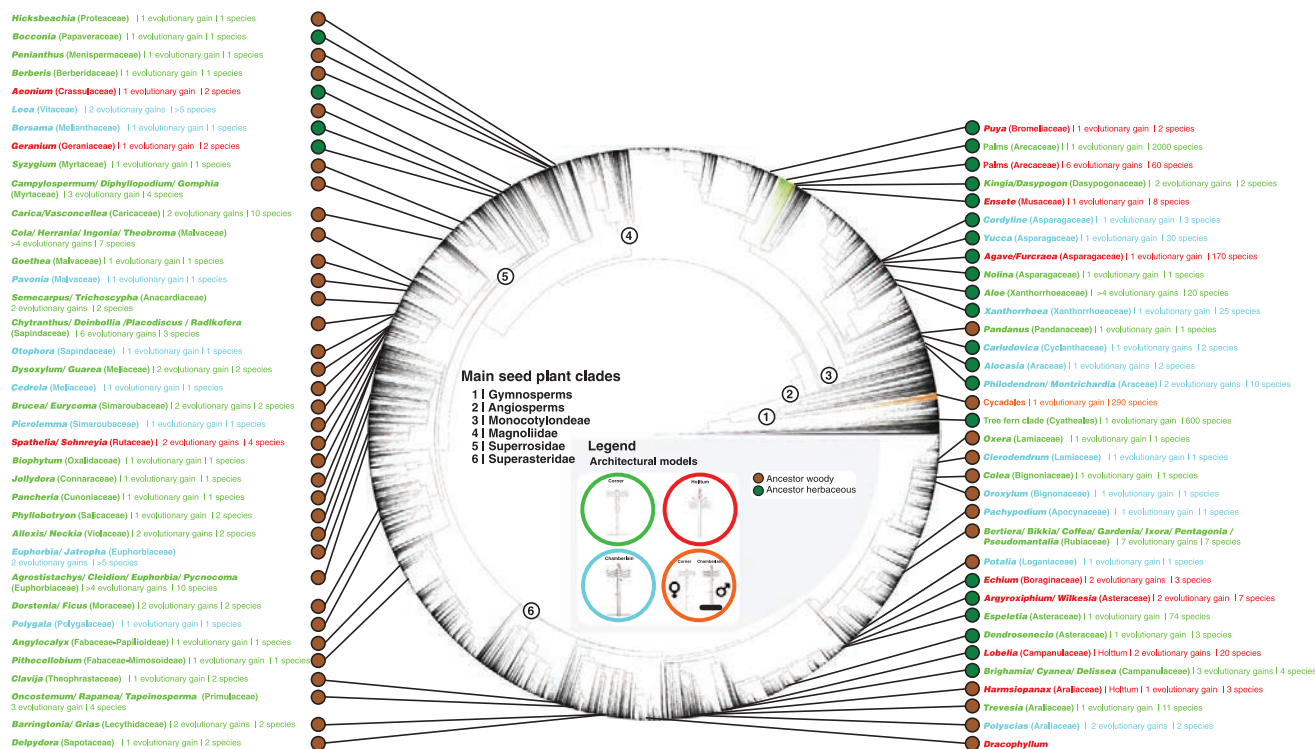


FIG. 20. The evolution of arborescent monoaxial plants. Monoaxial arborescent plants (Holttum's, Corner's and Chamberlain's models) are mapped on a >20 000 species seed plant dated tree (Zanne *et al.*, 2014).

frequency of Corner's model (monocaulous plants) through the fossil record, shown in Fig. 9B, reveals that this growth form probably originated in the mid-Devonian.

Further work in well-sampled clades is needed to resolve the evolutionary links between architectural models. Having a broad evolutionary framework for plant architecture will illuminate the evolutionary dynamics of plant growth forms, the ancestral growth forms of important groups, such as the angiosperms, and shed light on their potential adaptive values.

The macroecology of plant architecture

Plant architectural diversity is unevenly distributed across the Earth's surface (Brunig, 1976; Tranquillini, 1979), suggesting that some architectures are advantageous in certain habitats. This points to direct and indirect environmental and historical selective factors. Disentangling these factors to ask what drives the architectural disparity requires (1) precise quantification of plant architectures found under different conditions; (2) use of a phylogenetic framework and comparative methods to study the dynamics of shifts between architectural traits and biogeographic analyses to trace the evolution of architectures in space; (3) niche-modelling approaches to identify bioclimatic variables correlated with particular architectural traits; (4) eco-physiological studies quantifying associated functions; and (5) mathematical modelling to evaluate the evolutionary stability of alternative architectural strategies in given environments. While plant science is far from achieving this, scattered lines of evidence have been noted in the literature for decades, and they are summarized below.

Global disparity in plant architectures may largely result from direct and indirect effects of climate on plant growth. Seasonality, with the presence of an adverse season (either cold or dry) drastically affects plant growth. In woody plants, growth rhythmicity allows meristem protection in buds during the adverse season, and architectures with continuous growth are largely restricted to the tropics. Another strategy to cope with seasonality is the herbaceous habit, with much of the temperate herbaceous flora having evolved from ancestrally tropical lineages comprising mostly woody species. This trajectory has been shown in several families, including Apiaceae, Rubiaceae and Malvaceae (Smith and Donoghue, 2008; Beaulieu *et al.*, 2013; Zanne *et al.*, 2014). Several architectural models – for instance all those involving rhythmic growth – cannot be realized in herbs, which indirectly explains the important architectural disparities between temperate regions and the tropics. Shifts from trees to herbs could involve (1) miniaturization if the herb retains the identical architecture of the tree; (2) neoteny, where all axes will have an early reproductive phase leading to a short plant, with a potentially distinct architecture; (3) fragmentation when a fraction of the architecture of a tree is inherited in the herb, notably in the case of rhythmically growing tree ancestors; or (4) loss of tropism when a shift from an orthotropic to a plagiotropic habit drove a subsequent shift to the herbaceous habit (Hallé *et al.*, 1978). Of course, in all these cases, major anatomical changes are also involved in the origin of the herbaceous habit (Feild *et al.*, 2004), but they are not the focus of this review. Conversely, many plant lineages that lost the tree habit later reverted to it, for instance in *Echium*, where invasion of Macaronesia followed by the evolution of insular woodiness led to major architectural changes (Böhle *et al.*, 1996).

Besides climate, important factors affecting plant architecture include fire and herbivory. Fire-prone environments led to adaptations such as epicormic resprouting, which evolved synchronously with flammable biomes in *Eucalyptus* (Crisp *et al.*, 2011) and ‘underground trees’ (geoxyles) in Africa (Maurin *et al.*, 2014). Bud protection allowing fire tolerance is a key trait for species sorting in African fire-prone regions (Charles-Dominique *et al.*, 2015). Herbivory by large browsing mammals favoured highly branched ‘cage’ architectures (Staver *et al.*, 2012; Charles-Dominique *et al.*, 2017) and, in African savannah, a trade-off is evident between poorly branched ‘pole’ architectures that protect buds against fire and cage architectures that protect against herbivory (Staver *et al.*, 2012).

Another driver of architectural disparity involves selection on reproductive traits, including the rhythmicity and ‘volume’ of flowering and fruiting. Certain environments favour certain life histories and plant heights (Grime, 1973; Westoby *et al.*, 1990; Falster and Westoby, 2003), which indirectly affects a flora’s overall architectural diversity. The rhythm of reproduction with one inflorescence on monocarpic plants as in Holttum’s model vs. continuously produced inflorescences, associated with longevity, is under selection by biotic and abiotic parameters, such as pollen limitation, length and predictability of the growing season (Prusinkiewicz *et al.*, 2007), and type of pollinator (e.g. bat pollination is absent from herbaceous plants). Growth rhythmicity, besides its adaptive value in seasonal climates, is also the only means of allowing synchronous flowering, which is essential when plants grow at low conspecific densities, for instance in tropical rain forests (Borchert *et al.*, 2005). This could explain why most woody plants in aseasonal climates have retained rhythmic growth and, conversely, tropical plants growing in high population densities, such as some mangroves or some palm species, have lost it.

Plant architecture is also pivotal to efficient light capture, height, mechanical stability and hydraulics (Poorter *et al.*, 2003; 2006; Edwards *et al.*, 2014). Unsurprisingly, distinct architectural traits are involved in niche differentiation with for instance, orthotropy (Fig. 1D) associated with high light intensity, but plagiotropy (Fig. 1D, E) more common in shady environments (Fournier, 1979; Millet *et al.*, 1998). In trees, height extension and mechanical stability engage in a trade-off with light capture (Poorter *et al.*, 2003). The impact of plant architecture on functional traits structures niche differentiation not only in space but also in time. Thus, architectural traits correlate with forest succession (Millet *et al.*, 1998, 1999). The key architectural determinant of early successional species, as compared with late successional species, appears to be a species’ reiteration ability (see above). The rapid growth that characterizes early succession favours species with little potential for reiteration, whereas late successional species have high potential for reiteration, which imposes slower growth (Millet *et al.*, 1999). The potential for reiteration controls the degree of plasticity and life span (cf. section on ‘The functional importance of reiteration’), and therefore plays an important role in forest succession.

This section has highlighted some potential determinants of architectural disparity. In most cases, ‘architecture’ has not been studied from a developmental perspective as it has been here, but rather from quantitative measures such as crown width or branching level. The developmental diversity encapsulated in architectural models, however, does not directly reflect

realized architectural geometry because some species, such as *Terminalia catappa* and *Manilkara zapota*, share the same architectural model (Aubréville’s model) but have very different crown geometry; the opposite situation of similar crown geometry but different models also occurs (Fisher and Hibbs, 1982; Hamilton, 1985). Thus, the distribution and disparity of plant architectures through space appear to be the sum of environmental selective pressures acting on functional traits that are themselves dependent on architecture (mostly indirectly), and historical factors that have retained or lost architectural traits that are functionally redundant. This suggests that some aspects of plant architecture are adaptive whereas others might not be.

CONCLUSION

By its integrative approach, this study aims to show that architecture is a fundamental topic in plant biology where a dialogue between specialists in different sub-fields needs to be established. The research shows that architectural analysis can be extended to the fossil record and that dichotomously branched extinct plants present an understudied diversity of growth forms that can be summarized in 12 new architectural models. We have reviewed the developmental genetic basis of important architectural traits and pinpointed the potential molecular mechanisms controlling sympodial vs. monopodial growth, rhythmic vs. continuous growth, and axillary branching. Our exploratory phylogenetic analyses of the evolution of plant architecture in conifers, *Aloe* and monocaulous arborescent vascular plants show that some architectural traits are highly labile in given groups, whereas others are conserved, and the results reveal some of the relationships between architectural models. Ecological factors affect the distribution of plant architectural diversity and shape its evolution, and future work integrating phylogenetically informed architectural data with ecological variables will continue to unveil how plant architecture is shaped at a global scale.

SUPPLEMENTARY DATA

Supplementary data are available online at <https://academic.oup.com/aob> and consist of the following. Supplementary Materials and Methods document containing methodology for the following: epifluorescence microscopy; scanning electron microscopy; fossil phylogeny; ancestral state reconstructions of architectural traits; and branching mechanisms through time.

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