

LITERATURE ANALYSIS OF PHYLOTAXIS PATTERN VARIATION IN PLANTS: SYMMETRY, CLASSIFICATION, AND SPECIES REPRESENTATION

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ABSTRACT

Phyllotaxis, or the pattern of leaf arrangement along a plant stem, plays a crucial role in physiological efficiency and morphological adaptation. This study aims to examine the variation in phyllotactic patterns among plants, identify their relationship with morphological symmetry, and provide examples of species that exhibit each pattern. Through a systematic literature review method, various relevant scientific sources on phyllotaxis and leaf morphological symmetry were analyzed, including journals, textbooks, and previous review articles. The analysis revealed two main categories of phyllotaxis: alternate and whorled. In alternate phyllotaxis, patterns such as distichous, spiral, semidecussate, and orixate arrangements were identified, whereas whorled phyllotaxis included decussate, tricussate, and tetracussate patterns. Each pattern exhibits distinct symmetry characteristics, including reflection, rotational, and spiral symmetries. The study also found that variations in phyllotactic patterns demonstrate profound geometric regularities, which are associated with plant adaptive strategies for light capture and internal resource distribution. This review provides new insights into the understanding of phyllotaxis in the context of morphological geometry and the distribution of plant species exhibiting each pattern.

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Introduction

Phyllotaxis, or the pattern of leaf arrangement along the plant stem, is a fundamental aspect of plant morphology and development. This pattern not only influences the aesthetics and structural organization of plants but is also closely associated with the efficiency of light capture, respiration, and internal resource distribution (Kuhlemeier, 2017; Okabe, 2024). Phyllotactic patterns are formed through the interaction of genetic factors, hormonal regulation (such as auxin distribution), and biomechanical pressures during the growth of the apical meristem (Kuhlemeier, 2017). Leaf phyllotaxis are established during early development, primarily regulated by genetic factors. However, mechanical signals have also been proposed to influence cellular growth and morphogenesis during leaf initiation and patterning (Guo et al., 2022). In many species, these patterns are established consistently and repetitively, reflecting complex yet orderly geometric regularities, such as the Fibonacci spiral pattern observed in *Arabidopsis thaliana* (Kuhlemeier, 2017; Liu et al., 2021).

Various types of phyllotaxis have been identified in both classical and modern botanical studies, including alternate phyllotaxis such as spiral and distichous arrangements (Itoh et al., 2012), as well as more complex forms such as semidecussate, orixate, and Halophila-type patterns (Snow, 1958; Dengler, 1999; Yonekura et al., 2019). Other types include whorled

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phyllotaxis, such as decussate, tricussate, and tetracussate patterns, which exhibit more than one leaf per node and are characterized by distinctive rotational symmetry (Rutishauser, 1999; Zagórska-Marek et al., 2021).

From a structural perspective, variations in phyllotactic patterns can be analyzed through three main types of symmetry: rotational, reflectional, and spiral symmetry (Roberts et al., 1977; Jean, 1994). Each phyllotactic pattern exhibits distinct symmetry characteristics, and understanding these aspects is crucial for studying the regularity of plant development and the morphological adaptation strategies employed in nature.

Although previous studies have described individual phyllotactic patterns separately, there are relatively few comprehensive reviews that classify phyllotactic patterns based on their structural symmetries and distribution across plant species. Therefore, this article aims to provide a literature-based analysis of the variation in phyllotactic patterns among plants, examine their relationship with morphological symmetry, and present examples of species that exhibit each pattern.

Method

This study employed a descriptive qualitative approach using a systematic literature review method to identify, classify, and analyze phyllotactic patterns in plants and their structural implications for leaf morphological symmetry. This method allows for an in-depth understanding of the variation in phyllotactic patterns reported in the scientific literature, while also evaluating their relationship with plant symmetry.

Data were obtained from relevant secondary literature sources, including scientific journals, textbooks, and previous review articles discussing phyllotactic patterns and morphological symmetry in plants. Literature searches were conducted through various scientific databases, such as Google Scholar, ScienceDirect, SpringerLink, JSTOR, and PubMed.

The analysis was conducted to extract data regarding the characteristics of the identified phyllotactic patterns, including the number of leaves per node, the divergence angle between leaves, the number of orthostichies, and the types of symmetry involved, namely reflectional, rotational, or spiral symmetry. Additionally, the analysis also included the mapping of plant species exhibiting specific phyllotactic patterns, based on the morphological descriptions found in the reviewed literature.

Result and discussion

A. Alternate Phyllotaxis

Alternate phyllotaxis is a leaf arrangement pattern in which only one leaf grows at each node. In other words, new leaf primordia form alternately, one by one, at the apex of the stem. The distinctive feature of this pattern is the absence of rotational symmetry, as the leaves do not repeat regularly around the stem. Additionally, reflectional symmetry is only possible under certain conditions, such as when all the leaves are arranged on the same flat plane. This pattern is commonly observed in various plant species and serves as one of the fundamental forms in the study of phyllotaxis or leaf arrangement in plants.

1. Distichous Phyllotaxis

Distichous phyllotaxis is a form of alternate phyllotaxis in which leaves are produced alternately with a constant divergence angle of approximately 180° . In this arrangement, the leaves are positioned on two opposite sides of the stem, forming two vertical rows known as orthostichies. Distichous phyllotaxis is commonly observed in monocotyledonous plants, particularly in the Poaceae (grass) family. A representative example is rice (*Oryza sativa*) (Itoh et al., 2012). In rice, each leaf emerges from a node on the stem, known as the culm, which consists of a series of nodes, new leaves arise from nodes positioned above those bearing older leaves (Tokuyama et al., 2021). In certain moss species, the apical cell is lenticular and undergoes alternating divisions along two planes, producing opposite segments and resulting in a distichous phyllotaxis, as observed in *Fissidens* (Véron et al., 2021). Additionally, distichous phyllotaxis has also been identified in several species within the genus *Myrcia* (Wagner et al., 2023).

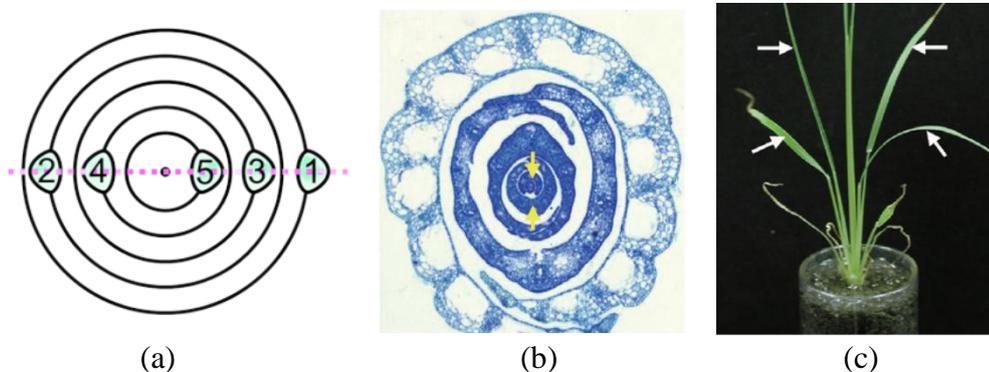


Figure 1. (a) Symmetry pattern in distichous phyllotaxis (Yonekura & Sugiyama, 2020), (b) Cross-section of wild rice (*Oryza sativa*) (Itoh et al., 2012), and (c) Leaf positioning in germinated rice (*Oryza sativa*) (Itoh et al., 2012).

In studies of structure and symmetry, distichous phyllotaxis is sometimes considered a special form of spiral phyllotaxis due to the similarity in the sequence of leaf emergence. However, in terms of symmetry, distichous phyllotaxis is distinctly different as it exhibits reflectional symmetry, where the arrangement of leaves can be symmetrically reflected across a plane, unlike the spiral pattern which lacks such symmetry.

2. Spiral Phyllotaxis

Spiral phyllotaxis is a phenomenon marked by symmetry, regularity, and spiral patterns, where the number of spirals often follows the Fibonacci sequence (Rozin, 2023). Spiral phyllotaxis is a form of alternate pattern in which leaves grow one by one with a constant divergence angle smaller than 180° . Unlike distichous phyllotaxis, which exhibits reflectional symmetry, spiral phyllotaxis only possesses symmetry resembling a corkscrew pattern, that is, a continuous circular pattern without reflectional symmetry.

The most commonly observed type of spiral phyllotaxis is the Fibonacci spiral, characterized by a divergence angle approaching the golden angle (approximately 137.5°). This pattern is referred to as the Fibonacci spiral because the golden angle is mathematically related to the Fibonacci sequence, while the divergence angles of developed leaves vary according to a sequence of Fibonacci fractions, such as $1/3$, $2/5$, $3/8$, $5/13$, etc. (Okabe et al., 2019). A clear example of a plant exhibiting the Fibonacci spiral pattern is *Arabidopsis thaliana* (Caselli et al.,

2025; Kuhlemeier, 2017; Liu et al., 2021). The Fibonacci spiral pattern has also been identified in the fossil *Sanfordiacaulis densifolia* based on reconstruction analyses (Gastaldo et al., 2024).

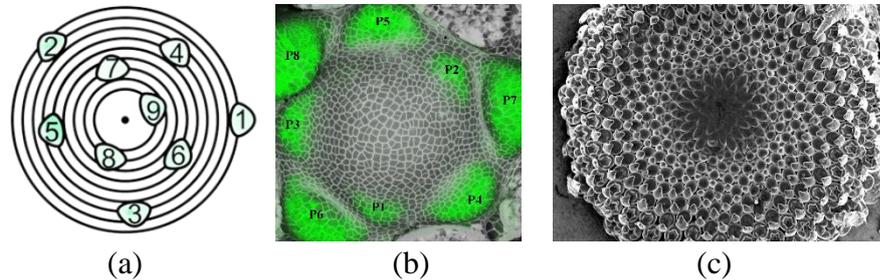


Figure 2. (a) Symmetry pattern in spiral phyllotaxis (Yonekura & Sugiyama, 2020), (b) Top view of the vegetative meristem of *Arabidopsis thaliana* (Kuhlemeier, 2017), and (c) Spiral pattern in sunflower (Kuhlemeier, 2017).

3. Semidecussate Phyllotaxis

Semidecussate phyllotaxis is a variation of the alternate phyllotactic pattern, in which the divergence angle between leaves alternates between two angular cycles, namely 180° and 90° (Roberts et al., 1977). As a result of this pattern, the leaves are arranged in four vertical rows known as tetrastichous or four orthostichies, and this arrangement is clearly visible when viewed from the top of the stem.

Similar to spiral phyllotaxis, semidecussate phyllotaxis also exhibits a spiral symmetry resembling a corkscrew pattern. However, its degree of symmetry is lower ($m=2$) compared to regular spiral phyllotaxis ($m=1$), indicating that its arrangement is slightly more complex, yet still orderly (Yonekura & Sugiyama, 2021).

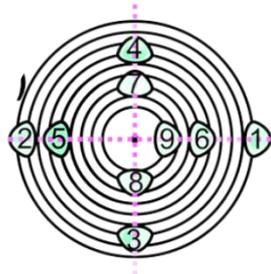


Figure 3. Symmetry pattern in semidecussate phyllotaxis (Yonekura & Sugiyama, 2020).

Semidecussate phyllotaxis is rarely encountered in nature and is found only in certain plant species. Some examples of species known to exhibit this phyllotactic pattern include *Kniphofia tubergeniana* (Snow, 1958).

4. One-sided Distichous Phyllotaxis

One-sided distichous phyllotaxis is a special form of alternate phyllotaxis, in which the divergence angle between leaves follows two different cycles, namely θ° and $(360-\theta)^\circ$, where θ is not equal to 180° . This pattern results in two vertical rows of leaves (two orthostichies), resembling true distichous phyllotaxis. However, unlike the symmetric distichous pattern, in one-sided distichous phyllotaxis, the two rows are not exactly opposite each other, thus losing reflectional symmetry.

One-sided distichous phyllotaxis is considered rare and has only been reported in specific structures of certain plant species. Examples include the floral arrangement (inflorescence) in *Thalia* (Kirchoff, 1986) and the branches of *Orchidantha chinensis* (Kirchoff et al., 2020).

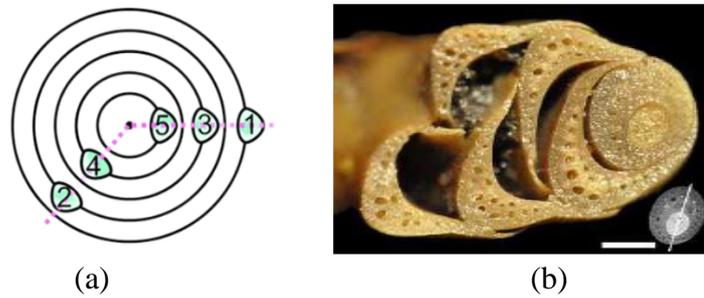


Figure 4. (a) Symmetry pattern in one-sided distichous phyllotaxis (Yonekura & Sugiyama, 2020), and (b) Cross-section of *Orchidantha chinensis* (Kirchoff et al., 2020).

5. Orixate Phyllotaxis

Orixate phyllotaxis is a unique form of alternate pattern, characterized by a change in the divergence angle following four consecutive cycles: 180° , 90° , 180° , and 270° . Similar to semidecussate phyllotaxis, this pattern results in four vertical rows known as tetrastichous or four orthostichies, but the sequence of leaf emergence in different directions distinguishes it structurally.

Although this pattern is rarely encountered, orixate phyllotaxis has been identified in several plant taxon from different phylogenetic groups. Some examples of species known to exhibit this pattern include *Orixa japonica* (Yonekura et al., 2019).

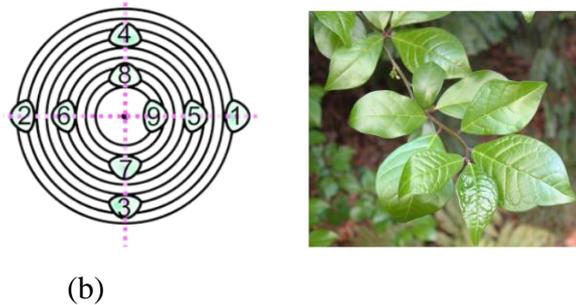


Figure 5. (a) Symmetry pattern in orixate phyllotaxis (Yonekura & Sugiyama, 2020), and (b) orixate phyllotaxis in *Orixa japonica* (Yonekura et al., 2019).

6. Halophila Phyllotaxis

Halophila-type phyllotaxis is an alternate phyllotactic pattern that is also tetrastichous, with four regular divergence angle cycles: 180° , θ° , 180° , and $(360-\theta)^\circ$, where the value of θ is not equal to 90° . In general, this pattern shares fundamental characteristics very similar to Orixate phyllotaxis, including the number of orthostichies (four vertical rows of leaves) and the type of symmetry displayed.

The main difference between Halophila and Orixate phyllotaxis lies in the orientation of the two pairs of opposing orthostichies. In the Orixate pattern, these two pairs of orthostichies are orthogonal or form a right angle. However, in Halophila phyllotaxis, the orientation of the orthostichies is not perpendicular, creating an arrangement that appears skewed or slightly deviated from the typical geometric symmetry.

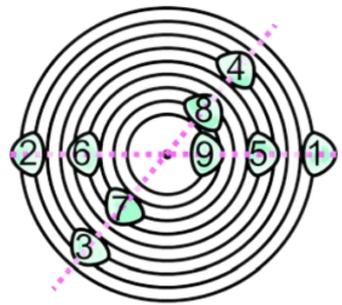


Figure 6. Symmetry pattern in *Halophila* phyllotaxis (Yonekura & Sugiyama, 2020).

This type of phyllotaxis is considered rare and has only been reported in a few species, such as *Anisophyllea disticha*, a woody plant from tropical forests (Dengler, 1999).

B. Whorled Phyllotaxis

Whorled phyllotaxis refers to a leaf arrangement pattern in which two or more leaves emerge simultaneously at each node. Unlike alternate phyllotaxis, which has only one leaf per node, whorled phyllotaxis displays a circular grouping of leaves around the stem.

In this pattern, all leaves at a single node are evenly arranged around the stem, creating a symmetrical structure. Therefore, whorled phyllotaxis naturally exhibits rotational symmetry, determined by the number of leaves emerging at each node. The greater the number of leaves in a whorl, the more complex the rotational pattern becomes, although the principles of regularity and balance are consistently maintained.

1. Decussate Phyllotaxis

Decussate phyllotaxis is one of the most common forms of whorled phyllotaxis found in plants. This pattern is classified as tetrastichous, as it forms four vertical rows of leaves (four orthostichies). In this arrangement, two leaves grow at each node, positioned opposite each other on opposing sides of the stem (Godin et al., 2020). What distinguishes this pattern is that the pair of leaves at the next node is rotated 90° relative to the previous pair, creating an alternating orthogonal arrangement of leaf pairs along the stem. Decussate phyllotaxis can be observed in plants such as *Verbena officinalis*, *Avicennia marina*, *Mesembryanthemum forsskalii*, and *Dendrophthoe pentandra* (AlZewar, 2024; Adiansyah et al., 2023; Alsanie, 2025; Fuenzalida et al., 2023; Zagórska-Marek et al., 2021).

Due to its regularity, decussate phyllotaxis exhibits all three major types of symmetry simultaneously: reflection symmetry, spiral symmetry, and rotational symmetry. This makes the pattern not only efficient in terms of physiological functions (such as light capture) but also highly ordered from a geometric and developmental perspective.

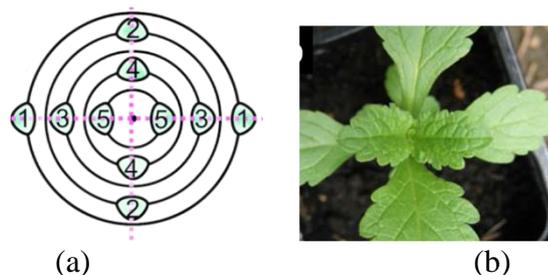


Figure 7. (a) Symmetry pattern in decussate phyllotaxis (Yonekura & Sugiyama, 2020) and (b) Decussate phyllotaxis in *Verbena officinalis* (Marek et al., 2021).

2. Oscillating Decussate Phyllotaxis

Oscillating decussate phyllotaxis is a variant of the tetrastichous whorled pattern that resembles true decussate phyllotaxis but exhibits a key difference in its regularity. In this pattern, as in true decussate arrangements, two leaves grow on opposite sides of the stem at each node. However, the divergence angle between successive pairs of leaves is not consistently 90° , but instead alternates between two angles: θ° and $(180-\theta)^\circ$. This alternating pattern creates four orthostichies (vertical rows of leaves), but with orientations that are not strictly perpendicular to each other as observed in true decussate phyllotaxis.

Due to the oscillation of the divergence angle, the two pairs of orthostichies formed are not orthogonal. As a result, this pattern lacks reflection symmetry, which is a characteristic feature of true decussate phyllotaxis. This phyllotaxis pattern has been clearly reported in *Selaginella martensii* (Dengler, 1999).

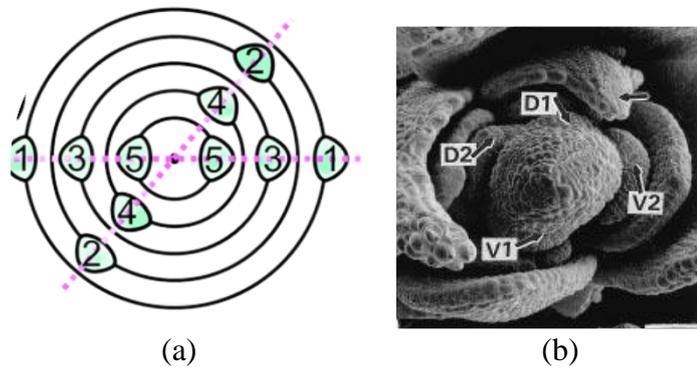


Figure 8. (a) Symmetry pattern in oscillating decussate phyllotaxis (Yonekura & Sugiyama, 2020) and (b) Oscillating decussate phyllotaxis in *Selaginella martensii* (Dengler, 1999).

3. Bijugate Spiral Phyllotaxis

Bijugate spiral phyllotaxis is a type of whorled phyllotaxis in which each node has two leaves growing in pairs on opposite sides of the stem, similar to the decussate pattern. However, what distinguishes it is that the divergence angle between leaf pairs in successive nodes is constant and smaller than 90° , typically approaching half of the golden angle, approximately 68.8° . As a result, these pairs of leaves are arranged in a regular double spiral pattern along the stem.

This pattern reflects spiral symmetry and rotational symmetry, as each pair of leaves consistently moves around the stem at a specific angle and distance. However, unlike in true decussate phyllotaxis, reflective symmetry is absent, as the leaf pairs are not positioned perpendicular to each other or symmetrically opposite between nodes.

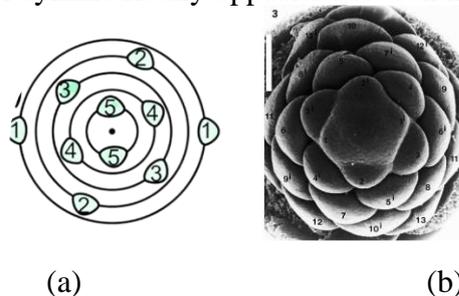


Figure 9. (a) Symmetry pattern of bijugate spiral phyllotaxis (Yonekura & Sugiyama, 2020) and (b) Bijugate spiral phyllotaxis in *Torreya nucifera* (Tomlinson & Zacharias, 2001).

Bijugate spiral phyllotaxis has been observed in various seed plant groups, including *Cephalotaxus* and *Torreya* (Tomlinson & Zacharias, 2001).

4. Tricussate Phyllotaxis

Tricussate phyllotaxis is a type of verticillate (whorled) phyllotaxis pattern in which three leaves grow simultaneously at each node, arranged evenly around the stem. This means that each leaf in a single whorl is separated by an angle of 120° , so when this pattern continues to the next node with a divergence angle of 60° between nodes, a formation of six vertical lines of leaves (hexastichous) is created along the stem. From a symmetry perspective, tricussate phyllotaxis is highly regular, as it exhibits all three primary forms of symmetry in phyllotaxis: rotational symmetry, reflectional symmetry, and spiral symmetry. This phyllotaxis pattern is relatively common in various plant species. One of the most well-known examples is *Sedum ternatum* (Messerschmid et al., 2020). In addition, Tricussate phyllotaxis can also be observed in *Siphocampylus flavescens*, a newly identified endangered species from southeastern Brazil (Coelho et al., 2022).



Figure 10. (a) Symmetry pattern in tricussate phyllotaxis (Yonekura & Sugiyama, 2020) and (b) Tricussate phyllotaxis in *Sedum ternatum* (Marlow, 2022).

5. Tetracussate Phyllotaxis

Tetracussate phyllotaxis is a leaf arrangement pattern in which four leaves emerge simultaneously at each node and are evenly distributed around the stem. In this pattern, each leaf within a quartette has a divergence angle of 90° between leaves at a single node, and the divergence angle between nodes is 45° , thus forming eight vertical orthostichous lines of leaves, also known as octastichous. Due to the high regularity of leaf placement, tetracussate phyllotaxis exhibits all three main types of symmetry: reflectional symmetry, rotational symmetry, and spiral symmetry. Some well-known examples include *Rubia cordifolia* and *Galium rubioides* (Rutishauser, 1999).

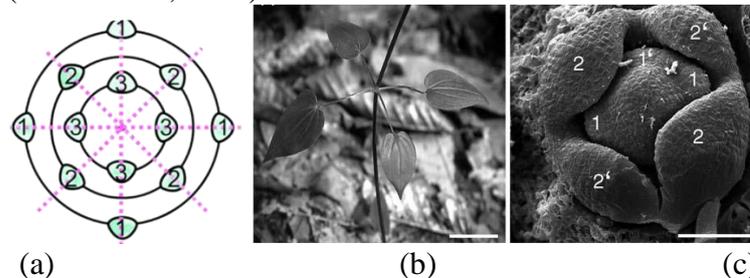


Figure 11. (a) Symmetry pattern in tetracussate phyllotaxis (Yonekura & Sugiyama, 2020), (b) Tetracussate phyllotaxis in *Rubia cordifolia* (Rutishauser, 1999), and (c) Tetracussate phyllotaxis in *Galium rubioides* (Rutishauser, 1999).

Conclusion

The variation in phyllotaxis patterns in plants plays a crucial role in morphological adaptation and physiological efficiency, closely related to light capture strategies and resource distribution. The two main categories of phyllotaxis patterns, alternate and whorled, exhibit various types of symmetry, including reflectional, rotational, and spiral, each influencing the structure and development of plants. Patterns such as distichous, spiral, and semi-decussate in alternate phyllotaxis, as well as decussate, tricussate, and tetracussate in whorled phyllotaxis, reflect the diversity in the geometrically regular arrangement of leaves. This analysis provides a deeper understanding of how phyllotaxis pattern variation supports plant physiological efficiency and optimal ecological adaptation strategies.

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