Quantitative Plant Biology

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Gymnosperms – A forgotten model for phyllotaxis research

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Review

Cite this article: A. Banasiak and E. M. Gola Gymnosperms – A forgotten model for phyllotaxis research. *Quantitative Plant Biology*, **7**:e23, 1–15
https://dx.doi.org/10.1017/qpb.2026.10056

Received: 18 May 2026 UTC
Revised: 12 August 2026 UTC
Accepted: 14 August 2026 UTC

Keywords:
pattern transitions; phyllotaxis diversity; shoot apical meristem (SAM); vascular system.

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Associate Editor:
Paula Elomaa

Abstract

Phyllotaxis, the regular arrangement of lateral organs initiated at the shoot apical meristem (SAM), has long served as a model for studying pattern formation in plants. Gymnosperms, due to their crystal-like organ arrangements, suitable for geometric analyses, were often used in phyllotactic research. In addition, the interrelationship between phyllotaxis and the primary vascular system became well-recognised. Here, we review classical morphological and anatomical data together with recent molecular findings to reevaluate gymnosperms as a model system for phyllotaxis regulation. We discuss the diversity and ontogenetic dynamics of phyllotactic patterns, their close relation with SAM structure and activity and the role of the vascular system as a potential constraint stabilising pattern propagation and chirality. Available evidence suggests that auxin-dependent mechanisms are evolutionarily conserved, but operate within diverse structural contexts. We propose that integrating classical datasets with modern experimental and modelling approaches, applied to gymnosperms, can reveal fundamental principles governing phyllotaxis regulation.

1. Introduction

Aerial plant organs are periodically initiated at the shoot apical meristem (SAM) and arranged according to the regular spatial patterns, which are termed phyllotaxis (e.g., Evert, 2007). The regularity in element distribution has aroused scientists' interest for decades, with research focusing on different aspects of phyllotaxis (for a review see Adler et al., 1997; Church, 1904; Gola & Banasiak, 2016; Refahi et al., 2016; Reinhardt & Gola, 2022). In the first decades of the 20th century, the main attention was paid to descriptions of gross plant morphology in relation to the inter- and intraspecific diversity of patterns as well as to their frequency. At that time, gymnosperms became intensively studied and due to regular, crystal-like arrangements of tightly packed organ primordia (needles) in a dormant bud, phyllotaxis was considered in developmental research. Furthermore, scientists were aware of the intimate relationships between the shoot apex activity, superficial (leaf) phyllotaxis and internal (vascular) organisation; thus, the gymnosperm vasculature was comprehensively analysed and described from this perspective (Crafts, 1943a, 1943b; Cross, 1939, 1940, 1941; Foster, 1938, 1939, 1940, 1943; Gifford, 1943; Gifford & Wetmore, 1957; Griffith, 1952; Gunckel & Wetmore, 1946a, 1946b; Kemp, 1943; Namboodiri & Beck, 1968a, 1968b; Owens & Molder, 1973a, 1973b, 1976; Parke, 1959, 1963; Romberger, 1963; Sterling, 1945a, 1945b, 1946a). Detailed analyses of different taxa generated a plethora of anatomical and developmental datasets that, combined with modern advanced experimental techniques, provide a good background for dissecting mechanisms involved in phyllotaxis regulation in gymnosperms and plants in general.

Development of molecular methods shifted the attention of researchers toward angiosperm plants, mainly the model organism Arabidopsis, in search of the mechanisms and factors underlying phyllotactic pattern formation. As a result, the first comprehensive auxin-based model of phyllotaxis was proposed (Kuhlemeier, 2007; Reinhardt, 2005; Reinhardt et al., 2003). Subsequently, other intrinsic factors potentially involved in phyllotaxis regulation have been identified, showing the necessity of modifying the classical model (Banasiak, 2011; Banasiak et al., 2019; Bhatia et al., 2016; Bhatia & Heisler, 2018; Cheng et al., 2006; Prusinkiewicz et al., 2022; Zhang et al., 2021). In addition, phyllotaxis has been studied from an evolutionary perspective in attempts to answer how the regularity of patterns and underlying mechanisms emerged (e.g., Kamamoto et al., 2021; Okabe, 2024; Véron et al., 2021). Rediscovery of gymnosperms as a model for phyllotaxis studies would help to address these questions. The well-known classical knowledge of the anatomical structure and phyllotaxis of gymnosperms, coupled with the modern techniques of experimental plant biology and currently available molecular data and tools will enable analysis of this group of plants at a much deeper level.

Based on combined results of molecular and morphological analyses, extant gymnosperms are classified into three classes, five subclasses, eight orders and 13 families (Yang et al., 2022, 2024). Importantly, information about phyllotactic arrangements of organs appears in the

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descriptions of different taxa representing all the families and refers to various structures – leaves, bracts and scales (Table 1). The data come not only from studies focused on phyllotaxis but also from works analysing other aspects of gymnosperm development (e.g., cone formation). The interrelation of phyllotaxis and the primary vascular system is also well-recognised. As a result of progress in molecular studies, the first complete genome of a gymnosperm representative, *Picea abies*, has been published (Nystedt et al., 2013). Since then, 17 taxa have been sequenced or published as draft genomes, including species from different families, for example *Pinus taeda, Pinus lambertiana*, *Abies alba, Sequoia sempervirens, Ginkgo biloba, Gnetum montanum* (Neale et al., 2022; Wan et al., 2022). In addition, experimental techniques and molecular markers, successfully used so far for angiosperms, have been implemented to study gymnosperms.

In this review, by combining classical data with recent molecular insights, we argue that gymnosperms constitute an underutilised quantitative system for dissecting the mechanism of phyllotaxis regulation.

2. SAM structure and organogenic activity

Phyllotaxis is an outcome of meristem organogenic activity; thus, SAM morphology is important for understanding pattern formation. The size and shape of the gymnosperm meristem varies from small and narrow conical apices, for example in *Cupressus*, *Thuja*, *Juniperus* or *Araucaria*, reaching ca. 120 μm (or less) in diameter and ca. 50–70 μm in height (Crafts, 1943b; Griffith, 1952; Pillai, 1963; Pillai, 1963a, 1964) to relatively huge, broad dome-like or even flat, 300–400 μm in diameter, as in *Pinus*, *Pseudotsuga*, *Torreya* (Crafts, 1943b; Kemp, 1943). The biggest meristems, exceeding even 3,000 μm in diameter, occur in cycads (Foster, 1940, 1943; Johnson, 1945). Importantly, depending on the meristem's divisional and organogenic activity, its size and shape show seasonal variations in some species (Curtis & Popham, 1972; Kemp, 1943; Owens, 1984; Owens et al., 1977; Owens & Molder, 1973b, 1976; Parke, 1959; Pillai, 1963a, 1963b, 1964; Pillai & Chacko, 1978; Romberger, 1963; Sacher, 1954; Sterling, 1946b).

The SAM structure in gymnosperms seems to be relatively less complicated than in angiosperms due to the presence of only one superficial group of initial cells (Evert, 2007; Romberger, 1963). Such a group usually contains a few impermanent apical initial cells, which could be replaced during ontogeny (Conway & Drinnan, 2017; Ruth et al., 1985; Zagórska-Marek & Turzańska, 2000). They occupy the central part of the meristem, forming the apical initial layer and divide in both planes: perpendicular (anticlinal division) and parallel (periclinal division) to the meristem surface (Figure 1). Anticlinal divisions of the initial cells provide cells to the peripheral zone (PZ), whose outer region is involved in organ primordia initiation, while the inner region is responsible for vascular meristem (procambium) development. On the other hand, periclinal divisions of the superficial initial cells supply cells to the central mother cell (CMC) zone, corresponding to the organising centre of the angiosperm SAM (Bäurle & Laux, 2005; Kean-Galeno et al., 2024; Kwiatkowska, 2008). This zone is characterised by a slower rate of cell divisions and thus a prolonged cell cycle. The CMC zone is delimited from the rib meristem, located below, by a narrow transition zone of intensively dividing cells, which extends to the PZ and can reach the meristem surface (Figure 1). Generally, the zonation pattern of the gymnosperm apex is distinguishable due to such pronounced cytohistological differences that they were

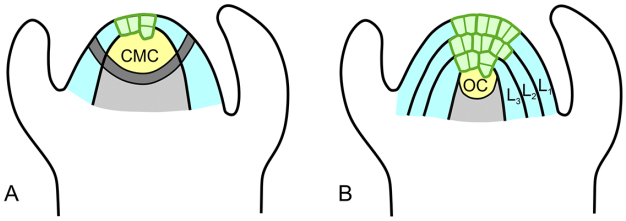


Figure 1. Schemes of the shoot apical meristem (SAM) structure in gymnosperms (a) and angiosperms (b). Initial cells for a superficial group of apical initials in gymnosperms and for three groups of initials in angiosperms are drawn in green. In gymnosperms, initial cells divide anticlinally and periclinally, while in angiosperms divisions in two outer groups of initials (in tunica) are anticlinal and in the inner group of initials (in corpus) anticlinal and periclinal. Central mother cell zone (CMC) and organising centre (OC) are labelled in yellow, peripheral zone in blue. Light grey colour marks the rib meristem; dark grey (in gymnosperm) shows the transition zone.

described for the first time in this plant group (not in angiosperms!) (Gifford & Wetmore, 1957). However, the distinctiveness of particular zones varies depending on the genus, apex shape and size, frequency of periclinal divisions and ontogenetic stage, and can be seasonally changeable. For instance, the well-defined zonation, mentioned above, was described in *Ginkgo* (Foster, 1938; Gunckel & Wetmore, 1946a; Romberger, 1963), and similar, though less pronounced patterning is visible, for example, in cycads and the Pinaceae family (Cross, 1943; Foster, 1939, 1940, 1943; Johnson, 1939, 1945; Kemp, 1943; Sacher, 1954; Sterling, 1945a, 1945b). Some genera from the Taxaceae and Cupressaceae have a discrete layer of superficial cells (so-called 'pseudotunica') formed due to limited periclinal divisions within the PZ. Extremely rare periclinal divisions in superficial cells of the adult SAMs of the Araucariaceae (and possibly in some Podocarpaceae and Gnetaceae) cause the structure of their meristems to resemble a tunica-corpus organisation of angiosperms (Cross, 1942; Griffith, 1952; Johnson, 1950; Pillai, 1964; Romberger, 1963; Romberger et al., 1993; Sacher, 1954; Sterling, 1958).

Lateral organ initiation starts in the PZ, by divisions of subsuperficial cells. The shoot vegetative meristem produces primordia of different identity, assimilating leaves and scales (cataphylls), while the reproductive apex initiates bracts (bract scales), seed (ovuliferous) or microsporangia-bearing scales and forms a strobilus or cone (Romberger et al., 1993).

As gymnosperms are long-lived trees or shrubs, composed of numerous branches subordinated to the main axis (monopodial branching), the SAM on each axis (branch) functions for many years, showing seasonal changes in its activity, size and shape. During the dormant period, the meristem ceases its activity and is usually covered by scales forming a bud. The meristem hidden within the bud can bear the leaf primordia, initiated during the prior vegetative season, which, however, will develop in the subsequent year (so-called predetermined growth). The axils of some leaf and/or scale primordia can contain initiated and partially developed axillary buds (Wenzel et al., 2024, 2026). As a whole, such a structure is treated as an embryonic (preformed) shoot with extremely shortened internodes (Romberger, 1963; Sterling, 1945a, 1958). After bud bursting, scales detach and the preformed shoot rapidly elongates. Then, the meristem resumes its divisional and organogenic activity and produces first the scales, which will form the bud, and finally leaves for the next vegetative season. Thus, along one continuously growing branch, alternating zones with assimilating leaves and short fragments covered with scars of scale leaves (seasonal borders) are present, being the outcomes

Table 1. Published phyllotactic patterns in gymnosperms

Taxon				Dominant phyllotaxis/organ type	Other patterns/remarks	References
Class Cycadopsida	Subclass Cycadidae	Order Cycadales	Family Cycadaceae			
			Cycas	Main Fibonacci (1,2,3,5,8,...)		Davis & Bose, 1971
			Cycadaceae	Leaves and microsporophylls spirally arranged		Yang et al., 2024
			Family Zamiaceae			
			Zamia	Leaves spirally arranged		Johnson, 1939
Class Ginkgoopsida	Subclass Ginkgoidae	Order Ginkgoales	Family Ginkgoaceae			
			Ginkgo	Main Fibonacci (1,2,3,5,8,...)		Gunckel & Wetmore, 1946b
				Leaves spirally arranged		Yang et al., 2024
Class Pinopsida	Subclass Cupressidae	Order Araucariales	Family Araucariaceae			
			Araucariaceae	Bracts spirally arranged		Tomlinson & Takaso, 2002
			Araucaria excelsa		Lucas (1,3,4,7,...)	Church, 1904
			Wollemia	Main Fibonacci (1,2,3,5,8,...)	Often irregular spiral phyllotaxis in orthotropic shoots and reversion of the ontogenetic helix	Tomlinson & Murch, 2009
				Decussate – plagiotropic shoots		
			Family Podocarpaceae			
			Dacrycarpus dacrydioides, *Dacrydium cupressinum*	2–3 cotyledons; leaves in number of cotyledons, spiral		Dörken & Parsons, 2016
				Bracts spiral, based on diagram main Fibonacci		Tomlinson, 1992
			Podocarpus japonica	Main Fibonacci (1,2,3,5,8,...)	Bijugy of main Fibonacci (2,4,6,10,...) and Lucas (1,3,4,7,....)	Church, 1904
				Cone scales decussate		Tomlinson, 1992
			Podocarpaceae	Main Fibonacci (1,2,3,5,8,...), in taxa with vegetative spiral phyllotaxis, bracts spirally arranged, occasionally decussate		Tomlinson, 1992
			Nageia	Decussate; vegetative and bracts		Tomlinson, 1992
			Microcachrys	Decussate, bracts in whorls of four		Tomlinson, 1992; Tomlinson & Takaso, 2002

Table 1. Continued

Taxon				Dominant phyllotaxis/organ type	Other patterns/remarks	References
Class Pinopsida	Subclass Cupressidae	Order Cupressales	Family Cupressaceae			
			Basal Cupressaceae (*Cunninghamia*, *Taiwania*, *Athrotaxis*, *Sequoia*, *Sequoiadendron*, *Cryptomeria*, *Glyptostrobus*, *Taxodium)* with exception of *Metasequia*	Spiral phyllotaxis in vegetative shoots and cones		Jagel & Dörken, 2014
					Lucas (1,3,4,7, . . .) (in *Cunninghamia*)	Fujita, 1939
			Metasequoia, *Metasequoia glyptostroboides*	Leaves bijugate (2,4,6,10, . . .), cone scales decussate		Takaso & Tomlinson, 1992
				Decussate leaves and seed scales		Jagel & Dörken, 2014; Yang et al., 2024
			Seqouia sempervirens	Main Fibonacci (1,2,3,5,8, . . .)		Crafts, 1943a
					Bijugy of main Fibonacci (2,4,6,10, . . .) and Lucas (1,3,4,7, . . .)	Sterling, 1945b
			Sequoia, *Sequoiadendron*	Spiral phyllotaxis, vegetative shoots and scale cones		Jagel & Dörken, 2014; Takaso & Tomlinson, 1992
			Taxodium Glyptostrobus		4:5 (1,4,5,9 . . . series)	Crafts, 1943b
				Main Fibonacci (1,2,3,5,8, . . .) in cones		Takaso & Tomlinson, 1990
			Subfamily Cupressoideae	Decussate or tricussate, spiral patterns absent (only in seedlings in some genera); Cone scales decussate		Jagel & Dörken, 2015a
			Thuja plicata, *Platycladus orientalis*	2 (3) cotyledons, first leaves in number of cotyledons, then exclusively decussate		Dörken, 2013a
			Cupressus vietnamensis	Needle leaves in tetramerous whorls (8 orthostichies), scale leaves decussate (4 orthostichies); Cone scales decussate		Dörken et al., 2017
			Juniperus	Decussate or tricussate (e.g., in sect. *Sabina*)	Transitions between both patterns within one shoot (e.g., *Juniperus squamata*)	Jagel & Dörken, 2015a; Ruth et al., 1985; After Yang et al. (2024): separate genus *Sabina*
			Subfamily Callitroideae	Decussate or tricussate (more frequent than in Cupressoideae), spiral phyllotaxis absent; Vegetative shoots and cones	Phyllotaxis not uniform, even within a taxon	Jagel & Dörken, 2015b

Table 1. Continued

Taxon				Dominant phyllotaxis/organ type	Other patterns/remarks	References
			Fitzroya, Callitris, Actinostrobus	Cone scales in trimerous whorls		Dörken et al., 2019; Jagel & Dörken, 2015b; Takaso & Tomlinson, 1989b
			Libocedrus group, *Austrocedrus*	Cone scales decussate		Jagel & Dörken, 2015b; Tomlinson et al., 1993
			Neocallitropsis, *Actinostrobus*	Tetracussate; Vegetative shoots and cones		Jagel & Dörken, 2015b
			Widdringtonia	Spiral arrangement in seedlings, whorled in mature branches; cone scales decussate		Jagel & Dörken, 2015b; Takaso & Tomlinson, 1989b
			Family Cephalotaxaceae			
			Cephalotaxus	Bijugy of main Fibonacci (2,4,6,10, . . .); vegetative shoots and bracts		Banasiak & Zagórska-Marek, 2006; Fujita, 1939; Namboodiri & Beck, 1968a; Tomlinson & Takaso, 2002; Tomlinson & Zacharias, 2001
					Main Fibonacci (1,2,3,5,8, . . .)	Fujita, 1939
			Family Taxaceae			
			Taxus, Taxus baccata	Main Fibonacci (1,2,3,5,8, . . .)	Bijugy of main Fibonacci (2,4,6,10, . . .)	Banasiak & Zagórska-Marek, 2006
				Decussate bracts		Tomlinson & Takaso, 2002
			Amentotaxus	Decussate leaves		Tomlinson & Zacharias, 2001
			Torreya	Bijugy of main Fibonacci (2,4,6,10, . . .) (assimilating leaves)		Banasiak & Zagórska-Marek, 2006; Kemp, 1943; Namboodiri & Beck, 1968a; Tomlinson & Zacharias, 2001
				Decussate (scale leaves); repetitive transition between both patterns	Main Fibonacci (1,2,3,5,8, . . .), Lucas (1,3,4,7, . . .), trijugy of main Fibonacci (3,6,9,15, ...)	Banasiak & Zagórska-Marek, 2006
Class Pinopsida	Subclass Pinidae	Order Pinales	Family Pinaceae			
			Pinaceae	Main Fibonacci (1,2,3,5,8, . . .)	Frequency ca. 95%	Fierz, 2015; Jean, 1994; Namboodiri & Beck, 1968a; Vakarelov, 1998; Zagórska-Marek, 1985
			Pinus austriaca		Tetrajugy of main Fibonacci (4,8,12,20, . . .)	Church, 1904
			Pinus halepensis		1,4,5,9 . . . series	Crafts, 1943b

Table 1. Continued

Taxon				Dominant phyllotaxis/organ type	Other patterns/remarks	References
			Pinus nigra	In cones main Fibonacci (1,2,3,5,8, . . .)	9 additional patterns: mostly bijugy of main Fibonacci (1,2,3,5,8, . . .), Lucas (1, 3, 4, 7, . . .); occasionally other patterns, e.g., 1,4,5,9, . . .; 1,2,5,7,12 . . .; 1,3,7,10,13, . . . and trijugy (3,6,9,15, . . .) and tetrajugy (4,8,12,20, . . .) of main Fibonacci	Fierz, 2015
			Larix decidua	In cones Fibonacci (1,2,3,5,8, . . .), ca. 78%, less stable than in *P. nigra*	7 additional patterns, mostly Lucas (1,3,4,7, . . .), bijugy (2,4,6,10, . . .) and trijugy (3,6,9,15, . . .) of main Fibonacci; less frequent 1,4,5,9, . . . and 1,2,5,7,12, . . .	Fierz, 2015
			Abies balsamea	Main Fibonacci (1,2,3,5,8, . . .); frequency ca. 95%	11 additional patterns; mostly bijugy (2,4,6,10, . . .) and Lucas (1,3, 4,7, . . .); occasionally other monojugate patterns, 1,4,5,9, . . .; 1,2,5,7,12 . . . and trijugy (3,6,9,15, . . .) and tetrajugy (4,8,12,20, . . .) of main Fibonacci; often pattern transitions	Zagórska-Marek, 1985; Zagórska-Marek & Banasiak, 2020
			Abies concolor	Fibonacci, frequency ca. 97%	Bijugy of main Fibonacci (2,4,6,10, . . .), Lucas (1,3,4,7, . . .) and 1,2,5,7,12, . . . series	Banasiak & Zagórska-Marek, 2006
			Abies alba, Picea abies	Fibonacci	Bijugy of main Fibonacci (2,4,6,10, . . .) and Lucas (1,3,4,7, . . .)	Zagórska-Marek & Banasiak, 2020
Class Pinopsida	Subclass Gnetidae	Order Ephedrales	Family Ephedraceae			
			Ephedra ssp., *Ephedra equisetina, E. distachya, E. sinica, E. pedunculata, E. chilensis, E. intermedia, E. przewalskii, E. ochreata*	Decussate, occasionally tricussate; vegetative shoots and bracts		Foster & Gifford, 1974 Yang et al., 2024
				Two opposite cotyledons, leaves decussate		Dörken, 2012
		Order Gnetales	Family Gnetaceae			
			Gnetum	Decussate, tricussate		Foster & Gifford, 1974 Yang et al., 2024
		Order Welwitschiales	Family Welwitschiaceae			
			Welwitschia	Decussate: whorls of different organs: cotyledons, a pair of strip-like leaves and bracts in female cones		Martens & Waterkeyn, 1963

Note: The taxonomic classification of gymnosperms follows Yang et al. (2022 , 2024).

of seasonal activity of meristem (Parke, 1959; Romberger, 1963; Romberger et al., 1993; Zagórska-Marek, 1985). In some species, for example in *Abies concolor, Pinus lamberghiana, P. ponderosa, Pseudotsuga taxifolia*, *Picea abies*, this sequence of lateral organ initiation is modified, and scale initiation takes place before or during the embryonic shoot elongation (Parke, 1959; Romberger, 1963; Sacher, 1954; Sterling, 1946b; Wenzel et al., 2024). Alternatively, in the Cupressaceae, the preformed, embryonic shoot and dormant bud are not formed. Meristem activity and organogenesis are temporally arrested under unfavourable environmental conditions and resumed afterwards (Stankova et al., 1999).

In the majority of gymnosperms (with the exception of *Pinus*), below the bud, in the central part of the stem, the collenchyma plate (crown) is formed. It separates the meristem from the mature tissues (mostly those of the pith) and is composed of a few cell layers with visibly thickened cell walls. Usually, the crown is located above the level of scale leaf insertion in the bud; thus, it does not isolate scale primordia from the mature shoot tissues during initiation (Kemp, 1943; Lewis & Dowding, 1924; Parke, 1959; Pillai & Chacko, 1978; Romberger, 1963; Sterling, 1945a, 1946b). By contrast, in *Torreya*, the crown is positioned at the level of scale leaf insertion in the bud; thus, the scale primordia develop in isolation from the mature tissues (Banasiak & Zagórska-Marek, 2006).

Upon transition to the reproductive phase, some axillary shoots start differentiating as reproductive ovule- or pollen-bearing structures (commonly referred to as cones; for discussion on homology and development of seed cones, see Dörken & Rudall, 2018; Leslie & Losada, 2019; Losada & Leslie, 2018; Matsunaga, 2026; for male cones see Schulz et al., 2014; Dörken & Nimsch, 2016, 2023; Dörken, 2024a, 2024b). The meristem increases in size, broadens and changes the shape to dome-like and although the zonation pattern remains relatively stable, the divisional activity within the CMC and PZ increases (Losada & Leslie, 2018; Mouradov et al., 1998). In the PZ, numerous bracts and ovuliferous scales are initiated, forming a complex, branched structure (Leslie & Losada, 2019). Upon bud breaking, the axis of a female cone starts rapid elongation that causes cone emergence; further scale differentiation and maturation result in reaching the final shape of the cone (Dörken & Rudall, 2018; Jagel & Dörken, 2014, 2015a, 2015b; Leslie & Losada, 2019; Losada & Leslie, 2018; Takaso & Tomlinson, 1989a, 1989b, 1990, 1992; Tomlinson et al., 1993; Tomlinson & Takaso, 2002).

The molecular regulation of the SAM transition from vegetative to reproductive phase has been intensively studied in order to elucidate the homology and evolutionary relationships of gymnosperm and angiosperm reproductive structures (Akhter et al., 2022; Matsunaga, 2026; Mouradov et al., 1998; Song et al., 2025; Vázquez-Lobo et al., 2007). The studies showed the role of C- class gene *AGAMOUS* in determining the identity of female (ovuliferous) structures (Matsunaga, 2026 and references therein), and the differential expression pattern of *LEAFY*-like (*LFY*-like; homologue of angiosperm *LEAFY*) and *NEEDLY* (*NLY*) genes that upregulate the B and C class MADS-homeobox genes (responsible in angiosperms for the identity of generative floral elements; Mouradov et al., 1998; Song et al., 2025; Vázquez-Lobo et al., 2007). In this context, an interesting developmental abnormality in gymnosperm cones is a resumption of vegetative growth after formation of several reproductive structures. Although a random and spontaneous process, the regrowth of vegetative shoots at the cone apex was described in several coniferous genera (Bateman et al., 2011; Dörken & Rudall, 2019; Rudall et al., 2011), and can be explained by spatiotemporal deviation in the functioning of the B and C class genes (Dörken & Rudall, 2019). Observations of reverted cones could be of interest in terms of the regulation of organ positioning versus their identity. In angiosperms, vegetative organs, formed after reversion, continue the whorled phyllotaxis of floral elements regardless of a vegetative pattern (e.g., spiral; Battey & Lyndon, 1990; Tooke et al., 2005), suggesting that both mechanisms are independent. In gymnosperms, although the type of vegetative and cone phyllotaxis is usually the same (Table 1), it is not known whether the expression, chirality of the pattern (for explanation of terms, see Figure 2), or the number of leaves per whorl is maintained or changes, especially given that the proportions at the SAM (i.e., the size of PZ versus primordia) change upon transition.

From a quantitative perspective, the large size, prolonged activity and distinguishable cytohistological zonation of gymnosperm SAMs provide a distinct geometric and temporal context for pattern formation, affecting both pattern stability and the occurrence of transitions.

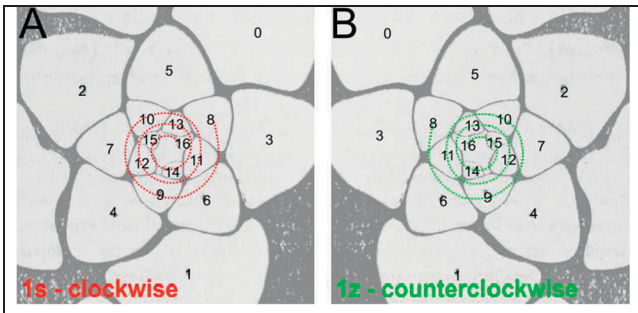
3. SAM self-maintenance regulation

Information on the genetic regulation of gymnosperm meristem functioning is fragmentary. The data come mostly from studies on somatic embryogenesis and de novo organogenesis in in vitro cultures or, alternatively, from transcriptomic analyses (Alvarez et al., 2018, 2020; Bueno et al., 2020; Hjortswang et al., 2002; Larsson et al., 2012). Recent studies showed that genetic SAM regulation relies on transcription factors belonging to the *WOX* (*WUSCHEL-related homeobox*) and *KNOX* (*KNOTTED1-like homeobox*) gene families, showing similarities to the regulatory mechanisms known in angiosperms (Alvarez et al., 2018; Bueno et al., 2020; Hedman et al., 2013; Xu et al., 2025). Analyses of different gymnosperm species showed the presence of the *WOX* genes, classified into three clades with specific expression profiles and functions. Importantly, homologues of angiosperm *WUS* and the gymnosperm-specific *WOXX* genes are possibly involved in SAM maintenance (Alvarez et al., 2018; Hedman et al., 2013; Xu et al., 2025).

Within the *KNOX* family, the first gene described for gymnosperms was *HBK1* (*Homeobox of KNOX class*) from *P. abies* (Sundås-Larsson et al., 1998). It shows high similarity to *KN1* (*KNOTTED1*) from maize in terms of both the homeodomain sequence and the expression pattern. It is expressed in the central population of undifferentiated cells in the SAM but not in sites designated for new primordia formation, suggesting a control of meristem versus leaf primordia initiation similar to that in angiosperms (Hjortswang et al., 2002; Sundås-Larsson et al., 1998). In recent studies, more genes from class I and II of *KNOX* have been identified in *Pinus* and *Picea*, but their function and tissue-specific expression remain to be established (Bueno et al., 2020).

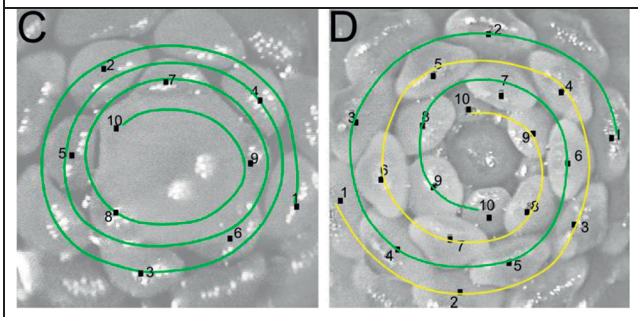
4. Phyllotactic pattern diversity

In gymnosperms, both spiral (helical) and whorled phyllotactic patterns occur; distichy is not reported. In the majority of taxa studied so far, one species-specific phyllotactic pattern dominates, regardless of the lateral organ type (scales, assimilating leaves, cone scales, etc.; Table 1). Spiral patterns can occur in two chiral configurations depending on the course of an ontogenetic helix (winding clockwise or counterclockwise; Figure 2a,b). In gymnosperms, the frequency of both helix chiral configurations is similar and random (Banasiak & Zagórska-Marek, 2020; Fierz, 2015; Gregory



Ontogenetic helix (spiral) – an imaginary line connecting all organs from the first initiated (the oldest) to the last one (the youngest).

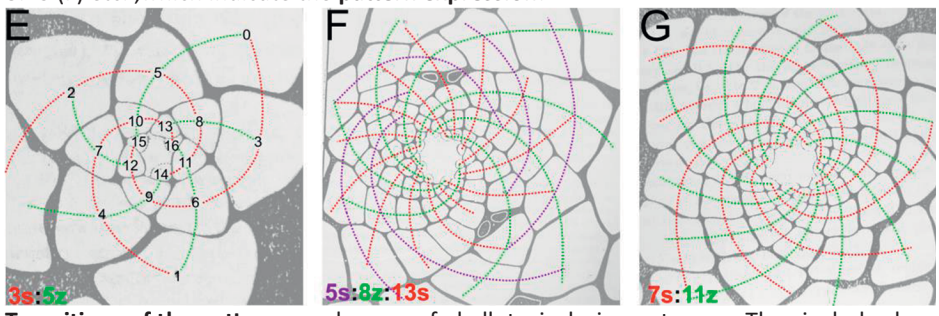
Chiral configuration (chirality) of the ontogenetic helix (spiral) – there are two mirror-like spatial configurations of the ontogenetic helix; it can wind up in a clockwise (**A**; an ontogenetic helix drawn in red; S configuration) or counterclockwise direction (**B**; an ontogenetic helix drawn in green; Z configuration).



Monojugy and multijugy refer to spiral phyllotaxis, where organs are initiated at the apex at a nearly constant angular distance one from another (a divergence angle). They can be initiated separately at the apex (**monojugy**; **C**) or in whorls of two, three etc. (**multijugy**; **D**); the number of ontogenetic helices linking all the organs equals to the number of organs per a whorl. **C, D** – dissected apices of *Picea abies*, **C** – the main Fibonacci pattern in expression 5s:8z, the ontogenetic helix drawn in green; **D** – the bijugy of the main Fibonacci pattern in expression 4s:6z, two counterclockwise ontogenetic helices are drawn (green and yellow lines), successive organs are numbered from the oldest to the youngest (the highest numbers in the picture). Note that in **D** two leaves are initiated at the same level (in pairs) in each whorl.

The main Fibonacci series is an arythmetic series, where each element is a sum of two preceding numbers: 1, 2, 3, 5, 8, 13..... In plants, it corresponds to the most common spiral phyllotaxis. The first element in the series refers to the ontogenetic helix, while other numbers in a series represent possible parastichy numbers. Other phyllotactic series are less frequent, e.g., the Lucas series with the numbers 1, 3, 4, 7, 11,.... (**G**), secondary series such as 1, 4, 5, 9, 14,....; 1, 5, 6,11,...., the bijugy of the Fibonacci pattern 2, 4, 6, 10,... (**D**) and others. For other patterns, their divergence angles and occurrence in plants, see, e.g., Jean, 1994; Zagórska-Marek, 1984.

Each phyllotactic pattern can be expressed by a pair of two successive numbers belonging to the same phyllotactic series (**contact parastichy pair**), e.g., the main Fibonacci pattern by 3:5 (**E**), 5:8 (**F**), 8:13 (**F**) etc. ,which indicate the **pattern expression**.



Transitions of the pattern are changes of phyllotaxis during ontogeny. They include changes of the pattern expression within the same phyllotactic series (**F** – a continuous change from 5s:8z to 8z:13s; **continuous transition**), or changes between two different phyllotactic patterns, e.g., from the Fibonacci series 3:5 to the Lucas series 3:4 (**discontinous transition**). In addition, the direction of the ontogenetic helix can change during transition.

Figure 2. Terminology related to spiral phyllotaxis used in the text. Drawings (a), (b), (e) – (g) after Church, 1904, modified; (b) is a mirror-image of (a).

& Romberger, 1972; Namboodiri & Beck, 1968a; Zagórska-Marek, 1985).

In species with spiral phyllotaxis, the main Fibonacci pattern is usually dominant (Church, 1904; Crafts, 1943b; Gola & Banasiak, 2016; Gregory & Romberger, 1972; Jean, 1994; Namboodiri & Beck, 1968a; Sterling, 1945a; Takaso & Tomlinson, 1990; Zagórska-Marek, 1985), although in some genera, for example *Torreya* and *Cephalotaxus*, the bijugy of this pattern prevails (Banasiak &

Zagórska-Marek, 2006; Kemp, 1943; Tomlinson & Zacharias, 2001; Table 1, Figure 2c,d). The other co-occurring patterns are less frequent, ranging from 3% to 5% in *Abies*, *Picea*, *Pinus* to ca. 20% in *Larix* (Banasiak & Zagórska-Marek, 2006; Fierz, 2015; Zagórska-Marek, 1985; Table 1). In general, several different patterns constitute a phyllotactic spectrum for a species, with additional patterns represented mostly by other monojugies (including rare phyllotactic series), multijugies (e.g., bijugies; Figure 2), and occasionally whorled patterns (e.g., decussate and tricussate).

For genera with whorled phyllotaxis, the decussate pattern is the most commonly occurring and dominant for a species (Dörken et al., 2017; Jagel & Dörken, 2014, 2015a, 2015b; Namboodiri & Beck, 1968b; Ruth et al., 1985; Takaso & Tomlinson, 1989b; Table 1). Some genera are generalised as having decussate or tricussate phyllotaxis, though the frequencies of the two patterns are not given (e.g., in *Juniperus*, subfamilies Cupressoideae, Callitroideae; Jagel & Dörken, 2015a, 2015b). In the Callitroideae, the tricussate pattern is more common than in the Cupressoideae, and this is the typical phyllotaxis of *Fitzroya*, *Callitris*, *Actinostrobus* (at least in cone bracts; Jagel & Dörken, 2015b; Takaso & Tomlinson, 1989b). Two genera, *Neocallitropsis* and *Actinostrobus*, are characterised by a tetracussate arrangement of leaves on adult vegetative shoots and of scales in cones (Jagel & Dörken, 2015b; Table 1).

4.1. Ontogenetic stability and transitions of phyllotaxis

The number of cotyledons in gymnosperm embryos is variable, in contrast to angiosperms with one (monocots) or two (dicots) cotyledons. In taxa with two (or occasionally three) cotyledons, e.g., in *Ephedra* (Dörken, 2012), *Welwitschia* (Martens & Waterkeyn, 1963), *Thuja* (Dörken, 2013a), the first initiated leaves continue the decussate (or tricussate) arrangement of cotyledons or, alternatively, develop spiral phyllotaxis, for example in *Dacrycarpus* (Dörken & Parsons, 2016), *Taxus* (Hakman et al., 2009) and *Ginkgo* (Dörken, 2013b). Interestingly, in the Pinaceae, the number of cotyledons in embryos varies from 2 to 23 (Hakman et al., 2009; Holloway et al., 2016, 2018, 2023). Their actual number is the outcome of the size of the primordia initiation zone and its location in relation to the meristem top. The primordia initiation zone is defined by interactions of *HD-ZIPIII* and *KANADI* genes, with cotyledon primordia emerging in the overlapping domain of their expression and induced by auxin concentration maxima (Holloway et al., 2023). Due to their complex phyllotaxis, conifer embryos are postulated to be a good model for analysing genetic interactions during lateral organ pattern formation (Holloway et al., 2023). It would be interesting to analyse how the number of cotyledons (embryonic phyllotaxis) relates to postembryonic phyllotaxis – the type of pattern and its expression (for explanation of terms, see Figure 2); in addition, to implement similar studies to gymnosperm taxa with a regular number of two (or three) cotyledons and whorled or spiral leaf arrangement. A similar initial condition is also present in lateral branches, where two opposite prophylls (i.e., the first leaves on lateral branches) usually start pattern formation, regardless of the following phyllotaxis (spiral or whorled).

In postembryonic development, the type of phyllotactic pattern and its chirality are usually continued along one axis in subsequent vegetative seasons, regardless of the possible organ identity change (needles, scales). However, the pattern expression (i.e., the number of contact parastichies) can change (continuous transition, Figure 2f) in relation to the size ratio between the meristem and organ primordium (Zagórska-Marek, 1985). Pattern transitions can also concern the type of phyllotaxis (discontinuous transition) and/or the ontogenetic helix chirality (Figure 2). Detailed studies on *Abies balsamea* shoots showed that, in ca. 8% of analysed cases, the pattern changed within the axis (particularly but not exclusively in the seasonal border zone), starting a new pattern that was propagated in the following vegetative seasons. Multiple transitions along the same axis were also observed. Interestingly, these transitions occurred according to the principle of minimal change in the number of parastichies in the pair (the second set of parastichies could be continued), regardless of the potential change of the ontogenetic helix chirality and the divergence angle (Zagórska-Marek, 1985). Less frequent transitions occurred in *Cephalotaxus*, *Taxus* and *A. concolor*, accounting for ca. 1% of all patterns analysed in each taxon (Banasiak & Zagórska-Marek, 2006). Changes in pattern expression, chirality or jugacy can be driven by shifts in meristem geometry or organogenic dynamics.

A particular case is *Torreya*, where repetitive gradual transitions from the bijugy of the main Fibonacci pattern to the decussate pattern occur in the scale leaf zone, and the leaf arrangement for a new vegetative season is established de novo every time. It is usually a main bijugy, with randomised orientation of the ontogenetic helices. Rarely, other patterns are formed, such as Fibonacci, Lucas or trijugy and maintained only in one growth increment. This phenomenon can be explained by SAM autonomy upon leaf initiation, resulting from the isolation of the active meristem, initiating bud scales and leaf primordia, from the mature vascular tissues by the crown, that is the specifically located collenchyma plate mentioned above (compare Fig. 3 in Banasiak & Zagórska-Marek, 2006). It seems that the collenchyma plate impedes differentiation of vascular elements within the apex and blocks the signalling possibly involved in the maintenance of the phyllotactic pattern (Banasiak & Zagórska-Marek, 2006).

4.2. Phyllotaxis chirality in the main versus lateral axes

In gymnosperms, shoot branching is monopodial (i.e., hierarchical with the dominance of the main axis), meaning that the SAM, through the mechanism of apical dominance, controls the axillary SAMs and the formation of lateral branches (Fraser, 1962; Romberger, 1963). As the same dominant phyllotaxis usually occurs in the main shoot axis of a specimen and in its lateral branches, it posed the question of whether the main axis controls the ontogenetic helix chirality in lateral axes. If the chirality in the main and lateral axes is the same, the correlation is positive (homodromy); if the helix orientations are opposite, the correlation is negative (antidromy). Detailed studies in *A. balsamea*, *A. alba, A. sachalinensis* and *P. abies* showed that, in lateral branches, both helix chiral configurations (clockwise, counterclockwise) had similar frequencies, suggesting randomisation of the helix course and a lack of the main axis influence on their pattern chirality (Banasiak & Zagórska-Marek, 2020). Interestingly, in *Cedrus libani* ssp. *atlantica*, more than 90% of lateral shoots showed antidromy in relation to the chirality of the main axis (Banasiak & Zagórska-Marek, 2020). These data show that the superior role of the main axis in phyllotaxis control is species-dependent and that other factors can be involved in this process (compare below).

5. Structure of the primary vascular system

The primary vascular system of gymnosperms is composed of discrete axial vascular bundles and regularly diverging leaf traces (i.e., vascular strands supplying lateral organs). Each axial vascular bundle, together with related leaf traces, forms a vascular

sympodium (Evert, 2007; Namboodiri & Beck, 1968a, 1968b). The close relation between superficial leaf arrangement (phyllotaxis) and the internal vascular supply of leaves is not surprising, as both structures develop within the PZ of the SAM and, in angiosperms, are related to a shared mechanism of polar auxin transport (PAT) (Banasiak & Gola, 2023; Reinhardt et al., 2003). Procambium, the vascular tissue progenitor, develops in the inner region of the PZ as strands of slightly elongated cells. Each procambial strand divides, and one part departs, forming a leaf trace (initiated in the outer region of the PZ), whereas the other part of a strand continues as the axial vascular bundle (Esau, 1965; Evert, 2007).

Interestingly, in some genera, for example *Taxus, Pseudotsuga, Sequoia*, the presence of procambial leaf traces was observed before the initiation of the corresponding leaf primordia (Gunckel & Wetmore, 1946a; Romberger, 1963; Sterling, 1945b, 1947). In addition, differentiated vascular elements could be present in the basal parts of such leaf traces (Sterling, 1946b). The opposite tendency in leaf trace differentiation was observed in *Abies*, where the youngest five or six initiated leaf primordia in the terminal bud were devoid of the procambial strands, which started developing later, during embryonic shoot elongation (Banasiak & Gola, 2023; Parke, 1963).

The primary vascular system in species with helical phyllotaxis shows high regularity: the number of sympodia belongs to the same phyllotactic series as the superficial leaf pattern, and their orientation agrees with the chirality of the same number of leaf parastichies in a given phyllotactic series, but departing leaf traces show the opposite chirality (Namboodiri & Beck, 1968a; Romberger et al., 1993). Only a single leaf trace supplies a leaf primordium, with the exception of *Ginkgo* (Gunckel & Wetmore, 1946b) and *Ephedra* (Dörken, 2012), where two leaf traces from neighbouring axial bundles supply a leaf. However, as there are no lateral connections between axial bundles or leaf traces (even in the case of *Ginkgo* and *Ephedra*), each sympodium maintains its discreteness (Namboodiri & Beck, 1968a).

The primary vascular system in species with whorled phyllotaxis is more variable. It can resemble that in gymnosperms with helical phyllotaxis (the number of sympodia corresponding to orthostichy numbers; single leaf traces supplying leaf primordia), but the chirality of leaf traces can be randomised. Importantly, in the evolutionarily advanced Cupressaceae, two leaf traces diverge from two neighbouring axial bundles toward the leaf (as in the case of *Ginkgo* and *Ephedra*), but they fuse, forming connections between axial bundles and closing the primary vascular system (Namboodiri & Beck, 1968b).

Interestingly, phyllotaxis and the primary vascular system are related to another internal system, present in some gymnosperm genera, that is axial cortical resin ducts. Their number is a member of the same phyllotactic series, always the one preceding the number of sympodia in the sequence and having an opposite orientation (Zagórska-Marek & Banasiak, 2000). The underlying cause of this interrelationship remains unknown, although spatiotemporal dependencies could suggest inductive interactions between these systems.

The structure of the primary vascular system was studied in search of the anatomical basis of the above-mentioned homo- and antidromic phyllotactic relations between the main and lateral axes. Surprisingly, regardless of the lack of correlations and the randomised course of the ontogenetic helix in *Picea* and *Abies*, their sympodial structure shows almost complete homodromy. The chiral orientation of sympodia in the main and lateral axes remains the same. Interestingly, the same correlation was observed in *Cedrus*, in which leaf phyllotactic antidromy occurred. Importantly, in the studied genera, if the chirality of sympodia changed, the orientation in lateral axes followed this change accordingly. This suggests that leaf phyllotaxis adjusts to the internal vascular organisation of the shoot (Banasiak & Zagórska-Marek, 2020).

These results imply that the primary vascular system can act as a structural constraint that cooperates with the SAM, affecting pattern stability, chirality maintenance and continuation along one axis. Understanding these interactions and underlying mechanisms requires, however, the creation and implementation of markers – not yet available for gymnosperms – for tracing subsequent stages of vascular system differentiation.

6. Phyllotaxis regulation

The auxin-dependent mechanism of phyllotaxis regulation in gymnosperms remains poorly studied and presents a great challenge due to a lack of model systems, huge genomes of gymnosperms and limited availability of genetic tools and molecular markers. In addition, the longevity of species, seasonal growth and methodological problems with the analysis of auxin transport result in limited knowledge of PAT and its role in phyllotaxis regulation in gymnosperms. Some information can, however, be inferred from the genomic and phylogenetic analyses.

The main sites of auxin biosynthesis are the SAM and young leaves, as in angiosperm plants. In addition, *YUCCA* genes, involved in the IPA-dependent main auxin biosynthetic pathway, have been identified in gymnosperms (Vijayanathan et al., 2025).

PAT has been detected in gymnosperms and, like in angiosperms, it involves three families of evolutionarily conserved proteins, PIN (PINFORMED), AUX/LAX (AUXIN1/LIKE-AUX1) and ABC (ATP-BINDING CASSETTE TRANSPORTER; Bennett, 2015; Carrillo-Carrasco et al., 2023; Salazar et al., 2019).

In *P. abies*, the PaPIN1 protein has been identified and characterised, and despite differences in structure, shows similarities to AtPIN1 in the expression pattern during embryogenesis. It has strong expression in the protoderm during cotyledons initiation and then in cotyledon tips and developing procambium (Palovaara et al., 2010). Experiments also show that the inhibition of PAT by NPA (N-1-naphthylphthalamic acid) in *P. abies* leads to embryonic SAM impediment, fusion of cotyledons and changes in procambial strands (Hakman et al., 2009; Holloway et al., 2018). Interestingly, NPA treatment causes overexpression of *PaPIN1* and *PaWOX2*, whose activity in embryos is PAT-related, suggesting a compensation mechanism (Hassani et al., 2022). The effects of PAT inhibition resemble those in angiosperms and can imply similar regulation of embryonic organ development (Hakman et al., 2009). Despite the variable number of cotyledons in gymnosperms, the PAT-dependent mechanism of their initiation seems to be evolutionarily conserved in both groups of plants. Other homologues of PIN proteins, PtPINE, PtPING and PtPINH, were identified in *P. taeda* (Bennett, 2015; Palovaara et al., 2010; Zhang et al., 2020). Used in heterologous complementing systems in Arabidopsis *pin1* mutant, PtPINE and PtPINH can rescue the phenotype, leading to organ formation and inflorescence development (Zhang et al., 2020).

Less information is available about the two remaining groups of auxin plasma membrane transporters. The AUX/LAX family in gymnosperms is represented by a lower number of proteins compared to angiosperms; for example in *Pinus radiata*, three transporters have been described: AUX1–1, AUX1–2 and AUX1–3, which participate in auxin maxima formation necessary for vascular tissue formation (Salazar et al., 2019). The ABC

transporters (group B) were identified in *Pinus* and *Picea*, where they are involved in cambium activity and secondary growth regulation (Dobrowolska et al., 2017; Salazar et al., 2019).

The auxin-dependent regulatory mechanism is studied using fusion proteins with GFP, GUS or luciferase. They are implemented in heterologous systems where gymnosperm proteins (e.g., from *Pinus taeda*) are expressed in model plants (mostly Arabidopsis), during somatic embryogenesis, and in callus tissues (Feng et al., 2026; Höfig et al., 2003; Lee et al., 2014; Taniguchi et al., 2004; Zhao et al., 2024). Although these systems are utilised to study different processes, the tool can potentially be modified to analyse SAM and phyllotaxis regulation. However, it would also require developing an experimental setup to study auxin-related processes and markers in mature plants, as so far mostly embryos have been analysed.

Developing stable and widely applicable transformation systems for gymnosperms remains a major challenge because of their complex biology, long life cycle and low efficiency of tissue regeneration in culture. The other problems are low efficiency and stability of transformation (often related to the particular genotype; thus, no single universal protocol is available for all species), the lack of a gymnosperm model system and gymnosperm biochemical specificity. Despite this, the first reports of stable gymnosperm transformation came from the end of the 20th century, when transgenic *Larix* plants were obtained (Huang et al., 1991; Levée et al., 1997). Since then, several gymnosperm species (e.g., *Pinus taeda, P. sylvestris, P. radiata, P. abies, Pseudotsuga menziesii*) have been successfully transformed. Gymnosperm transformations as well as gene editing by the CRISP/Cas9 system have been successfully used to analyse different developmental and physiological processes, specifically gene functions and the regulatory mechanisms of growth and reproduction (Rodríguez et al., 2022; Zhao et al., 2024). Thus, gymnosperms offer a system in which conserved molecular machinery, acting within spatiotemporal and anatomical constraints, can reveal principles of organ patterning regulation that are unavailable in short-lived angiosperm models.

7. Conclusions and perspectives

The classical auxin-dependent model, developed mostly based on Arabidopsis, seems to be universal in its principles across seed plants. However, it has become generally accepted that the model requires the incorporation of additional factors, not all of which are yet known. The extension of research into gymnosperms – the other, distantly related group of plants – will possibly enable analysis of the emergence and evolution of phyllotaxis regulatory mechanisms from a different perspective. In this context, gymnosperms are promising, although forgotten, models for understanding phyllotaxis regulation.

Gymnosperm SAMs are structurally similar to those in angiosperms but devoid of tunica layers (whole structure is similar to the angiosperm corpus); however, due to limited periclinal divisions in some species, a pseudotunica can be formed that resembles the L1 layer of the angiosperm meristem. This structural similarity could be translated into a similar regulatory mechanism of leaf patterning, assuming the presence of homologue PIN proteins and PAT in gymnosperms.

Relatively huge SAMs and the availability of numerous organ primordia for organogenesis manipulation are beneficial for implementing different experimental setups for analyses of the regulation of leaf positioning, both empirical and computational. Furthermore, well-described phyllotaxis diversity and its ontogenetic changes, together with the well-recognised structure and development of internal systems, constitute huge datasets for future analyses.

Research on gymnosperm phyllotaxis can reach a new level, as genomes of some coniferous species have now been sequenced (at least partially), and methods of transformations and gene editing, as well as techniques for visualising gene/protein expression, have become available. Although developed to analyse other developmental or cellular processes, this knowledge can be advantageous in the search of the molecular background of organ patterning regulation in gymnosperms.

Open peer review. To view the open peer review materials for this article, please visit http://doi.org/10.1017/qpb.2026.10056.

Acknowledgements

We would like to thank two anonymous reviewers and the editor for constructive comments, and Piotr Otręba for English checking and copyediting.

The authors acknowledge the use of an artificial intelligence-based tool (Copilot, Microsoft Corporation, ver. 148.0.3967.54) for limited support in language editing of the abstract, without influencing the scientific content or conclusions of the work.

Author contributions. AB and EMG designed the review, gathered literature data and wrote the manuscript.

Competing interest. The authors declare none.

Data availability statement. The review is prepared based on published, publicly available sources. Further inquiries can be directed to the corresponding author.

Funding statement. This work was supported by the University of Wrocław research subvention 501/73/10110/MPK 2599150000/2026.

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