

Developmental transitions during the evolution of plant form

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THE INVASION OF LAND

Land plants evolved from aquatic algal ancestors. The algae are a polyphyletic group from which the transition to land, and acquisition of developmental features associated with land plants, have occurred many times (Lewis and McCourt 2004). Recent phylogenetic evidence points to the charophyte algal lineage as the sister group to the land plants (Figure 16.1). Developmental features shared by charophytes and land

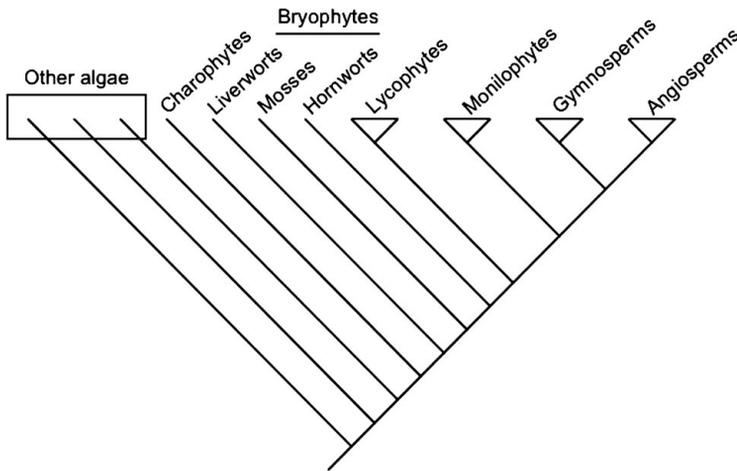


Figure 16.1 Phylogenetic relationships between extant land plants. The diagram has been compiled from phylogenies aimed at resolving particular nodes of the plant tree (Pryer *et al.* 2001, Lewis and McCourt 2004), although there is still conflict between topologies retrieved by different researchers. Angiosperm species mentioned in the text are *Arabidopsis thaliana*, *Populus tremuloides*, *Zea mays*, *Antirrhinum majus*, *Nicotiana sylvestris* and *Pisum sativum*.

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plants are cell cleavage by phragmoplasts, plasmodesmatal connections between cells, and a placental link between haploid and diploid phases of growth (Marchant and Pickett-Heaps 1973). These and other features of derived charophytes, in particular growth from an apical cell in the gametophyte (Graham 1996, Graham *et al.* 2000), suggest that many of the cellular characteristics required for the development of land plants may have evolved within the charophyte lineage.

FROM HAPLOID TO DIPLOID

The major character that distinguishes land plants from charophyte algae is the development of a diploid embryo. In charophytes, the majority of the life cycle is represented by the haploid gametophyte and only the unicellular zygote is diploid, undergoing meiosis immediately after formation. Embryo development represents a major growth transition in that meiotic division of the zygote is delayed and diploid sporophytic cells divide by mitosis, giving rise to a multicellular body. Although in the earliest land plants the gametophyte generation remained dominant, this transition in growth pattern led to a dramatic change in life history such that the sporophyte generation gradually became the dominant form (Graham 1985, Kenrick 1994, Graham and Wilcox 2000). Consequently, the dominant part of the life cycle became diploid and thus was better protected against deleterious mutations.

The transition from growth in water to growth on land required innovations that aided reproductive success in a new, drier environment (see Figure 16.2 for a schematic sequence of character acquisitions). Most land plants have waxy cuticles enclosing vegetative tissue and sporopollenin-coated spores, both of which protect against desiccation. Cuticle formation subsequently necessitated the development of stomata to permit gaseous exchange with the environment. Cuticle formation, and the re-localisation of sporopollenin deposition from the zygote in charophytes to the spores in land plants, are shared ancestral character states (plesiomorphies) of land plants. Possession of stomata may also be a land-plant plesiomorphy but because liverworts do not possess true stomata, this scenario would imply a loss in this group. The alternative explanation is that stomatal formation is homoplastic. Either way, cuticle, sporopollenin-coated spores and stomata are considered to be key innovations that conferred desiccation resistance on vegetative and reproductive structures, and so assisted in the colonisation of land (reviewed in Cronk 2001).

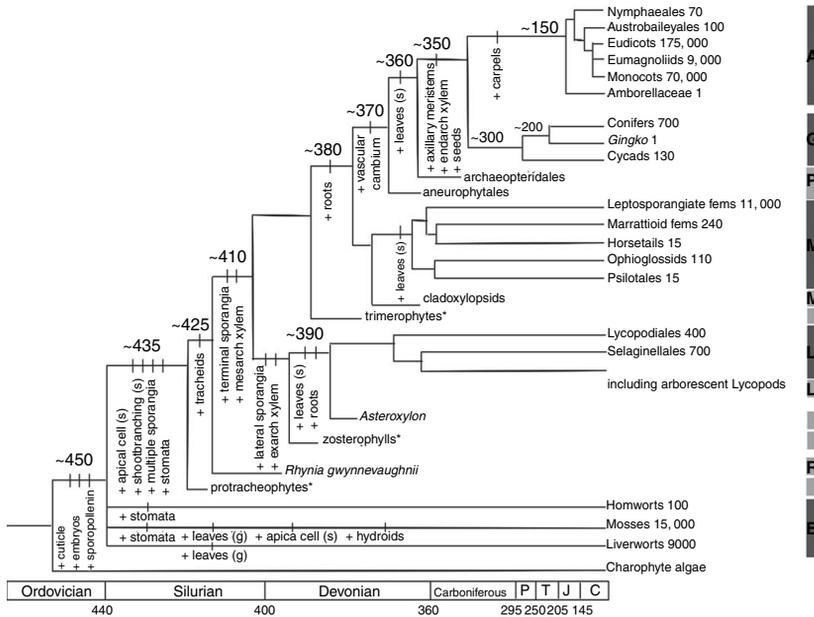


Figure 16.2 Phylogeny of selected extant and fossil land-plant taxa, showing predicted character acquisitions on each branch (in grey, s: sporophyte; g: gametophyte). Approximate timing of acquisition is given and is reflected by the bar at the base of the figure (P: Permian; T: Triassic; J: Jurassic; C: Cretaceous) using the time scales of Gradstein *et al.* (2005).

Numbers after taxon names indicate the number of extant species within the taxon, taken from Palmer *et al.* (2004). Asterisks indicate groups that are putatively paraphyletic.

Protracheophytes refers to non-vascular polysporangiates including *Aglaophyton major*, *Horneophyton lignieri* and some non-vascular *Cooksonia*-like fossils; zosterophylls refers to Zosterophylloids and Lycopytina; trimerophytes refers to taxa such as *Psilophyton* and *Pertica* (Crane *et al.* 2004). Cladoxyloids refers to *Cladoxylon*, *Hyenia*, *Pseudosporochmus* and *Lorophyton goense* (Fairon-Demaret and Li 1993). On the bar at the right, dark boxes indicate extant taxa and light bars indicate fossil taxa. A: angiosperms; P: progymnosperms (paraphyletic grade); G: gymnosperms; M: monilophytes; L: lycophytes; R: Rhyniaceae; B: bryophytes. Bryophytes are depicted as paraphyletic in accordance with Qiu *et al.* (2006); lycophte relationships are in accordance with Bateman (1994) and DiMichele and Bateman (1996); monilophyte and seed plant relationships are in accordance with Palmer *et al.* (2004).

The earliest land plants were bryophytes (mosses, liverworts and hornworts), and extant bryophytes form a paraphyletic grade at the base of land-plant phylogenies (Wellman *et al.* 2003, Qiu *et al.* 2006). Recent evidence points to the hornworts as the vascular plant sister group (Qiu *et al.* 2006). In bryophytes, as in the charophytes, the conspicuous phase of

growth is gametophytic (haploid), and plants have filamentous, thalloid and/or leafy form and bear egg-producing archegonia and sperm-producing antheridia. The diploid embryo remains attached to the gametophyte and develops into a single naked sporophytic axis that subtends a sporangium. In contrast, tracheophytes have conspicuous sporophytes and reduced gametophytes. Such sporophyte dominance is most pronounced in seed plants where the sporophyte can be a large ancient tree, yet the gametophyte lives for at most several months and can consist of just a few cells.

In the context of land-plant evolution, the significance of the transition from unicellular to multicellular growth in the sporophyte cannot be disputed. One of the most important questions to address in plant evo-devo is therefore how cell division is regulated following fertilisation of the zygote. The plane of the first cell division in bryophytes is variable; cleavage in mosses and liverworts is transverse, whereas cleavage in most hornworts is longitudinal (Kato and Akiyama 2005). The importance of such early divisions has recently been demonstrated by work with the angiosperm *Arabidopsis thaliana*, where the zygotic cell is usually cleaved unequally and transversely to give a small apical and larger basal cell. In *gnom* mutant zygotes, division is symmetrical, and as a consequence, embryos fail to develop a shoot or root. The GNOM protein functions as an auxin response factor (Geldner *et al.* 2003, 2004) suggesting that recruitment of an auxin pathway may have been pivotal in the transition to multicellular development in the sporophyte (Cooke *et al.* 2003). However, without studying GNOM function in species other than *A. thaliana*, this is wild speculation – particularly since early cell division patterns in the *A. thaliana* embryo represent only one of six patterns recognised in angiosperms (Johri 1984) and may be unrelated to patterns in other plants. It may be more relevant to study the basis of multicellularity in bryophytes, particularly as the bryophyte sporophyte presents a relatively simple morphology.

GROWING FROM THE TOP

Although bryophyte sporophytes are united by having a single axis of growth that terminates in sporangium formation, distinct growth patterns are seen in each of the main groups. Liverworts grow from cell divisions throughout the structure, mosses grow from both an apical cell and an intercalary meristem at the base of the sporophyte, and hornworts grow from the base (Kato and Akiyama 2005). In contrast, all tracheophytes grow from one or more apical cells, and this mode of sporophytic growth is a

plesiomorphy of vascular plants that had evolved by the mid Silurian (~420 million years ago [mya]).

Apical growth in most lycophytes, monilophytes and gymnosperms is thought to be restricted to one or few cells in the surface layer of the meristem, but how these meristems function is poorly understood. In contrast, angiosperm meristems are layered and have distinct zones of specialised function, and their development is reasonably well understood. In the layered meristem of *A. thaliana*, apical growth is sustained through activity of the WUSCHEL (WUS)/CLAVATA (CLV) pathway (Mayer *et al.* 1998, Brand *et al.* 2000, Schoof *et al.* 2000). The homeobox transcription factor WUS acts non-cell autonomously to promote stem-cell activity in cells overlying the WUS expression domain. In addition, WUS activity indirectly induces expression of the CLV₃ ligand in cells at the surface of the meristem. CLV₃ itself acts non-cell autonomously to activate the presumed CLV₁ receptor in cells surrounding the WUS domain. CLV activity then restricts WUS activity to a small region of the meristem; in this way, a regulated population of stem cells is maintained. Recent reports suggest that a WUS/CLV-like feedback pathway also operates in meristems of other angiosperms (Taguchi-Shiobara *et al.* 2001, Bommert *et al.* 2005, Kieffer *et al.* 2006).

Meristems in early diverging land-plant lineages are structurally different from angiosperm meristems and arguably less complex. They are more likely to resemble the ancestral growth form that existed in the late Silurian (~400 mya). In this context, it will be interesting to see whether components of the WUS/CLV pathway function to maintain stem-cell activity in non-layered meristems that facilitate apical growth or whether this pathway is a synapomorphy (acquired shared character state) of angiosperms.

BRANCHING OUT

Whereas bryophytes have unbranched sporophytes, protracheophyte fossil sporophytes from the Silurian have multiple branches that terminate in sporangia, and are therefore named polysporangiates (reviewed in Crane *et al.* 2004). Unlike extant polysporangiates, the protracheophyte fossils *Aglaophyton major* and *Horneophyton lignieri* are non-vascular. From a developmental perspective, this observation is important because in combination with the phylogenetic position of these fossil taxa, it implies that axial branching evolved before vascularisation. The switch from unbranched to branched growth habit required at least a transient switch from determinate to indeterminate shoot development. In the absence of extant leafless

polysporangiates, it is not possible to determine exactly how this was achieved at the molecular level. Presumably, either the activity of apical cells was altered, or cells in the stem were partitioned to form two distinct axes. Regardless of the exact process, such sporophyte branching mechanisms evolved before vascular tissue.

Branching occurs by different developmental mechanisms in different plant groups. In lycophytes and some monilophytes, sporophytes branch as a consequence of equal or unequal bifurcation of the shoot apex. In contrast, angiosperms branch from axillary meristems that are formed as part of what can be visualised as the phytomer unit that also includes a leaf, node and internode (Galinat 1959). These distinct mechanisms of branching suggest that the developmental toolkit adopted for branching may have been different in each case.

At least in *A. thaliana*, formation of the axillary meristem is associated with axis formation in the leaf. Transcription factors such as PHABULOSA (PHB) and KANADI, which function to distinguish and maintain adaxial (upper) and abaxial (lower) leaf domains thus play a role in axillary meristem formation (Eshed *et al.* 2001, McConnell *et al.* 2001). Specifically, adaxialisation promoted by PHB activity is required for axillary meristem formation. Once formed, outgrowth from axillary meristems is inhibited by the plant growth regulator auxin, and this inhibition is mediated by a novel plant hormone that is regulated by the MAX pathway (Booker *et al.* 2005, Bennett *et al.* 2006).

In contrast to our understanding of branching processes in angiosperms, the mechanism of bifurcation in lycophyte meristems is poorly understood with respect to the underlying genetic and physiological mechanisms. In monilophytes the actual mechanism of generating new axes of growth is disputed, with evidence of meristem bifurcation in some species and branching from rhizomes in other species (Bierhorst 1977). Clearly, both developmental and genetic analyses need to be carried out with carefully selected lycophyte and monilophyte species to determine whether similar pathways are used to promote branching in distinct plant lineages, and to provide insight into the developmental module that was first recruited to facilitate branching.

VASCULAR HIGHWAYS

Branching led to increasingly complex body plans and competition for light, which then led to the evolution of taller plants. As a consequence, the need for mechanical support and for transport of water intensified. Coupled with the origin of lignin in vascular plants, these drivers led to the evolution of

lignified conducting cells (tracheids). Whereas moss and some liverwort gametophytes transport water through conducting hydroids consisting of elongated cells with just primary cell walls, and protracheophyte fossils show evidence of a similar system (Boyce *et al.* 2003), true tracheophytes transport water through xylem cells that have lignified secondary walls.

Tracheophyte fossils indicate that tracheids first evolved in the mid-Silurian (~420 mya) (Edwards *et al.* 1983). In fossils such as *Rhynia gwynnevaughnii*, tracheids possess two layers of secondary cell wall – an inner degradation-prone layer and an outer degradation-resistant layer (Kenrick and Crane 1991). Because tracheids in well-studied extant seed plants have a single lignified secondary cell wall, the singularity of tracheid evolution has been questioned. However, tracheid secondary walls in at least one lycophyte and at least one monilophyte are bilayered as in tracheophyte fossils, supporting the argument that tracheids per se have a single origin (Cook and Friedman 1998, Friedman and Cook 2000).

The developmental mechanisms that specifically contribute to tracheid (xylem) formation in extant plants include cell-wall pitting and lignin deposition. Recent work in the angiosperms *A. thaliana* and *Populus tremuloides* has shown that the activity of two transcription factors – VASCULAR-RELATED NAC-DOMAIN6 (VND6) and VND7 – is sufficient to induce trans-differentiation of various cells into protoxylem or metaxylem vessel elements (Kubo *et al.* 2005). The relative simplicity of this switching mechanism is consistent with the reported single origin of xylem formation. However, developmental patterns vary in different plant groups. Xylem differentiation in lycophytes is exarch, in that the earliest maturing xylem (protoxylem) is at the periphery of the vascular bundle and the later maturing metaxylem is at the centre. In contrast, xylem formation in monilophytes is mesarch, with metaxylem developing both inward and outward of protoxylem relative to the centre of the bundle; and is endarch in seed plants, with protoxylem at the centre of the bundle and metaxylem at the periphery. Whether the VND system ubiquitously regulates xylem formation in land plants remains to be determined.

Although lignification is a defining characteristic of tracheids and other water-conducting cells in seed plants, biochemical analyses suggest that xylem lignification in late Silurian fossils (~400 mya) is minimal compared with that seen in extant plants (Boyce *et al.* 2003). The inferred increase of lignin deposition in xylem cells through evolutionary time (Boyce *et al.* 2003) and the developmental mechanisms operating in extant plants (McCann 1997) both suggest that cellulose secondary thickenings are a prerequisite for lignin deposition. Thus, the evolution of xylem lignification

most likely required the transfer of a pre-existing lignin biosynthesis pathway to cellulose-thickened conducting cells and the development of a mechanism for targeted cell wall deposition.

Lignified vasculature paved the way for plants to increase in height. However, without an accompanying capacity for increased girth, and hence support, an increase in height is biomechanically untenable. Expansion in girth is facilitated by growth from a secondary meristem known as the vascular cambium. The most significant cambial development is seen in the trees of extant seed plants and in fossil lycophytes that evolved tree form independently (Phillips and DiMichele 1992, Bateman 1994). The developmental processes that regulate cambial development are poorly understood, but genes that regulate shoot meristem activity also play a role in regulating cambial activity and lignin biosynthesis (Mele *et al.* 2003, Oh *et al.* 2003, McHale and Koning 2004b, Groover and Robischon 2006). This suggests that although cambial meristems arise *de novo* in growing tissue, the developmental mechanism used may be the same as that recruited during embryogenesis to form the shoot apical meristem.

DIGGING DEEP

Whereas tracheids provided a conduit for water transport in aerial parts of the plant, increasingly complex body plans and greater sporophyte surface areas demanded greater water absorption from the environment and additional mechanical support at the base of the plant. The ecological driver was thus in place for the evolution of sporophyte roots.

Charophyte algae and free-living gametophytes develop root-like structures, but 'true' roots are only found in tracheophyte sporophytes. Gametophyte 'roots' are single-celled rhizoid-like structures that are analogous to root hairs, multicellular rhizoid-like projections from a subterranean rhizome, or mycorrhizas formed following a fungal association (Raven and Edwards 2001). In these cases, the rhizoids provide conduits for water and nutrient transport but only the subterranean rhizomes enhance mechanical support. In contrast, true roots provide both transport capability and mechanical support. By definition they are multicellular, have a defined endodermis (with the exception of extant Lycopodiaceae roots), produce lateral organs endogenously and have a root cap.

Sporophyte roots first appear in the fossil record in the early Devonian (~390 mya). Earlier rootless fossils are classified into two groups, the zosterophylls and trimerophytes (Banks 1975), the xylem arrangement and sporangial position of which are reflected in extant lycophytes and euphylllophytes,

respectively. These observations suggest that the lycophyte and euphyllophyte lineages may have diverged before roots evolved (Raven and Edwards 2001). This suggestion is further supported by evidence of lycophyte roots in *Asteroxylon* fossils found in the early Devonian Rhynie Chert in Aberdeenshire (Kidston and Lang 1920), in contrast to the earliest evidence of euphyllophyte roots from the mid-Devonian cladoxylopsid fossil *Lorophyton goense* (Fairon-Demaret and Li 1993).

To date, our understanding of genetic mechanisms regulating root patterning is restricted to seed plants. In this case, work carried out mainly with *A. thaliana* has shown that a stem-cell niche is established during embryogenesis and that differentiation of cells produced from that niche depends on positional signals (van den Berg *et al.* 1997). The stem-cell niche consists of a small group of slowly dividing cells known as the quiescent centre (QC) plus four sets of initials that give rise to the cell types of the mature root (Dolan *et al.* 1993, Scheres *et al.* 1994). Stem-cell activity is regulated by the activity of two related transcription factors – SCARECROW (SCR) and SHORTROOT (SHR) (Sabatini *et al.* 2003). SCR acts cell autonomously within the QC to regulate QC identity. The QC then acts in a non-cell autonomous manner to maintain stem-cell activity of the surrounding initials. Derivatives of the initials are physically separated from the stem-cell-inducing QC and thus differentiate. SCR and SHR also play a role in regulating cell-type differentiation in these derivatives and thus contribute to radial patterning in the root (Helariutta *et al.* 2000, Nakajima *et al.* 2001). Superimposed upon the SCR/SHR system is the PLETHORA/auxin system which regulates stem-cell activity and longitudinal patterning in the root (Aida *et al.* 2004), and the WOX system (Kamiya *et al.* 2003). Significantly with respect to understanding the evolution of root structures, SCR and SHR play a role in radial patterning of the shoot (Wysocka-Diller *et al.* 2000). WOX genes are related to WUSCHEL, and components of a CLV-like pathway are involved in maintaining root meristem activity (Casamitjana *et al.* 2003). Root evolution in the euphyllophytes may therefore have involved co-option of mechanisms already functioning in the shoot. Whether similar genetic mechanisms operate in lycophytes awaits investigation but the developmental anatomy of lycophyte roots suggests that they are derived from shoots.

HARVESTING ENERGY

The next significant phase of land-plant evolution could have been driven by a large drop in atmospheric CO₂ and temperature, or by competition for light

(Beerling *et al.* 2001, Beerling 2005). Whatever the cause, lateral flattened photosynthetic organs (leaves) evolved. The evolution of leaves followed a similar trajectory to that of roots in that small leaf-like structures are present on some extant free-living gametophytes, but 'true' leaves, exhibiting lignified vasculature and multiple cell layers, are found only on tracheophyte sporophytes. Like roots, sporophyte leaves have multiple origins.

Leaves evolved on at least two separate occasions in the Devonian, once in the lycophytes and once in the euphyllophytes (monilophytes, progymnosperms and seed plants). The independent origins and morphological differences between extant lycophyte and euphyllophyte leaves have led to several theories to explain how leaves evolved. Lycophyte and euphyllophyte leaves are traditionally termed microphylls and megaphylls, respectively. Most microphylls have a single vascular trace and no leaf gap at the point of insertion in the stem whereas megaphylls have complex venation and stem leaf gaps. The utility of the microphyll/megaphyll dichotomy is questionable, particularly since microphylls are seen in some euphyllophytes and some lycophytes have leaves with complex venation. However, the distinction fuelled leaf evolution theories for many years. Bower (1935) first proposed that microphyllous leaves arose as enations from the stem that later became vascularised. Kenrick and Crane (1997) challenged this theory, arguing instead that microphylls were derived from bracts subtending sporangia and that sterilisation of one member of a sporangial pair resulted in the leaf. Megaphylls, however, were proposed to derive as a consequence of modified stem branching patterns. The proposed mechanism was first put forward in Zimmermann's telome theory, which invoked the idea that one branch in a dichotomously branched axis became overtopped, and then went through a progressive series of planation, webbing and fusion events to form a complex flattened lateral organ (Zimmermann 1965, Kenrick 2002). Notably, there is fossil evidence to support all of the intermediate stages but there are several criticisms of the theory (see Stein and Boyer 2006 for discussion). Despite conflicting theories of evolutionary mechanism, the separate origin of lycophyte and euphyllophyte leaves has rarely been questioned.

As with most other developmental processes, leaf development is best understood in a few model angiosperms. In this case, however, the mechanism has been examined in several different species and a shared process has been revealed. Determinate leaves are formed on the flanks of indeterminate shoot apical meristems (SAM). Indeterminacy in the SAM is maintained through the activity of *KNOTTED1*-like homeobox (*KNOX*) transcription factors, whereas determinacy in the leaf is maintained by repressing

KNOX activity (Smith *et al.* 1992, Jackson *et al.* 1994). In *A. thaliana*, *Zea mays* and *Antirrhinum majus*, the orthologous myb transcription factors ASYMMETRIC LEAVES 1, ROUGH SHEATH 2 and PHANTASTICA (ARP) were found to mediate KNOX repression in the leaf (Waites and Hudson 1995, Schneeberger *et al.* 1998, Timmermans *et al.* 1999, Tsiantis *et al.* 1999, Byrne *et al.* 2000). Later studies showed that similar mechanisms operate in *Nicotiana sylvestris* (McHale and Koning 2004a) and *Pisum sativum* (Tattersall *et al.* 2005), leading to the suggestion that the KNOX/ARP module may be a fundamental requirement for leaf development, at least in angiosperms.

Unlike many other developmental processes, the genetic basis of leaf development has also been studied in non-seed plants, most notably in the lycophyte *Selaginella kraussiana*. Despite *S. kraussiana* having meristems and leaves that are morphologically distinct from those seen in angiosperms, the KNOX/ARP pathway also regulates the switch from indeterminate shoot to determinate leaf growth (Harrison *et al.* 2005). As lycophyte and seed-plant leaves are thought to have evolved independently, this observation implies that the same mechanism was recruited twice in parallel, and thus suggests that there was a developmental constraint on leaf evolution. In this context, it will be interesting to determine the role of the KNOX/ARP pathway in monilophytes. However, the observation that the same developmental mechanism underpins leaf development in at least one lycophyte and in various seed plants also supports the view that leaves per se, or at least the potential to produce leaves, is a plesiomorphy of tracheophytes.

REPRODUCTIVE TRANSITION

Before the late Devonian, plants reproduced via spores, with most lineages being homosporous and some heterosporous (Bateman and DiMichele 1994). Fertilisation required water, or at least moist conditions, because sperm swim. The evolution of seed plants, the oldest fossils of which date from the late Devonian (~360 mya) (Gillespie *et al.* 1981), changed both the developmental and environmental landscape. In seed plants the female gametophyte develops inside a modified and protected megasporangium (the nucellus). The male gametophyte is the pollen grain that develops within the microsporangium (the pollen sac). Female and male reproductive organs are borne on condensed and modified branching systems that are flowers or cones in gymnosperms, and flowers in angiosperms (reviewed in Bateman *et al.* 2006). These modifications permitted radiation of the seed plants by allowing dispersal of pollen and seed, and specialisation to

attract animal pollinators. Genetic events that led to specialised functions on reproductive shoots in angiosperms, such as reproductive fate modified organ fate and enclosure of floral organs, are reasonably well characterised in model angiosperm species. This work has been extensively reviewed in recent literature and will not be discussed here (Endress 2001, Albert *et al.* 2002, Theißen *et al.* 2002, Frohlich 2003, Irish 2003, Irish and Litt 2005, Bateman *et al.* 2006). Suffice to say that the data obtained have provided a foundation for exciting advances in species that represent transitional evolutionary stages, and have provided a framework for addressing questions about floral evolution and development.

FUTURE CHALLENGES

As can be seen from the overview provided, the field of plant evo-devo currently offers more questions than answers. This is particularly true in relation to macro-evolutionary questions. So what are the major challenges for the future? Most noteworthy is the conflict between phylogenetic hypotheses suggesting which bryophyte lineage is sister group to tracheophytes. Until this is known, hypotheses of character state transitions within the bryophytes, and between bryophytes and vascular plants, cannot be critically examined. Elsewhere, the phylogeny is well resolved at deep nodes and the major limitations are those concerning the ease with which non-flowering plant species can be grown in the laboratory and can be experimentally manipulated. Owing to the amount of time needed to establish different species as experimental organisms, this is an area that needs wide consultation and agreement. Despite these limitations, the field is expanding, not only to ask questions of how developmental mechanisms evolved but also to look at the variety of mechanisms operating in extant plant lineages, particularly in response to changing environments. With genomes currently being sequenced in selected mosses, lycophytes and gymnosperms, and RNAi technologies being developed in several relevant species, the future is both exciting and unpredictable. Furthermore, there are plenty of empty niches available for young investigators who are not afraid to work with non-model systems.

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