Acta Societatis Botanicorum Poloniae

DOI: 10.5586/asbp.3529

Publication history
Received: 2016-12-05
Accepted: 2016-12-19
Published: 2016-12-31

Handling editors
Beata Zagórska-Marek, Faculty of Biological Sciences, University of Wrocław, Poland
Przemysław Prusinkiewicz, Faculty of Science, University of Calgary, Canada

Authors' contributions
EMG and AB planned, disscussed, and wrote the article

Funding
This work was supported by the University of Wrocław (grant No. 1068/S/IBE/16).

Competing interests
No competing interests have been declared.

Citation
Gola EM, Banasiak A. Diversity of phyllotaxis in land plants in reference to the shoot apical meristem structure. Acta Soc Bot Pol. 2016;85(4):3529. https://doi.org/10.5586/asbp.3529

INVITED REVIEW

Diversity of phyllotaxis in land plants in reference to the shoot apical meristem structure

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Abstract

Regularity and periodicity in the arrangements of organs in all groups of land plants raise questions about the mechanisms underlying phyllotactic pattern formation. The initiation of the lateral organs (leaves, flowers, etc.), and thus, their spatio-temporal positioning, occurs in the shoot apical meristem (SAM) and is related to the structure and organogenic activity of the meristem. In this review, we present some aspects of the diversity and stability of phyllotactic patterns in the major lineages of land plants, from bryophytes to angiosperms, in which SAM structures differ significantly. In addition, we discuss some of the possible mechanisms involved in the formation of the recurring arrangement of the lateral organs.

Keywords

phyllotaxis; shoot apical meristem (SAM); apical cell; initial cells; land plants

Introduction

Formation of the lateral organs (leaves, flowers, etc.) at the shoot apical meristem (SAM) is a spatially and temporally controlled iterative process [1,2]. Because of its periodic nature, the lateral organs are arranged in regular patterns at the shoot surface. This intriguing phenomenon, called phyllotaxis, is found in all major lineages of land plants. The same major categories and types of phyllotactic patterns occur in various phylogenetically distant groups of plants, regardless of their SAM structures and type of the initiated organs. Surprisingly, the same phyllotactic organ arrangements occur even in a thallus-forming brown alga, *Sargassum* (see this issue), suggesting that the formation of phyllotactic patterns is a universal process across the plant kingdom. However, most phyllotaxis-related research has focused on several groups of angiosperms and conifers for which empirical data on the frequency and diversity of phyllotactic patterns are available, as are proposed putative mechanisms to explain their formation. Much less attention is paid to other land-plant lineages, for which information about phyllotaxis diversity and pattern frequency is scattered and incomplete, if available at all. Research on those groups of plants, however, is of great value, as it can shed light on the mechanisms that regulate phyllotactic pattern formation. Here, we focus on the universal patterns of organ arrangements in all major land-plant lineages, from bryophytes through lycophytes and monilophytes, to gymnosperms and angiosperms. Importantly, SAM organization varies significantly among these groups of plants in terms of the numbers and shapes of the initial cells; for example, meristems in bryophytes, monilophytes, and some lycophytes have a single structurally and functionally distinct apical cell (AC), whereas meristems of lycopods and seed plants have multiple initial cells [3]. As the meristem is the site of organogenesis and formation of leaf primordia, its structure and divisional activity are important in determining subsequent leaf arrangement and phyllotactic pattern.

Here, we review the relationship between phyllotactic arrangement and SAM structure in land plants, and discuss the possible factors and/or mechanisms involved in the formation of recurring phyllotactic patterns among phylogenetically distant lineages.

Types of patterns: terminology

Two major categories of phyllotactic patterns are recognized in plants, spiral and whorled, both of which include several different types of patterns [4–6].

Spiral phyllotaxis is formed when organs successively initiated at the apex are circumferentially displaced from one another by an angular distance known as the divergence angle. These successively initiated organs can be connected with an imaginary spiral (helical) line, which is called an ontogenetic spiral (helix) (Fig. 1a). If one organ is initiated per node then one ontogenetic spiral is sufficient to link all elements, resulting in a monojugate phyllotactic pattern (monojugies) (Fig. 1a); when more elements are initiated in a node, more parallel lines are necessary to link all elements, resulting in a multijugate phyllotactic pattern [7,8] (Fig. 1b). Because of limited elongation of the internodes, the ontogenetic spiral(s) are usually indiscernible; instead, secondary spiral lines (parastichies), which wind in both clockwise (S chirality) and counterclockwise (Z chirality) directions, become apparent. Sets of the most conspicuous oppositely directed parastichies, intersecting at the angle close to 90°, are denoted by two numbers, m:n (where $m \leq n$), forming a contact parastichy pair [9] (Fig. 1c,d). Numbers of parastichies, denoting a particular phyllotactic pattern (m:n) are not random; rather, they belong to one of several phyllotactic series, in which each number is a sum of two preceding elements. The most common and best known monojugate phyllotaxis is associated with the main Fibonacci series, with the numbers 1, 1, 2, 3, 5, 8, …, etc. (Fig. 1c), whereas the best known multijugate phyllotaxis is the bijugy of this series, where subsequent numbers are duplications of the Fibonacci series: 2, 2, 4, 6, 10, …, etc. (Fig. 1d).

Whorled patterns are formed when two or more organs are simultaneously initiated in a single node; in successive whorls, organs are located exactly halfway between the elements of the previous whorl (Fig. 1e), so that every second whorl overlaps. Imaginary vertical lines along the stem that connect the organ bases of the overlapping whorls are called ortostichies (Fig. 1e). As the number of elements per node varies among plants, a wide diversity of whorled phyllotaxis occur; for instance, decussate phyllotaxis is formed when two organs are initiated per node (Fig. 1e), tricussate patterns emerge when there are three elements, etc., and they are respectively denoted as 2:2, 3:3, and so on.

A special type of phyllotaxis that is intermediate between whorled and spiral is called distichy or distichous phyllotaxis. This pattern develops when only one organ is initiated in a node, but the next is initiated at the opposite side of the stem, thus, circumferentially displaced exactly 180° from the previous element. As a result, organs are arranged in two alternating ranks along the stem (Fig. 1f). A similar exception, called tristichy, occurs when the distance between successively initiated organs is equal to 120°, and thus, three ranks of organs are formed along the stem.

Phyllotactic patterns of the major land-plant lineages in the reference to SAM structure

Bryophytes

This lineage of early land plants includes the liverworts (Marchantiophyta), hornworts (Anthocerophyta), and mosses (Bryophyta), which differ from one another primarily in morphology of the gametophyte, which is dominating generation [10]. In hornworts, as well as some liverworts, the gametophyte forms a thallus, whereas in most liverworts and mosses, the gametophyte is differentiated into leaf-like and stem-like

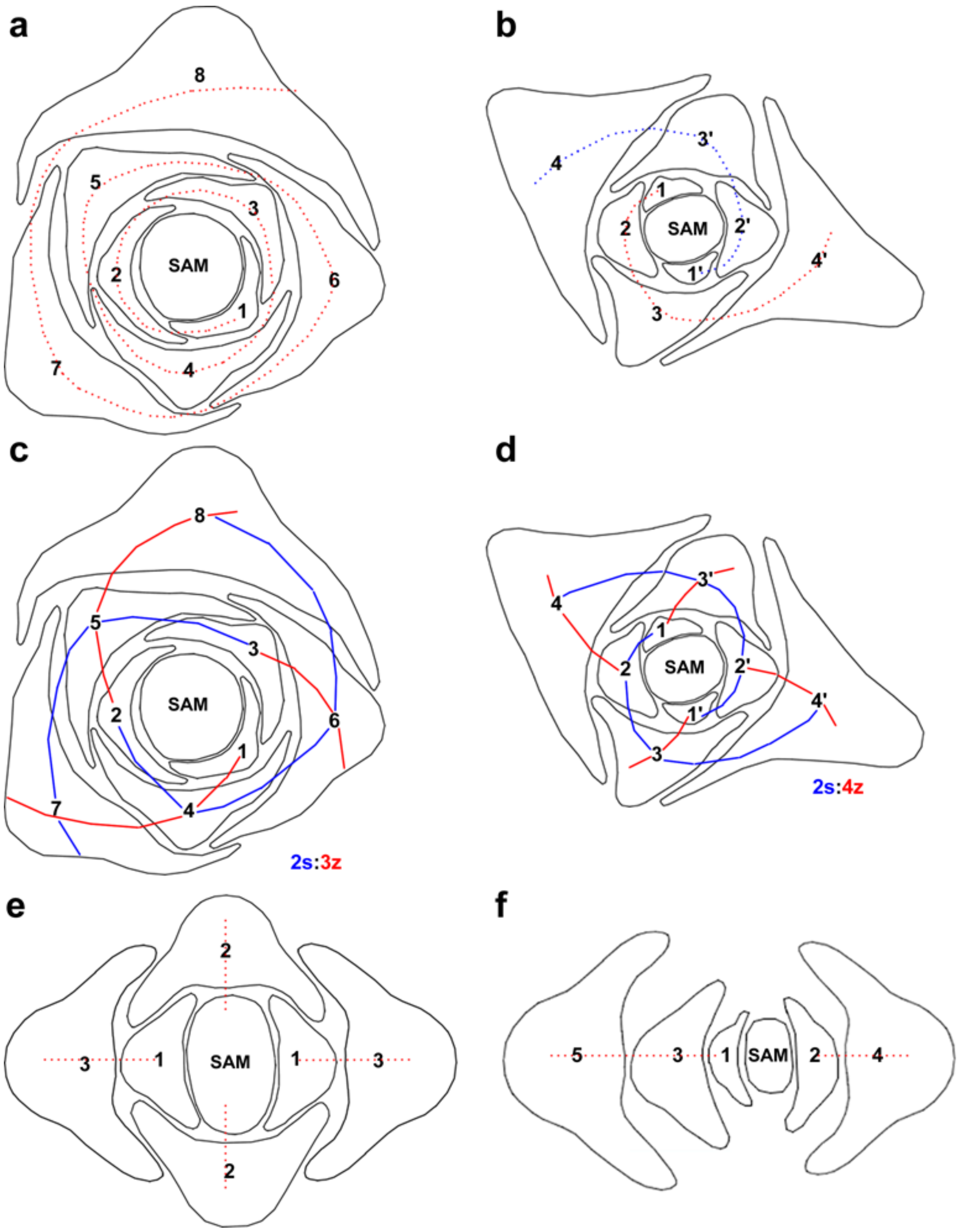

Fig. 1 Diagrams of the major categories of the phyllotactic patterns. **a,c** Monojugate spiral phyllotaxis represented by the main Fibonacci pattern. **a** A single ontogenetic spiral (red dotted line) connects all successively initiated leaves at the SAM. **c** Two sets of oppositely directed and intersecting spiral lines (parastichies) are conspicuous at the apex and form a pair of contact parastichies: two parastichies wind clockwise toward the apex (chirality S, blue lines) and three are counterclockwise (chirality Z, red lines), denoted as 2s:3z. Leaves are numbered according to the sequence of their initiation at the meristem, with the lowest number (1) referring to the youngest leaf. **b,d** Multijugate spiral phyllotaxis represented by the bijugy of the main Fibonacci series. **b** Two parallel ontogenetic spirals are necessary to connect all initiated leaves (red and blue dotted lines), as leaves are initiated in pairs. **d** Two sets of oppositely directed and intersecting spiral lines (parastichies) are conspicuous at the apex and form a pair of contact parastichies: two parastichies wind clockwise toward the apex (chirality S, blue lines) and four are counterclockwise (chirality Z, red lines), denoted as 2s:4z. Leaves in a pair are arbitrarily marked by a numeral and a numeral with a prime (e.g., 1 and 1′, etc.). Successively initiated pairs of leaves are numbered with the subsequent numbers, 1 and 1′, 2 and 2′ etc., where 1 and 1′ refer to the youngest pair of leaves. **e** Whorled phyllotaxis represented by the decussate pattern, where leaves are initiated in pairs and successive whorls are placed exactly in the half circumferential distance to the elements of the previous whorl; as a result, every second whorl overlaps, thereby forming vertical lines along the stem (ortostichies, red dotted lines). **f** Distichous phyllotaxis; distichy is formed when successive leaves are alternately initiated at the meristem 180° from one another, and thus are arranged in two ranks (ortostichies, red dotted lines) along the stem. Leaves are numbered according to the sequence of their initiation, with the youngest leaf assigned the number 1. SAM – shoot apical meristem.

structures [10]. Although these leafy organs originate from gametophytes and thus are not homologous to leaves of vascular plants [11], here they will be referred to as "leaves."

Phyllotaxis in the leafy shoots of bryophytes is shaped by the activity of a single AC within the apical meristem of the gametophyte. The AC is characterized by a stable sequence of divisions that produce regularly arranged segments (Fig. 2a–d), with a single leaf developing within each segment (Fig. 2a,b) [12–14]; thus, the shape and pattern of the AC divisions largely determine the resulting spatial arrangement of the leaves. Bryophyte ACs differ in size and shape, consisting of lens-like ACs with two planes of division, tetrahedral ACs with three cutting faces, and polyhedral ACs. Bryophytes exhibit only a handful of phyllotactic patterns, and little is known about their frequencies, as phyllotaxis in this group is generally presented in terms of the AC shape and its divisional pattern [13,14].

Distichy. This pattern is usually formed when the AC is lenticular with two planes of divisions, which gives rise to alternating segments and leaves, as in the moss Fissidens [13,14]; alternatively, this pattern can also arise when only two out of three segments, cut-off by the tetrahedral AC, develop (e.g., *Rhizogonium novae-hollandiae*) [13], or when tetrahedral AC has only two cutting surfaces (e.g., *Distichum*) [14]. Regardless of the mode of pattern formation, leaves are arranged in two ranks (i.e., two ortostichies) along the stem.

Tristichy. Leaves can be arranged in three ranks (i.e., three ortostichies) when the AC is tetrahedral and its divisions are parallel to all internal cell walls, resulting in

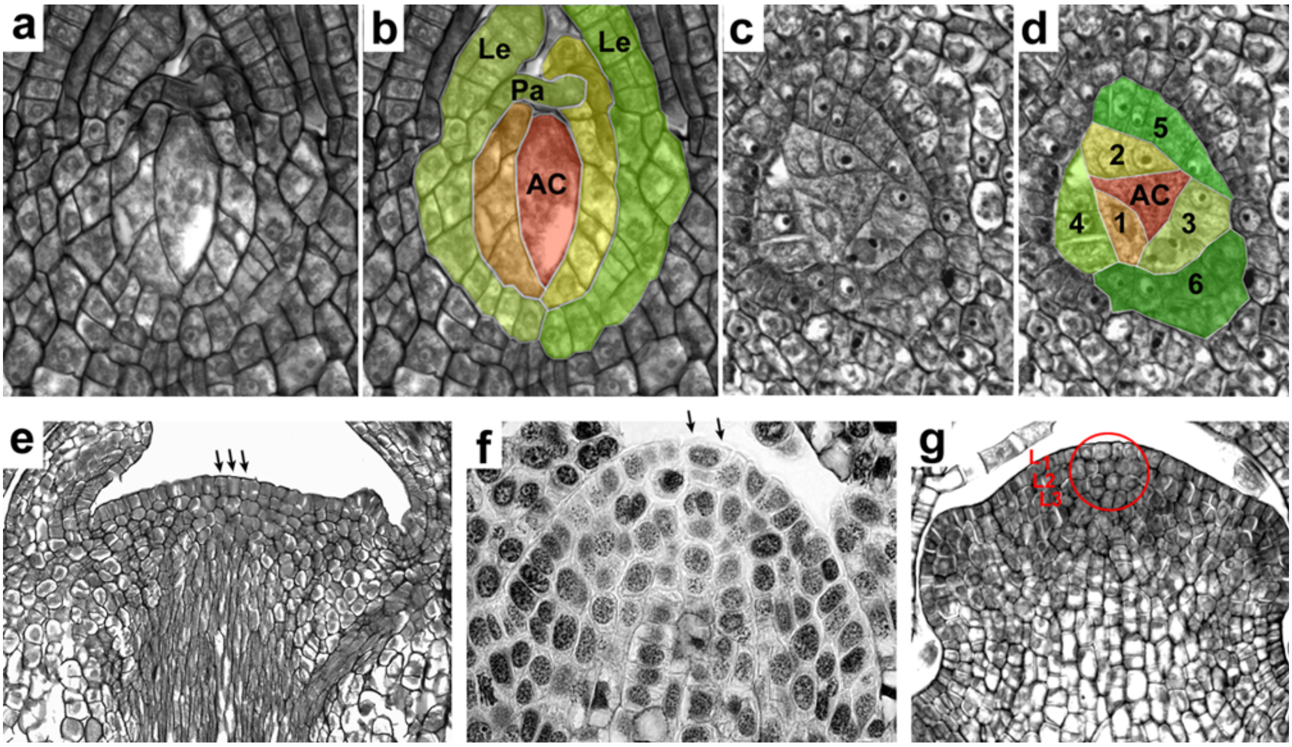

Fig. 2 Different SAM structural types in land plants. **a–d** Meristems with a distinct single apical cell (AC), exemplified by the bryophytes, presented at the longitudinal (**a,b**) (*Rhacomitrium* sp.) and transverse (**c,d**) (*Atrichum undulatum*) sections. For each sectional view (**a,c**), a corresponding diagram is presented (**b** and **d**) showing the AC and segmentation pattern of the meristem. Successively cut-off segments (merophytes) are colored and numbered with consecutive numerals, starting with the youngest segment. Leaf primordia (Le) are clonally related to the segments; in addition, between subsequent leaves, leaf-like or trichome-like structures (paraphyllia; Pa) are initiated. At the transverse sections (**c,d**), the slightly oblique divisions of the AC are visible, resulting in a spiral arrangement of the segments and the leaves related to them. **e,f** Meristems with a single group of superficial initial cells, exemplified by the lycopod, *Huperzia lucidula* (**e**) and the gymnosperm, *Picea abies* (**f**). Potential initial cells are indicated by arrows. **g** Meristems with initial cells (encircled in red) arranged in several layers (labeled with L1, L2, and L3) at the center of the meristem, exemplified by the angiosperm, *Verbena* sp. Photographs (**a–d,f,g**) are courtesy of M. Turzańska.

every third cut-off segment (and leaf) having the same circumferential position. True tristichy is, however, characteristic of only few bryophytes, such as *Fontinalis* [13], but is a more typical pattern among the leafy liverworts [12,15].

Spiral phyllotaxis. In bryophytes, divisions of the tetrahedral AC are usually not perfectly parallel to the side walls, and thus, slightly oblique, resulting in circumferential displacement of the segments (Fig. 2c,d), as for example in a model moss species *Physcomitrella patens* [11] or in *Polytrichum* [13]. As a result, the initiated leaves are positioned ca. 137° from one another [12] and usually arranged in three spirals. Such a divergence between subsequent leaves results in an arrangement of the visible parastichies in a Fibonacci sequence [12,13]. It remains however the matter of debate if it is a true spiral (Fibonacci) pattern or if it is a case of spirotristichy. Alternatively, spiral phyllotaxis is formed as a consequence of polyhedral AC activity [13].

Phyllotactic transitions. Developmental changes in leaf arrangement, such as transitions in *Fissidens*, from tristichous [13] or spiral [12] to distichous phyllotaxis have been observed. These transitions are related to changes in the shape of the AC from tetrahedron to lens-like [12]. Alternatively, patterns can be developmentally modified due to the torsion of regularly cut-off segments, resulting in leaves that are spirally arranged at the stem apex becoming displaced and distichous below the apex, as in *Schistostega disticha* [14].

Only three phyllotactic patterns are known to occur in bryophytes: distichy, tristichy, and spiral Fibonacci, which reflect the specificity of AC shape and its planes of division [12]. Interestingly, in bryophytes, similar leaf arrangements can be achieved via different pathways simply by modifying AC activity and/or segment growth, suggesting supracellular regulation of phyllotactic pattern formation.

Lycophytes

These early land plants, sister to all other vascular plants [16], are represented by three extant classes, the Selaginellales, Isoëtales, and Lycopodiales, which differ in SAM structure. In sporophytes, which are predominant generation, one to two AC forming regularly segmented shoot meristems are present in the *Selaginellales* [17–20], whereas the Lycopodiales have multiple superficial initial cells (Fig. 2e) [19,21,22], with four transient initial cells having been reported [23]. Moreover, regular shoot dichotomous branching in these groups results in repetitive reorganization of the SAM structure and the exchange of functioning initial cells. In Isoëtales, the SAM contains one (or two) AC or, alternatively, one group of superficial initials [17,19,24], depending on the age of the plant [25]. Unique to the lycophytes is the presence of microphylls, an evolutionary distinct type of leaf [16,19,24,26] that is initiated by one or two superficial cells in the peripheral zone of the meristem [18,22,27]. In *Selaginella*, in the SAM with distinct AC, microphylls develop in derivative segments with no particular correlation to the segmentation pattern [28]. For those species with two functioning ACs, each sagittal sector of the stem is generated by a separate initial cell, and thus, microphylls in these sectors are clonally related to different ACs [18].

Little attention has been paid to the phyllotactic patterns of the Selaginellales and Isoëtales, but more information about pattern diversity and frequency is available for the Lycopodiales. Because these groups differ in SAM organization, we discuss them separately.

Two types of phyllotactic patterns have been reported in the genus *Selaginella*. Spiral arrangements of microphylls occur in species characterized by radially symmetrical shoots, and represent Fibonacci patterns, for example in *Selaginella rupestris* [29]. On the other hand, in species that exhibit dorsiventral shoot symmetry, microphylls are initiated in pairs and are typically arranged in a slightly oblique decussate pattern, as e.g. in S. martensii [27,29]. Interestingly, dichotomous splitting of the SAM does not disturb the regular microphyll arrangement, as continuation of the pattern is ensured in both derived branches by the position of the last pair of microphylls (angular microphylls) prior to dichotomy [29].

In *Isoëtes*, microphylls develop from the specific basal meristem and in young plants are usually distichously arranged [25,29,30]. In older plants, however, microphyll arrangement transforms into a spiral pattern that is accompanied by the change in the SAM structure from that with a single AC to that composed of the group of initial cells at the apex surface [25].

A substantial degree of intergeneric and interspecific diversity in phyllotactic patterns is recognized among the Lycopodiaceae, for instance in *Huperzia lucidula* [22], *H. selago* [29], *Lycopodium clavatum* and *L.* (*Spinulum*) *annotinum* [31], and *Diphasiastrum digitatum* [32]. In addition, whorled and spiral patterns co-occur within a single species and form a wide spectrum of patterns; as many as 29 different phyllotactic patterns have been observed in *L. clavatum* [31]. The diversity of whorled and spiral phyllotactic patterns in the Lycopodiaceae is discussed below.

Whorled phyllotaxis. Different numbers of elements per whorl, from 2 to 12, occur in lycopods, with a few patterns predominant within a given species; for instance, decussate and tricussate patterns are the most common whorled phyllotaxes in *Diphasiastrum digitatum* [32]; four or five microphylls typically occur in a single whorl in *Huperzia lucidula* [22] and *Lycopodium* (*Spinulum*) *annotinum*; and five or six microphylls occur per whorl in *L. clavatum*, although as many as 12 whorl elements have been observed in the plagiotropic shoots of this species [31].

Spiral phyllotaxis. Numerous spiral patterns have been reported in various lycopod taxa, including 3:4 (*Diphasiastrum* [32]), 4:5 and 5:6 (*Huperzia* [22], *Lycopodium* [31], *Diphasiastrum* [32]), 6:7 (*L. clavatum* [31]). These patterns are unrelated to shoot type (e.g., vegetative shoots, strobilus), although higher numbers of contact parastichies are generally observed in the plagiotropic axes. Notably, Fibonacci sequences do not predominate in the lycopods, but in fact occur at a relatively low (typically <1%) frequency [31,32]; however, Fibonacci sequences do repeatedly occur in the early developmental stages of vegetative gemmae (bulbils) in *Huperzia selago* [33], but are transformed to a non-Fibonacci pattern in later stages of gemmling development. Interestingly, the multijugate patterns, which are quite common in the seed plants, have not been reported so far in the lycopods.

Phyllotactic transitions. Phyllotactic patterns can change in the ontogeny of a particular SAM, for instance just below the border of annual increment or during bulbil development. The majority of transitions (e.g., ca. 87% in *Lycopodium annotinum* and ca. 60% in *L. clavatum*) occur between whorled and spiral patterns, for example shifting from 4:4 to 4:5, or from 4:5 to 5:5 or to 4:4; phyllotactic transitions between two spiral or two whorled patterns are less common [31]. A gradual change in the parastichy numbers, from 2:2 to 5:5, has also been reported during gemmling development in *H. lucidula* [22]. Phyllotactic transitions may also be related to shoot dichotomous branching; in lycopods, changes in SAM geometry prior to dichotomy increase the frequency of phyllotactic transitions and pattern diversity [31,32].

Evolutionary changes in the structure of the lycophyte SAM, reflected in the increasing numbers of initial cells (e.g., [19,24]) and relatively small microphyll primordia [32], seem to enlarge the diversity of phyllotaxis in these taxa; these factors may also be driving the frequent phyllotactic transitions caused by dichotomous branching in this group of plants. On the other hand, in *Selaginella*, where the meristem is segmented, phyllotaxis is stable and no phyllotactic transitions have been observed, even during dichotomous branching.

Monilophytes

This group, which contains the four lineages of eusporangiate ferns consisting of the marattioids, ophioglossoids, horsetails, and whisk ferns (*Psilotum*), as well as the leptosporangiate ferns [34], encompasses a wide range of growth forms with some species adapted to extreme environments. Generally, the SAM of monilophytes contains a single AC, which is usually tetrahedral and distinct within the meristem, and derived segments [35–37]. The exceptions to this characteristic AC shape are members of the Salviniaceae family, which have a lenticular AC with two cutting surfaces, relating to the dorsiventral symmetry of the shoots [36,38]. Regardless of the shape, the AC divides parallel to the anticlinal sides and gives rise to segments (merophytes), which in species with relatively flat or concave apices are more rectangular and elongated, forming a distinct superficial layer of prismatic cells [36,37]. Interestingly, additional potential ACs, formed by the anticlinal oblique divisions can occur at the SAM surface in some filicalean ferns [35]. Leaves are formed in the merophytes by a constant sequence of divisions and can be in close clonal relationship to the successively cut segments, as, e.g., in *Ceratopteris* [36,37,39]. Typically, however, more than one merophyte is involved in leaf formation, and thus the impact of segmentation on the leaf spatial arrangement is less pronounced and strict, e.g., in *Dicksonia*, *Osmunda* [35–37,40].

Research and plant descriptions to date suggest a relatively small diversity of phyllotactic patterns within the monilophytes (e.g., [37]), but only several taxa have been intensively analyzed in this respect; their phyllotaxes are presented here.

Whorled phyllotaxis. The best-known whorled phyllotaxis in this group occurs in the genus *Equisetum* (horsetails) [41–43]. In horsetails, leaf arrangement is independent of segmentation pattern [41]. Leaves are reduced, discernible as the teeth of the stem sheath, and arranged in regular whorls, ranging from 4 to 12 elements (e.g., *E. arvense*) [26,41–43] or to 36 elements (e.g., *E. telmateia*) [43] per whorl. The number of sheath teeth differs among *Equisetum* species and vary within a particular shoot, between successive whorls [42,43].

One intriguing modification of the whorled pattern occurs in *Salvinia* (aquatic floating fern) [38]. Each whorl in this genus has two floating leaves, one submerged leaf, and a lateral bud, and all of these structures are strictly clonally related to the divisions of a lenticular AC. Elements of one whorl are initiated in two neighboring sagittal segments (merophytes): one floating leaf, a submerged leaf and a bud are initiated in one segment, whereas the second floating leaf is formed in the neighboring merophyte. Their position is mirrored in the next whorl. Such modifications in leaf form and arrangement are most likely adaptions to aquatic environments [38].

Distichy. Distichous phyllotaxis often occurs in ferns with a creeping rhizome. In such species, leaves are usually initiated in two ranks and form a true distichous pattern (leaves positioned 180° from one another, e.g., in *Stromatopteris*, *Microgramma* [37,44,45]) or its modification (successive leaves slightly shifted to the dorsal side with the circumferential distance between them less than 180°, as in *Davallia* [46]). Alternatively, tristichous pattern may be formed, such as in *Lomagramma* [47], or in some cases, only a single row of dorsal leaves develops in the rhizome [37].

Spiral phyllotaxis. Spiral phyllotaxis has been reported in the leptosporangiate tuft-forming ferns, such as *Ceratopteris*, *Osmunda*, and *Dryopteris* [37,39,48], and is also apparent in the arrangement of the leaves (leaf scars) on the trunk-like stems of the tree-ferns, such as *Dicksonia* [40]. However, in *Ceratopteris* [37], the spiral leaf arrangement can be rather a case of spirotristichy, than the true spiral pattern because the leaf initiation is clonally related to the merophytes. Phyllotactic pattern formation has been studied in detail in *Dryopteris*, for which, apart from the main Fibonacci pattern, both the bijugy of this pattern and the Lucas pattern (3:4) have also been reported [48,49], as have ontogenetic transitions between them [49].

Despite monilophytes being highly diversified morphologically, the range of phyllotactic patterns within this group is surprisingly limited. It is possible that the segmented structure of the SAM and the resultant geometric proportions may be responsible for the scarcity of pattern diversity, despite the lack of strict clonal relationships between segments and leaves in the majority of taxa; leaf primordia are quite large compared to SAM circumference, and thus only several phyllotactic patterns can occur. Moreover, leaf arrangement is often modified and then stabilized in parallel to the particular growth form, reflecting the remarkable degree of specialization of ferns and their adaptation to specific environments (e.g., epiphytic, rhizomatous, aquatic floating ferns).

Gymnosperms

The extant gymnosperms are a complex group that encompasses four subclasses: Cycadidae (order Cycadales), Ginkgoidae (order Ginkgoales), Gnetidae (orders: Welwitschiales, Gnetales, Ephedrales), and Pinidae (orders: Pinales, Araucariales, Cupressales) [50]. The meristem of gymnosperms is characterized by a distinctive zonation pattern, including a group of superficial initial cells at the top of the SAM and a peripheral (organogenic) zone where organ primordia develop (Fig. 2f) [3]. The meristem continues its organogenic activity throughout the entire life of the axis, varying in seasonal activity and changing the identity of initiated lateral organs (e.g., leaves, scales, etc.). Three or four initial cells function in the SAM at any given moment, as shown in *Picea* [51], but initial cells may be impermanent and exchanged into different initials during the ontogeny of a particular shoot [51,52]. Leaves are initiated by periclinal divisions in the subsuperficial cells within the organogenic (peripheral) zone of the meristem [3]. The size and shape of the SAM vary among the different groups of gymnosperms, resulting in numerous variations in the geometrical proportions between the organogenic zone and initiated primordia.

The diversity and frequency of phyllotactic patterns, as well as their ontogenetic changes, are relatively well known in gymnosperms, and especially in conifers. These are presented in the following sections.

Whorled phyllotaxis. This type of phyllotaxis occurs in the two Cupressaceae subfamilies Cupressoideae and Callitroideae [53,54]. Phyllotaxis in the subfamily Cupressoideae is stable and typically represented by the decussate pattern, although in some species of *Juniperus* [52,54], or in some branches of junipers that normally exhibit a decussate pattern [55], three leaves can be initiated per node, forming a tricussate pattern. Phyllotactic patterns in the subfamily Callitroideae are more variable, with decussate, tricussate (e.g., in *Fitzroya*, *Callitris*, *Actinostrobus*), and, in some genera (*Callitris*, *Neocallitropsis*), tetracussate patterns occurring [54]. Although spiral patterns have not been reported in the adult shoots of species in this subfamily, they have been observed in the seedlings of *Widdringtonia* [54]. Whorled phyllotactic patterns also occur in the Gnetales [56,57]; for instance, leaves in species of *Gnetum* are arranged in a decussate manner [57,58], although tricussate phyllotaxis can also be present in this genus [57]. The decussate pattern is also characteristic of *Welwitschia*, although in that case it refers to the arrangement of three whorls of different organs, consisting of cotyledons, a pair of strip-like leaves that function continuously throughout the entire life of the plant, and bracts [59]. Leaves among species of *Ephedra* are reduced to a scale-like form, and arranged in a decussate pattern (e.g., *E. equisetina*, *E. distachya*, *E. sinica*, *E. pedunculata*, *E. chilensis*) or on occasion in trimerous whorls (tricussate phyllotaxis; e.g., *E. intermedia*, *E. przewalskii*, *E. ochreata*) [57,58]. The decussate pattern is also a characteristic arrangement of the bracts in female cones of *Ephedra* and *Welwitschia* [57].

Distichy. This phyllotactic pattern has yet to be observed in gymnosperms. Leaves in plagiotropic shoots of some coniferous species (e.g., *Taxus*, *Cephalotaxus*, *Torreya*, *Abies*) are arranged in two rows that resemble the distichous pattern, but this arrangement results from post-initial modifications of developing leaves, and the bases of the leaves remain spirally distributed along the stem surface.

Spiral phyllotaxis. Among spiral patterns, the main Fibonacci pattern is known to occur in *Cycas* [60] as well as in *Gingko* [61]. In the majority of taxa belonging to the families Pinaceae and Araucariaceae, this phyllotactic pattern is predominant in both vegetative shoots and cones, usually at a frequency of ca. 95% [4,8,62–64]. Detailed case studies of *Abies balsamea* shoots [8], and *Pinus nigra* and *Larix decidua* cones [64], demonstrated that besides the dominant Fibonacci pattern, a wide spectrum of additional phyllotactic patterns can also be found; for example, 12 different patterns were identified in *Abies balsamea* [8], 10 in *P. nigra*, and eight in *L. decidua* [64]. *Larix* cones had a less stable phyllotaxis, comparing to other studied conifers, with higher frequency of additional phyllotactic patterns (ca. 22%) [64]. The most common additional patterns in these coniferous species were the bijugy of the Fibonacci series (2, 4, 6, 10, …) and the Lucas series (1, 3, 4, 7, …) [4,8,64]. Other spiral patterns occurred less frequently but include both monojugies (e.g., 4:5, 5:7) and multijugies, the latter consisting primarily of the trijugy and tetrajugy of the Fibonacci pattern [8,63,64]. Two rare spiral monojugate patterns, 7:10 and 8:11, which are thought to be impossible under natural conditions [4], have been identified in both *A. balsamea* shoots [8] and *P. nigra* cones [64]. In two genera of conifers, *Torreya* and *Cephalotaxus*, the bijugy of the Fibonacci series is the dominant phyllotaxis [63,65,66], although in other conifers it is usually the second pattern in respect to its frequency, and is usually the result of developmental transformations of phyllotaxis [8].

It is worth mentioning that in newly discovered *Wollemia* (Araucariaceae) spiral phyllotaxis can only develop at the main orthotropic axis, whereas in the lateral plagiotropic branches, a strict decussate pattern occurs [67].

Phyllotactic transitions. Transformations of phyllotactic patterns have been reported in many coniferous plants and involve both whorled and spiral patterns [8,65]. Such transitions occur the most commonly at the annual borders, and may possibly be related to changes in the identity of initiated organs. In conifers, because of the seasonal activity of the SAM, assimilating leaves (needles) alternate with scale leaves, which cover the winter bud with the pre-formed shoot for the subsequent season, along one axis. Regardless of initiated-organ type (leaves, scales), the dominant pattern is usually maintained during meristem activity [8,63], but in some conifers (e.g., *Picea*, *Abies*, *Cephalotaxus*), phyllotactic transitions have been reported to sporadically occur at the borders of annual increments. Notably, the resultant pattern was often maintained thereafter, regardless of the type of organ initiated [8,63]. Repetitive phyllotactic transitions have been reported for *Torreya*, in which the phyllotactic pattern consistently transformed from a spiral bijugate pattern in the zone of the assimilating leaves to a whorled decussate pattern in the zone of the scale leaves [63,66]; even more interesting, the spiral bijugate pattern returned when the subsequent set of assimilating leaves developed. This phenomenon of periodic shifts in phyllotactic patterns was repeated in successive annual increments. Sporadically needles can also be arranged according to other spiral patterns, including the main Fibonacci series and trijugy, but these patterns are maintained only in the zone of the assimilating leaves during a single annual increment [63].

In conifers, phyllotactic pattern transitions are also known to occur within one annual increment and without alterations in organ type [8,65,68]. These transitions are often related to developmental aberrations, for instance, the increased frequency of transitions was observed in dichotomizing shoots of *A. balsamea* and was accompanied by the occurrence of many rare phyllotactic patterns [8].

In general, gymnosperm species exhibit either a spiral or a whorled pattern, with other patterns occurring much less frequently. The additional patterns can vary immensely in some species, and thus, a wide spectrum of patterns can be found among the gymnosperms. The dominance of one phyllotactic pattern, its stability, and the range of diversity of additional patterns all seem to be related to the geometrical proportions at the SAM, i.e., to the ratio between the size of the peripheral (organogenic) zone and the leaf primordia [6,69]. Wide spectra of phyllotactic patterns tend to occur in species in which meristems are large relative to the leaf primordia, as in *Abies* or *Picea*, which facilitates the formation of various patterns; in contrast, leaf primordia that occupy a broad area of the organogenic zone, as in *Cephalotaxus* and *Torreya*, seem to restrict the number and variety of phyllotactic patterns.

Angiosperms

Given the intensity with which the phylogenetic interrelationships among this complex group of plants are examined, taxonomic positions are often reshuffled and subject to future changes, and thus, to avoid confusion, we refer only to the genus/species or family level, depending on the phyllotactic data currently available.

Angiosperms have the most complex SAM structure. The initial zone contains several cell layers, each containing its own group of initial cells; one or more external layers form a tunica, which covers the internally located corpus. Leaves are initiated in the peripheral (organogenic) zone of the SAM due to periclinal divisions in the second and third layers of the tunica (Fig. 2g) [3]; the outermost layer of the tunica normally contains only three or four initial cells [51,70]. Attempts to identify correlations between the stability of the initial cells and the most common and stable phyllotaxes have revealed that the number and permanency of the initial cells in the tunica do not affect the phyllotactic pattern, which is formed at the meristem [70]. During plant development, the meristem undergoes successive transitions from the seedling through the juvenile and adult vegetative stages to the generative (flowering) phase, at which axis growth is terminated. These transitions are accompanied by remarkable changes in SAM geometry and growth rates [71], which are also reflected in the various phyllotactic arrangements of the initiated organs. The key evolutionary novelty of angiosperms is the formation of flowers as the reproductive structures; these usually contain sterile elements (tepals or sepals and petals) and generative elements (stamens and carpels). The arrangement of these elements in a flower can be whorled and/or spiral depending on the type of the element and the taxonomic position of the species. Even within the same species, phyllotactic patterns within the generative structures usually differ from those of the vegetative leaves, thereby increasing overall phyllotactic diversity. Thus, vegetative and generative phyllotactic patterns will be discussed separately.

Whorled phyllotaxis. The most common whorled pattern in the vegetative parts of a plant is a decussate phyllotaxis. This pattern is typically found in several families (e.g., Lamiaceae, Hypericaceae, Caryophyllaceae, and others), in which it is often considered to be a characteristic feature. Three leaves per node have been reported in *Nerium oleander*, resulting in a tricussate phyllotaxis [72]. Whorls with multiple leaves often occur in aquatic angiosperms [43,73]; in *Hippuris*, for instance, the number of elements in subsequent whorls can vary between 4–16, depending on the size of the apex [43,74]. Polymerous whorls are also found in other genera, for example *Acacia* or *Gallium*, in which the origins of the whorl elements often differ and the whorls are normally the result of post-initial developmental modifications [43].

Whorled phyllotaxis in which three or more elements are initiated per whorl is a characteristic trait of flowers, with four whorls of different organs – consisting of sepals, petals, stamens, and carpels, starting at the outside of the flower and moving progressively toward the center – commonly initiated at the flower meristem. Both the number of elements per particular whorl and their whorled or spiral spatial arrangement are strictly preserved in ontogeny and depend on the taxonomic position of the plant; for instance, trimerous perianth is characteristic of some monocots (e.g., *Cyperus*, *Lilium*, *Colchicum*) [61] and magnolias [6,75,76], tetramerous of some basal angiosperms and the Brassicaceae (including *Arabidopsis*), and five floral elements per whorl are typical of the Ericaceae, among others. Sometimes, however, limited internode elongation of separately and spirally initiated elements can result in a seemingly whorled arrangement of flower elements [71,77].

Distichy. This phyllotactic pattern is common to the family Poaceae, as well as representatives of a few other families, including the Orchidaceae and Flagellariaceae [78]. Although generally rare in dicots, distichy is a typical phyllotactic pattern of *Pisum sativum* [71] and species of *Utricularia* (Lentibulariaceae), as well as a few members of the Podostemaceae [79,80]. Distichy is also a common transitory phyllotaxis in seedling development, occurring between the opposing arrangements of cotyledons and the spiral arrangement of leaves, as, e.g., in Cuscuta [81]. Furthermore, distichous patterns can also be seen in the plagiotropic branches of *Trema floridana* (Ulmaceae) and *Dicranolepis persei* (Thymelaeaceae), whereas the spiral phyllotaxis is present on the orthotropic stems in these species [82]. Distichous phyllotaxis also co-occurs in vegetative branches of *Magnolia* and *Ulmus* [83]. Tristichy is a rather rare pattern in angiosperms, although it may be a characteristic phyllotaxis of the Cyperaceae, as three regular ortostichies typically occur in this family.

Distichous phyllotactic patterns can also be found in the inflorescences of the Poaceae, and may represent a continuation from the previous vegetative phyllotaxis [71]. In addition, the arrangements of bracts and/or flowers in the inflorescences of members of the Bromeliaceae (e.g., *Vriesea*) and *Heliconia* are oftentimes distichous.

Spiral phyllotaxes. Leaf arrangement in the majority of angiosperms is relatively stable and primarily represented by the Fibonacci pattern (ca. 95%), with additional patterns occurring only infrequently and most times appearing as the bijugy of the main Fibonacci pattern and the Lucas pattern [4]. However, an enormous diversity of genus-dependent phyllotactic patterns can be found in the vegetative organs of cacti; for example, *Mammillaria* species display a relatively narrow spectrum of phyllotactic patterns dominated by, as with most angiosperms, the main Fibonacci pattern, whereas a wide spectrum of phyllotactic patterns, many of which are non-Fibonacci, can be found in the *Rebutia* genus [84].

Uneven elongation of the internodes may result in bunching of spirally initiated leaves at one level of the stem, forming pseudowhorls (false whorls). The number of leaves per pseudowhorl depends on the type of the spiral phyllotaxis, for example, with three or four leaves at one level in the case of Fibonacci or Lucas series, respectively, as occurs in *Anagallis* [85]. Interestingly, in *Peperomia verticillata*, pseudowhorls are formed in shoots with both spiral and whorled patterns; in the latter case, pseudowhorls are formed when internodes between neighboring whorls are shortened resulting in gathering of leaves at one level [86].

Much more diversified are the spiral patterns in the generative structures of angiosperms. Extensive analyses of *Magnolia* flowers have revealed the vast diversity of phyllotactic patterns within the gynoecium; moreover, the patterns of stamen arrangement are also highly diversified. As such, it has been proposed that *Magnolia* may be an ideal model for research on phyllotactic diversity [6]. *Magnolia acuminata* in particular exhibits a wide range (ca. 15) of phyllotactic patterns, including almost all patterns described to date, as well as some thought to be mathematically all but impossible, such as 7:10 and 8:11 [4]. Interestingly, the prevailing phyllotactic pattern, whether Fibonacci, bijugy, or trijugy, is maintained within any given *M. acuminata* tree [75]. Within the *Magnolia* genus, there are also species with a much narrower spectrum of patterns, such as *M. salicifolia*, in which only about six patterns have been observed [75], as well as species that adhere strictly to the main Fibonacci phyllotaxis, as in *M. virginiana* and *M. hypoleuca* [5]. A wide diversity of phyllotaxes has also been shown to exist in the generative structures of another Magnoliaceae species, *Michelia fuscata* [87,88], and in the inflorescence (capitulum) of *Carlina acaulis* (Asteraceae) [89]. The latter is particularly interesting because of the fact that in this family, the dominance of the Fibonacci pattern is maintained over the entire course of plant development, from the vegetative shoot through the bracts of the capitulum to the flower distribution [7,71,90].

Phyllotactic transitions. Phyllotactic patterns often undergo ontogenetic transition(s) in angiosperms, which can involve changes in initiated-organ identity or even within structures of the same type. Such modified phyllotactic patterns are often related to reorganizations of the SAM structure, particularly during crucial transitions between subsequent developmental stages [71]. For instance, at the beginning of seedling post-embryonal organogenesis, leaf arrangement alters from opposing cotyledons to a spiral in many dicots [91]; and during transition to flowering or inflorescence formation, decussate patterns of the vegetative shoots (e.g., in *Epilobium* [92] and *Antirrhinum* [93]) are transformed into spiral phyllotaxis in the inflorescence. In some species, the sequence of ontogenetic transitions takes place during development of the particular SAM; in *Magnolia*, for example, the vegetative distichous or spiral Fibonacci phyllotaxes [83] are replaced by the trimerous whorled arrangements of tepals or sepals and petals [76], and subsequently, within the androecium and gynoecium parts of the flower, to highly diversified spiral phyllotaxes [6,75]. Notably, stamen arrangements oftentimes differ from those of carpels even within the same flower [6]. This sort of phyllotactic transition is most likely associated with alterations in the ratio between the size of the organogenic surface of the meristem and the initiated organ primordia of different identity (type) [5,6,69]. However, ontogenetic changes in organ size and identity do not always lead to transformations in phyllotactic pattern (e.g., in the Ranunculaceae), but rather the main Fibonacci pattern is maintained throughout plant development and expressed in the arrangements of vegetative leaves and floral parts [94]. Less frequent are phyllotactic transformations that are unrelated to a particular developmental phase; these occur spontaneously at the shoot or within the gynoecium, as often happens in species of *Magnolia*. It is likely that ontogenetic transformations occur more frequently in species that encompass a wide spectrum of phyllotactic patterns.

Phyllotaxis in angiosperms is extremely diversified, reflecting various morphological modifications and degrees of specialization within this extensive group of land plants. Despite the enormous range of phyllotactic patterns both between and within taxa, some patterns are strongly associated with and preserved in specific taxon, especially in regard to the phyllotaxis of floral elements.

Regulation of the phyllotactic pattern formation – similarities and differences in plants differing in SAM structure

Given the universality of phyllotaxis in land-plant lineages, it is surprising that the mechanisms responsible for regulation of phyllotactic pattern formation are not yet fully understood. The level of phyllotaxis diversity corresponds with SAM organization; there is a much greater pattern diversification in plant species that have layered meristems than in species that have segmented meristems and a single AC. In the latter plants, occurrence of various patterns is most likely limited by the clonal interrelationships between the leaves and the segments. When such strict sectorial correlation between the initial cells and leaves is absent or limited, all cells in the peripheral (organogenic) zone become theoretically capable of forming primordia, thus increasing the probability of formation of diverse phyllotactic arrangements at the SAM. Interestingly, even within this group, some species exhibit a high diversity of phyllotactic patterns, suggesting that additional factors are involved in the control of phyllotaxis formation and/or its stability. The geometrical proportions at the SAM may be just such a factor, for instance: the ratio between the organogenic surface and the size of primordium (geometrical and/or the area of its impact) can determine the primordia distribution at the SAM [5–7,69,95,96]. Theoretically at least, relatively small primordia can be variously arranged within a large SAM, leading to the formation of a wide range of phyllotactic patterns, as happens in *Abies* and *Picea*, or the inflorescences of *Carlina* (Asteraceae). Further evidence that these geometrical proportions may influence pattern formation has emerged from studies on the *Zea mays* mutant *abphyl1* (*abph1*) [97–99]; whereas distichy is a typical phyllotaxis in *Zea*, the *abph1* mutant expresses a decussate pattern, which appears to be linked to the significantly larger SAM in the mutant compared to the normal plants. ABPH1 is believed to regulate the cytokinin-induced expansion of the SAM; thus, in the mutant, the ratio between the size of the meristem and the size of the leaf primordium changed, making the formation of alternative phyllotactic patterns possible [100]. The significance of the geometrical proportions at the SAM for pattern formation is further evidenced by studies on the genes (e.g., *WUSCHEL*, *CLVAVATA*, *ARGOS*, *ORGAN SIZE RELATED*) that regulate SAM and primordia size, as well as meristem structure and activity [101–103]. On the other hand, species with similar geometrical proportions at the SAM can differ in the degree of phyllotaxis diversity and/or stability; for instance, in inflorescences of some Asteraceae species, the primordia packing usually reflects the main Fibonacci series [7,71,104]. In addition, the geometrical proportions alone do not explain pattern frequencies, which are genet-specific in different *Magnolia* species [6]. All such evidence suggest that the geometrical proportions prevalent in the SAM may be only one of several factors responsible for the formation of phyllotactic patterns.

Experiments on the regulation of organogenesis in *Arabidopsis* and tomato revealed that leaf primordium size is dependent on auxin [105], leading to the development of the auxin-dependent regulation model of phyllotaxis. According to this model, which has been experimentally confirmed in *Arabidopsis* [105–109], the position of the leaf primordium is determined by auxin, which is acropetally transported in the L1 layer to the organogenic zone of the meristem [106]. This polar transport of auxin is facilitated by the membrane protein PIN1. The cells of the organogenic zone, with higher auxin level, become sinks that deplete this hormone from neighboring regions. Local maximum of auxin concentration, formed in this way, induces initiation of the organ primordium. Depletion of auxin in the surrounding tissues inhibits organogenesis in the vicinity, with the next local maximum formed beyond the region of depletion determining the position of the next primordium. The subsequent formation of local maxima of auxin is a self-organizing process, which likely depends on the regulatory loop between auxin, *PIN1* gene expression, and PIN1 protein polarization [1,2,110–112].

The damage of polar auxin transport (PAT) has been shown to inhibit organogenesis in the inflorescence stem of *Arabidopsis* and in vegetative shoots of tomato, suggesting that the same PIN1-protein-dependent mechanism regulates lateral organ formation in different developmental phases [105]. Furthermore, in light of the fact that similar developmental impairments have been shown in some monocots [113–117] and that homologs of *PIN* genes have been identified in gymnosperms [118,119], it is generally thought that the auxin mechanism of phyllotaxis regulation may be universal throughout the seed plants. Sequencing analyses have suggested that *PIN* genes may be present in the seedless land plants as well [119], and PAT has been shown to be present in *Physcomitrella* [120] and *Selaginella* [121], indicating that the auxin mechanism of phyllotaxis formation may be common to all land-plant lineages. However, localization of PIN proteins in the plasma membranes in the seedless plants has to date only be confirmed in *Physcomitrella* [120]. Notably, PAT has also been identified in *Chara* (Characeae, green alga) [122], which shares a common ancestor with land plants, although PIN proteins in *Chara* are localized in the endoplasmic reticulum [123,124]. Although the auxin-regulated model of phyllotaxis formation is generally accepted for the seed plants, it does not explain all aspects of pattern formation; for instance, how the spatio-temporal polarization of PIN1 is regulated during organogenesis remains unknown, although several explanatory models have been proposed (e.g., [108,109,125–128]). It is likely that additional factors which cooperate with the formation of self-organizing auxin maxima, must be involved in phyllotactic patterning [2].

One such factor is the vascular system. Plants for which there are strict correlations between the vascular system and phyllotaxis, e.g., poplars or conifers [129–132], are characterized by having very stable phyllotaxes, in which one pattern dominates (ca. 95%). Other patterns may occur, but only at very low frequencies and are usually associated with developmental abnormalities, e.g., dichotomy of shoots [8]. On the other hand, when the correlation between the vascular system and leaf formation is weaker, phyllotaxis appears to be more flexible. In *Torreya*, for instance, vascular system differentiation is delayed relative to leaf formation, resulting in temporal loosening of the mutual interrelations and possibly in the autonomy of the SAM in regard to phyllotactic pattern formation. As a consequence, phyllotaxis is established de novo at the SAM, at every change of the type of initiated organs (scales vs. leaves) [63]. Similarly, the relationship between microphylls and the internal (stelar) vascular system is relatively unstable in lycopods, which display a high diversity of phyllotactic patterns and possibly independence of the SAM in pattern formation [133]. Moreover, extremely diversified phyllotactic arrangements in the carpels of *Michelia fuscata* may be related to the instability and flexibility of vascular system structure during carpel initiation [88]. These examples suggest that stabilization of phyllotactic patterns depends on the stability of the spatial organization of the vascular system (e.g., relatively constant number of vascular bundles), and the strict association between the differentiated vasculature and the SAM organogenic zone [63,134], which form the framework for meristem functioning. It should be noted that some land-plant lineages, namely the bryophytes, do not have the vascular system yet are still capable of producing regular phyllotactic patterns. Interestingly, connections via true leaf traces between the leaves and the specialized water-conducting cells (hydroids) in the gametophyte stem have been identified in *Polytrichum*, but it is not known if these are related to the phyllotaxis regulation [135].

What influence the vascular system has on phyllotaxis formation remains, for the most part, unknown. The results of analyses of poplar [131,132,136] and *Linum* [137] have led to suggestions that the acropetally differentiating vascular system determines the site of primordium initiation at the SAM, thereby regulating phyllotactic patterning. The importance of the vascular system in phyllotactic pattern formation has recently been re-discovered, but interpretations of its actual function vary [63,127,134]. According to the dual pathway of auxin transport hypothesis [134], the vascular system acts as an additional auxin transport pathway to that in the L1 layer, and thus is involved in the organogenic process at the meristem. Only the impairment of both pathways (in L1 and in the vascular system) completely inhibits organogenesis, as one can compensate for the other, at least to some extent; if only the external pathway is damaged (i.e., in L1) but auxin transport via the vascular system is still effective, as seems to be the case for the vegetative rosette of the *Arabidopsis pin1* mutant, organs are initiated but their phyllotactic arrangement is disturbed [134]. In contrast, when internal transport of auxin in vasculature is blocked but external transport via L1 is undamaged, organs are initiated but their phyllotactic pattern is unstable, as in *Torreya* [63]. According to an alternative theory, the differentiated vascular tissue below the meristem is necessary to drain off the auxin from the site of primordium formation (local maximum of auxin at the meristem), which is necessary for primordium formation [127]. During leaf development, auxin flowing from the superficial layers to the internal tissues is directed by PIN1 proteins polarized by the mechanism “with the flux” toward the nearest mature vascular tissue. In this way, concentrations of auxin optimal for organ development are maintained at the initiation site [127]. These interpretations of the role of the vascular system are not mutually exclusive and together may significantly supplement the model of the regulation of phyllotactic pattern formation by auxin.

This review on phyllotaxis diversity clearly shows that the formation and the main types of patterns are universal across the major lineages of the land plants, regardless of the structure of the meristem (from which these patterns are generated), leaf origin, and the type of organ (leaf, flower, etc.). This universality strongly points to the importance of the regular and iterative organ arrangements. Over the course of their evolutionary history, plants have gained and developed specific mechanisms to form and maintain these patterns within existing structural and functional constraints, and thus it is difficult to explain all aspects of phyllotactic patterns formation, stabilization, and diversity. To fully elucidate and understand the reason(s) for and regulation of this spatio-temporal patterning would require detailed examinations of this process in all groups of land plants, and possibly in their ancestors as well. Of particular interest would be to trace the origin and evolution of auxin-regulated phyllotaxis formation from the angiosperms back through the ancestral lineages, as auxin appears to be a factor common to all land plants [138,139].

Acknowledgments

We thank our colleagues from the Department of Developmental Plant Biology, University of Wrocław, for their critiques of the manuscript; special thanks to Magda Turzańska for providing the images of meristems, and comments about the bryophytes.

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