

The Regulation of Compound Leaf Development¹

Geeta Bharathan and Neelima Roy Sinha*

Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794–5245 (G.B.); and Section of Plant Biology, University of California, Davis, California 95616 (N.R.S.)

In higher plants, the shoot apical meristem generates the radially symmetrical stem and also produces, in succession, bilaterally symmetrical lateral organs called leaves. Photosynthetic light capture occurs in leaves. In addition, leaves may also function to perceive and transmit environmental signals to other plant organs. Leaves come in two basic forms, simple (blade or lamina not subdivided into multiple units or leaflets) and compound (lamina subdivided into leaflets). The two leaf types can be found in related species of the same genus. In addition, certain heterophyllic aquatic species can switch from making simple leaves to compound leaves on transfer from terrestrial to aquatic environments (Allsopp, 1965). Compound leaves may confer an advantage in air exchange (Gurevitch and Schuepp, 1990) and reduce herbivore damage (Brown and Lawton, 1991). Given the wide ranging implications of variation in leaf form, an interesting question is whether the leaf in ancestral angiosperms (and other groups) was simple or compound.

MORPHOLOGY OF COMPOUND LEAVES

Compound leaves consist of a petiole and several leaflets, each of which may or may not have a short petiolule. Leaflets may be arranged along a main axis, the rachis (pinnate), or emerge from one point at the distal end of the petiole (palmate). Most compound leaves are determinate, bilaterally symmetrical structures and usually produce a defined number of leaflets. In dicots, compound leaves are very similar to simple leaves in initiation and growth patterns. Leaflets can be produced by one of three routes: acropetal, basipetal, or divergent (Gifford and Foster, 1988). In ferns and angiosperms, the marginal meristem dilates shortly after primordial initiation and fractionates to produce pinnae (Hagemann, 1984). As pinnae are generated, marginal meristem thickness declines until the last period of growth leads to pinnae lamina formation. In the palmately compound leaf in the monocot *Arisaema* spp., a member of the Araceae, the apex of the primordium becomes hood like and plicately folded at right angles

to its surface (Peraisamy and Muruganathan, 1986). Each fold gives rise to a leaflet by differential growth of different parts of the fold. This is in marked contrast to palm leaf development. Kaplan et al. (1982a, 1982b) have shown that pleated folds appear on the palm leaf primordium. The folds are then dissected into individual laminas by abscission of a layer of cells from one surface of the pleated primordium. Thus, palms and aroids (both monocots) have very different compound leaf development. Certain tropical plants in the family Meliaceae have pinnately compound leaves in which leaflet initiation at the apex continues for years (Fisher and Rutishauser, 1990). Some fern fronds show almost indefinite growth from an apical zone of mitotic activity, and all ferns have acropetal leaflet initiation (Steeves and Sussex, 1989).

HOMOLOGY OF COMPOUND LEAVES

Morphological Analyses

There is some discussion in the literature regarding the nature of highly dissected versus compound leaves. Leaves bearing distinct leaflets are termed compound leaves by some researchers (Steeves and Sussex, 1989; Bell, 1991). Others have preferred to treat leaves as a continuum between simple and highly dissected (Kaplan, 1975). The dicot simple leaf has been suggested to be derived phylogenetically from a pinnately compound leaf, with smooth-edged leaf blades arising by suppression of marginal meristem fractionation (Hagemann, 1984). An opposing view suggests that the simple leaf is the ancestral form, which is maintained in ontogeny, and that leaflets in compound leaves develop by similar mechanisms, as do lobes in a simple leaf (Eames, 1961). The ontogenetic relationship of the dicot compound leaf to the simple leaf is unclear (Merrill, 1986a, 1986b). The true homologies of compound leaves have been a matter of debate. They have been considered true lateral organs with homologies to simple leaves (Kaplan, 1975; Hagemann, 1984) or structures that are intermediate between leaves and shoots (Fisher and Rutishauser, 1990; Lacroix and Sattler, 1994).

Phylogenetic Analyses

The primary photosynthetic structures of the earliest vascular plants were branched axes, and the first

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* Corresponding author; e-mail nrsinha@ucdavis.edu; fax 530-752-5410.

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identifiable leaves in the fossil record are believed to represent modified three-dimensional lateral branch systems (Zimmerman, 1952). Extant vascular plants exhibit an enormous range of leaf forms broadly grouped into two categories, compound and simple leaves. The evolutionary transition from lateral, flattened branch systems to compound leaves, now identified as distinct organs, is represented in the extant groups, ferns and cycads, in which it occurred independently (Stewart and Rothwell, 1993; Kenrick and Crane, 1997; Doyle, 1998). In other words, compound leaves of vascular plants are not all homologous. Do different mechanisms underlie their development? Many angiosperms also produce compound leaves, and the same question may be asked for this group.

Fossil evidence suggests that the ancestral angiosperm leaf type was simple (Doyle, 1998). The scattered occurrence of compound/complex leaves in families such as Solanaceae and Asteraceae, on the one hand, and Ranunculaceae, on the other, points to several independent origins of this feature in the dicots. Preliminary results from phylogenetic analyses using recent hypotheses of angiosperm relationships support this idea (Goliber et al., 1998). The occurrence of multiple origins of compound/complex leaves in angiosperms permits tests of hypotheses about their mode(s) of origin. For instance, it has been suggested that the evolution of the compound/complex leaf in dicots is the result of homeosis—expression of “leaf” programs within the shoot-like compound/complex leaf (Lacroix and Sattler, 1994; Rutishauser, 1995). These leaves might represent reversals to an ancestral condition such as that in cycads, or they might be the result of mechanistic innovations. On the other hand, deeply lobed or compound leaves could have arisen from simple leaves by a suppression of the blade expansion program in certain regions of the leaf primordium. These hypotheses are not mutually exclusive.

These analyses suggest that compound leaves are derived from either elaborated simple leaves or reduced branch systems. With the identification of genes that play a role in morphogenesis, it is now possible to propose hypotheses for the mechanistic bases of compound leaf development and test them using developmental and evolutionary tools.

Genes Regulating Morphogenesis in Vascular Plants

We expect that the basic set of components involved in the regulation of leaf morphology would include key regulatory genes, such as *KNOX*, *LEAFY*, and *PHANTASTICA*.

KNOTTED1-like class I homeobox genes (*KNOXI* genes) have a fundamental role in shoot meristem formation and axis development. Homeobox proteins are fundamental to multicellular eukaryotic development and have been characterized from ma-

ior eukaryotic groupings (Bürglin, 1994). Plant homeobox genes of the *KNOTTED* family (*KNOX*) belong to the *TALE* superclass of homeobox genes, which also includes *PBC*, *TGIF*, *MEIS*, and *IRO* in animals and *BELL* in plants (Bürglin, 1994, 1997). Phylogenetic analyses reveal that these homeobox genes were already present in the common ancestor of plants, animals, and fungi (Bharathan et al., 1997), and, therefore, study of their function should increase understanding not only of plant development but also of multicellular eukaryotic organisms in general. The *KNOX* genes fall into two classes (Kerstetter et al., 1994). Although no function is known for the class II *KNOX* genes, the class I *KNOX* genes (*KNOXI*, e.g. *STM1*, *RS1*, *KN1*, *LeT6*) appear to play a fundamental role in shoot apical meristem formation, maintenance, and segmentation (Vollbrecht et al., 1990; Jackson et al., 1994; Schneeberger et al., 1995; Long et al., 1996; Chen et al., 1997). Some of these genes may also determine leaf characteristics as fundamental as simple versus compound morphology (Sinha et al., 1993; Chuck et al., 1996; Hareven et al., 1996; Chen et al., 1997). *KNOXI* genes are expressed only in the shoot apical meristem and unexpanded shoots, and not in the incipient leaf primordium, of simple leaf-producing apices in both dicots and monocots (simple-type pattern; Jackson et al., 1994; Lincoln et al., 1994a; Hareven et al., 1996; Chen et al., 1997). Overexpression of *KNOXI* in these plants results in the formation of leaves with lobes and ectopic shoots (Sinha et al., 1993; Lincoln et al., 1994b; Chuck et al., 1996). In contrast, in the complex-leafed tomato (*Lycopersicon esculentum*), *KNOXI* genes are expressed in the apical meristem and in leaf primordia (Hareven et al., 1996; Chen et al., 1997), and overexpression results in increased ramification of the complex morphology (Hareven et al., 1996; Chen et al., 1997; Janssen et al., 1998). These differences in *KNOXI* expression and effect in leaves of contrasting morphology suggest that *KNOXI* genes may provide a degree of indeterminacy to the leaf primordia in tomato, thereby leading to an extended stage of morphogenesis and a more complex leaf form.

The *FLORICAULA/LEAFY* gene encodes a protein with a transcriptional activation domain (Coen et al., 1990; Weigel et al., 1992). Mutations in *FLO/LFY* result in replacement of flowers with leaf-bearing shoots and a reiteration of the inflorescence phase of development. The *FLO/LFY* gene product appears to be necessary for the production of determinate floral meristems. Whereas *FLO/LFY* expression is absent from vegetative meristems in Arabidopsis and *Antirrhinum majus*, the gene is expressed in newly initiated leaf primordia (Blazquez et al., 1998). In tobacco (*Nicotiana tabacum*) meristems, the *FLO/LFY* homologs *NFL1* and *NFL2* are expressed in vegetative shoot apical meristems in cells that may be precursors to procambium, as well as in the peripheral zone

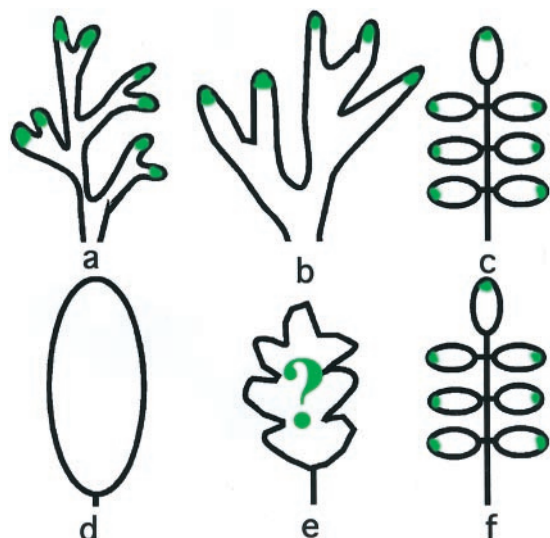


Figure 1. Hypothetical stages in evolution of simple leaves from shoot systems and their subsequent elaboration into compound leaves. a, A three-dimensional branching reproductive or vegetative shoot system. b, Reduction in branching and flattening of the branches. c, A complex leaf in ferns or cycads. d, Reduction of *KNOX/FLO/LFY* expression to lead to a simple leaf in angiosperms. e, It is unclear whether there was a hypothetical angiosperm ancestor with lobed leaves or is its *KNOX/FLO/LFY* expression state known. f, The elaboration of a compound leaf by acquisition of *KNOX/FLO/LFY* expression in the leaf primordium giving rise to leaflets. Green represents *KNOX/FLO/LFY* expression (hypothetical in a–c and e; observed in d and f). Although the mature forms are depicted, the expression would occur in earlier stages (primordia) of these structures.

of the shoot apex. It has been proposed that the role of *NFL* may be to establish determinacy for recent derivatives of apical initial cells (Kelly et al., 1995). Hofer et al. (1997) have shown the *unifoliata* mutation in pea (*Pisum sativum*) to be caused by deletions or alterations in the *PEAFLO* gene (the pea homolog of *FLO/LFY*). Alterations in flower development accompany leaf abnormalities in the *uni* mutation. *PEAFLO* is expressed in initiating leaf primordia and becomes restricted to the more distal (leaflet or tendril initiating) regions of the leaf in older primordia. Whereas loss of *FLO/LFY* function leads to indeterminacy in inflorescence and floral meristems, loss of *PEAFLO* function prevents the acquisition of a transient phase of indeterminacy in pea leaves, preventing leaflet initiation and leading to production of a single lamina in the *uni* mutation (Hofer et al., 1997). This effect of *PEAFLO* on pea leaf architecture may be the result of interactions with other, locally restricted, genes such as *COCH*, *AF*, and *TL*. Furthermore, unlike tomato, the pea compound leaf does not express *KNOX* genes (Gourlay et al., 2000).

PHANTASTICA, an MYB domain-encoding gene, has also been shown to play a role in leaf development (Waites and Hudson, 1995). Mutations at the *PHANTASTICA* locus in *A. majus* lead to loss of ab-adaxial polarity in leaves and floral organs

(Waites and Hudson, 1995). It has been suggested that the juxtaposition of abaxial and adaxial fates allows for blade growth (Waites and Hudson, 1995; McConnell and Barton, 1998). Although a role for the *PHAN* gene in leaf initiation events has not been elucidated, the gene is expressed in a pattern complementary to that seen for *STMI* (Waites et al., 1998). The maize *PHAN* ortholog (*RS2*) serves to down-regulate class I *KNOX* gene expression in leaf primordia (Taylor, 1997; Schneeberger et al., 1998; Timmermans et al., 1999; Tsiantis et al., 1999; Byrne et al., 2000). *PHAN* has been shown to play a role in generation of the leaf blade in *A. majus*, and reduced *PHAN* leads to suppression of blade growth (Waites and Hudson, 1995). Other genes displaying similar roles in generating blade growth are the *YABBY* (Sawa et al., 1999; Siegfried et al., 1999) and *PHABULOSA* (*PHAB*) gene families (McConnell and Barton, 1998; McConnell et al., 2001).

THE INVOLVEMENT OF AS YET UNKNOWN LOCI IN LEAF EVOLUTION

Although it is reasonable to presume that genes with known functions/expression patterns will have a role in the morphogenesis and evolution of leaf complexity, it is likely that a number of as yet unknown loci also play a role. With near-saturation mutagenesis in maize (*Zea mays*) and *Arabidopsis* (both model systems with simple leaves), no mutation has been found that causes compound leaves to be produced. Furthermore, although we know that increased expression of *KNOX/LEAFY* genes is seen to occur in compound-leaved species (like tomato/pea), experimental overexpression of these genes in simple-leaved maize or *Arabidopsis* does not cause the production of compound leaves. In addition, genes such as *CLAVATA*, by interacting with *KNOX* genes (Clark et al., 1996), may also have a minor role in regulating leaf complexity. We hypothesize that

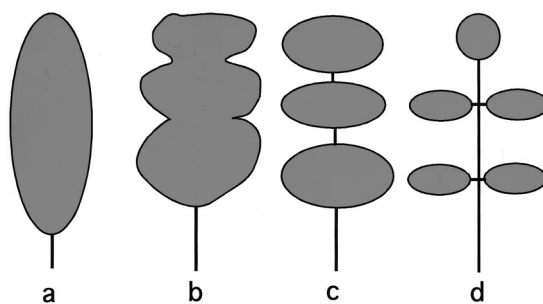


Figure 2. Hypothetical stages in compound leaf evolution by regulation of *PHAN* expression. a, A simple leaf with ab-adaxial polarity throughout, leading to uniform blade expansion. b, Reduction in ab-adaxial polarity in certain regions leads to suppression of blade formation. c, Further reduction in ab-adaxial polarity leads to regions with no blade. d, In the final state, rachis and petiolules represent regions of reduced blade, whereas leaflets are regions with expanded blade.

differences in leaf morphology are related, at least in part, to differential expression of key genes, such as *STM*, *LFY*, *PHAN*, *YABBY*, and *PHAB*, during development of the different leaf types. This hypothesis is reasonable in the light of data suggesting that the expression of *KNOXI* genes and *PHAN* in tomato is unique and different from that seen in maize and *Arabidopsis* (Hareven et al., 1996; Chen et al., 1997; Parnis et al., 1997; Koltai and Bird, 2000).

HYPOTHESES FOR COMPOUND LEAF MORPHOGENESIS

According to the telome theory (Zimmerman, 1952) complex leaves originated from indeterminate shoots, and these events occurred independently in the fern and seed plant lineages (Stewart and Rothwell, 1993). These indeterminate shoots likely expressed the *KNOXI* genes (known to play a role in shoot meristem maintenance and organization). In the angiosperms, the ancestral leaf form was simple (perhaps generated by suppression of *KNOXI* expression in some appendages), and complex leaves arose independently multiple times in this group (Goliber et al., 1998). We propose that this ancestrally simple leaf became complex by one of two routes. The primordium may have acquired indeterminacy by gaining either *KNOXI* or *FLORICAULA/LEAFY* function in leaf primordia and thus became complex (Fig. 1). Alternatively, *PHAN* expression was regulated in the primordium so that blade growth was interrupted in parts leading to a dissected leaf (Fig. 2).

Analysis of gene expression patterns in a phylogenetic context might help answer this question. The role of the *KNOX* genes and *LFY/FLO* in leaf evolution and development and the role of *PHAN/YAB/PHAB* in regulating dissection particularly in relation to simple versus compound leaves should help discriminate between the two alternative hypotheses proposed above. It should be noted that, because *PHAN* has been shown to regulate *KNOXI* expression, the role of these two kinds of genes may not be mutually exclusive in the context of compound leaf generation. It has been shown that several mutations that cause the *Arabidopsis* leaf to become lobed show ectopic *KNOX* expression in these lobed leaves (Ori et al., 2000). With an improved understanding of vascular plant relationships (Kenrick and Crane, 1997; Pryer et al., 2001) and molecular regulation of development (Ori et al., 2000), new ways will be utilized to analyze unique morphological features in plants.

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