

Aberrant phyllotactic patterns in cones of some conifers: a quantitative study

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Abstract

The scale patterns of 6000 cones from one single tree of *Pinus nigra* Arn. have been examined. Apart from the main Fibonacci pattern with 8 and 13 parastichies, nine aberrant spiral patterns with Fibonacci-type sequences have been found. They are quite rare and occur with different frequencies. The parastichy quotient 8/13 of the prevalent pattern is very close to the golden ratio 0.618. In case of the black pine it appeared that the greater the deviation of the parastichy quotient m/n from 0.618, the rarer the pattern. Similar results obtained for the sample of 1506 cones collected from three individual trees of larch (*Larix decidua* Mill.) suggest a true correlation between the frequency of a pattern and the deviation of its parastichy quotient from the golden ratio.

Keywords: phyllotaxis; phyllotactic diversity; *Pinus nigra* Arn.; *Larix decidua* Mill.; rare cone patterns; Fibonacci-type sequences; golden ratio

Introduction

Looking at European black pine cones from below (Fig. 1), curved rows of scales running in two opposite directions can be observed, one clockwise, the other counter-clockwise. These conspicuous rows are called contact parastichies. When counted, they are found in paired numbers of the Fibonacci sequence: in open *Pinus nigra* cones there are usually 8 parastichies running in one direction and 13 parastichies the other way round. Personal observations of the author of the present study have shown (unpublished data) that in other species of conifers, the patterns are often seen in lower expression of the Fibonacci sequence, e.g. with 5 and 8 parastichies (*Picea abies* or *Larix decidua*) or 3 and 5 parastichies (*Sequoia sempervirens*). However, there are exceptions to the rule: in most species of conifers, always quite rarely but in different frequency, aberrant patterns of cones show different parastichy numbers. They belong to the “Fibonacci-type” sequences [1]; as in the main Fibonacci sequence, each number is the sum of the previous two (Fig. 2). The aim of the present study was mainly to compare the phyllotactic diversity of one single *Pinus nigra* tree with pooled data of other species.

Material, methods and results

In search for aberrant patterns in European black pine, 6000 cones from one single tree have been examined, almost its whole cone production of about two years. This tree was planted more than 60 years ago in a garden in Küsnacht near Zürich, Switzerland at 560 m altitude.

The open *Pinus nigra* cones have been selected for the study because their patterns can be neatly documented with single photographs and do not need unrolled surface techniques like vegetative shoots or magnolia floral cones [2].

Apart from the usual pattern 8:13 nine different types of aberrant patterns have been found (Fig. S1, Fig. S2, Fig. S3). The bijugy pattern 10:16 (69 cones), the first accessory pattern 7:11 (20 cones) and the trijugy pattern 9:15 (9 cones) were the most frequent. The patterns 8:12, 9:14 and 7:12 followed with 3–5 cones, and the rarest patterns were 9:13 (2 cones), 6:11 (one cone) and 7:10 (one cone).

The wide and distinct difference in frequency of aberrant patterns was the reason to start searching for possible correlations with mathematical or geometrical properties of the parastichy pattern. Looking at the opposite parastichy pairs (called m and n) of the various patterns, an apparent correlation of the parastichy quotient m/n with the frequency of the pattern can be found. Generally, the greater the deviation of the m/n quotient from the value of 0.618 (the golden ratio ϕ), the less frequent a pattern, with very few exceptions (Tab. 1).

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Fig. 1 *Pinus nigra* – a cone with the expression 8:13 of the main Fibonacci sequence (1, 2, 3, 5, 8, 13, 21, ...). Three photographs of the same cone seen from below. In the middle and right photograph, the contours of the parastichies are marked in both directions for better visibility. The scales are numbered from the edge to the cone base (center).

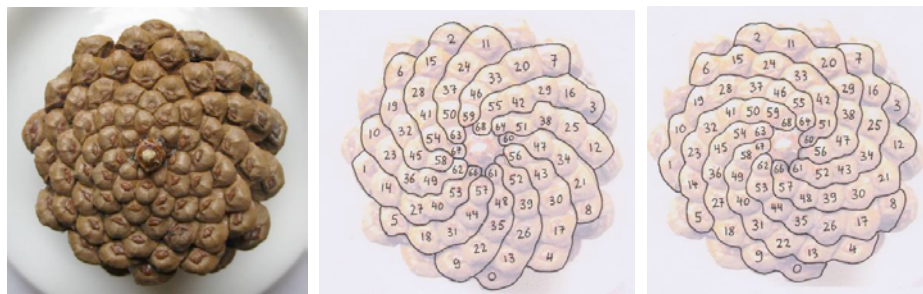


Fig. 2 *Pinus nigra* – a cone with the very rare spiral pattern 9:13 (numbers of the Fibonacci-type sequence 4, 9, 13, 22, 35, 57, ...).

Tab. 1 Deviation of m/n quotient from the golden ratio ϕ (= 0.618), and $m:n$ pattern frequency in 6000 *Pinus nigra* cones.

Fibonacci or Fibonacci-type sequence	Spiral pattern $m:n$	Parastichy quotient m/n	Deviation from 0.618	Number N of <i>Pinus nigra</i> cones
1, 2, 3, 5, 8, 13, ...	8:13 normal	0.615	-0.003	5838 (97%)
2, 4, 6, 10, 16, ...	10:16	0.625	+0.007	69
1, 3, 4, 7, 11, ...	7:11	0.636	+0.018	20
3, 6, 9, 15, ...	9:15	0.600	-0.018	9
1, 4, 5, 9, 14, ...	9:14	0.643	+0.025	3
2, 5, 7, 12, ...	7:12	0.583	-0.035	3
4, 8, 12, 20, ...	8:12	0.667	+0.049	5
1, 5, 6, 11, 17, ...	6:11	0.545	-0.073	1
4, 9, 13, 22, ...	9:13	0.692	+0.074	2
3, 7, 10, 17, ...	7:10	0.700	+0.082	1
Not readable	irregular			49

The greater the deviation, the rarer the pattern, with very few exceptions. The deviation indicates the relative order of pattern frequency only within the same species. Compared with *Larix decidua* cones (Tab. 2), deviation is generally lower in *Pinus nigra* cones with all patterns in higher expression of the same sequences.

Tab. 2 Deviation of m/n quotient from the golden ratio ϕ ($= 0.618$), and $m:n$ pattern frequency in 1506 *Larix decidua* cones.

Fibonacci or Fibonacci-type sequence	Spiral pattern $m:n$	Parastichy quotient m/n	Deviation from 0.618	Number N of <i>Larix decidua</i> cones
1, 2, 3, 5, 8, 13, ...	5:8 normal	0.625	+0.007	1181 (78%)
2, 4, 6, 10, 16, ...	6:10	0.600	-0.018	79
1, 3, 4, 7, 11, ...	4:7	0.571	-0.047	69
3, 6, 9, 15, ...	6:9	0.667	+0.049	30
1, 4, 5, 9, 14, ...	5:9	0.555	-0.063	11
2, 5, 7, 12, ...	5:7	0.714	+0.096	15
2, 6, 8, 14, ...	6:8	0.750	+0.132	1
1, 6, 7, 13, ...	6:7	0.857	+0.239	1
Not readable	irregular			119

The greater the deviation, the rarer the pattern, with very few exceptions. The deviation indicates the relative order of pattern frequency only within the same species. Compared with *Pinus nigra* cones (Tab. 1), deviation is generally higher in *Larix decidua* cones with all patterns in lower expression of the same sequences.

For comparison with other species of conifers, 1506 larch cones produced by three different individuals of *Larix decidua* Mill. growing in a forest near the location of the *Pinus nigra* tree in the study, were examined. It appeared that even though *Larix decidua* produces aberrant patterns in a much higher proportion (22%) than *Pinus nigra* (3%), the order of frequency of the different patterns remains mainly the same. It is identical for the first three patterns, and again the parastichy quotients m/n of the most frequent patterns are very close to the golden ratio 0.618. The m/n quotients of the very rare patterns 6:8 (bijugy of the first accessory pattern) and 6:7 are quite far removed from 0.618 (Tab. 2). All *Larix decidua* patterns are observed in lower expression than the *Pinus nigra* patterns (e.g. 4:7 instead of 7:11), and their parastichy quotients generally deviated more from 0.618 than those of *Pinus nigra* patterns.

The distribution of different phyllotactic patterns can be illustrated with a phyllotactic grid [2–5]. The squares in the grid (Fig. 3) represent the individual “home address” of a given pattern. Into the grid a black line from square 0:0 to square 34:55 (outside this graph) has been drawn. We might call this line the “Fibonacci line” because it represents an m/n parastichy quotient of 0.618, or golden ratio, in good approximation. The lower expressions of the main Fibonacci sequence (black squares 1:2, 2:3, 3:5) zigzag visibly around the black line. In higher expressions, the zigzag approaches the black line more and more but will never reach it quite exactly. Thus, the pattern 8:13 (*Pinus nigra*) with its higher expression of the main Fibonacci sequence is nearer the black line than the pattern 5:8 (*Larix decidua*). It can be seen on the grid that all other patterns – observed or not – deviate less from the black line in their higher expressions (e.g. 7:11) than in their lower expressions (e.g. 4:7).

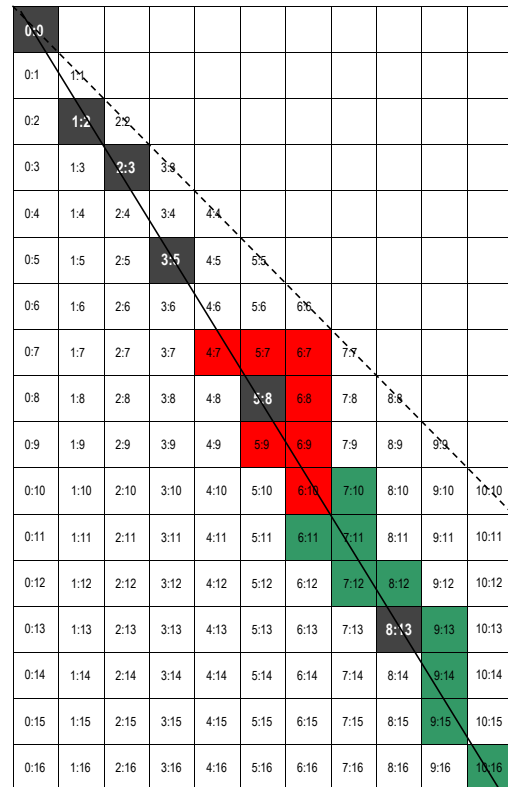


Fig. 3 Phyllotactic grid with aberrant patterns of *Larix decidua* (red squares), and *Pinus nigra* cones (green squares). Patterns of the main Fibonacci sequence (black squares) lie almost (but never quite exactly) on the black line which represents an m/n quotient of 0.618. Frequent aberrant patterns (6:10 and 4:7 for *Larix decidua*, 10:16 and 7:11 for *Pinus nigra*) are positioned near the black line. Rarest patterns (6:8 and 6:7 for *Larix decidua*, 6:11, 7:10 and 9:13 for *Pinus nigra*) lie far off the black line. The dotted line shows the symmetry axis of the phyllotactic grid.

Quite obviously, the possible range for aberrant cone patterns is limited. Observed aberrant patterns (red on Fig. 3 for *Larix decidua*, and green for *Pinus nigra*) are clustered around the main Fibonacci pattern with its species-specific expression. The further away from the black line, the greater the deviation of the parastichy quotient m/n from 0.618, and the rarer the pattern of a cone within the species-specific spectrum of patterns. The patterns most distant from the Fibonacci line are the *Larix decidua* patterns 6:8 (bijugy of the first accessory pattern) and 6:7, and the *Pinus nigra* patterns 6:11, 9:13 and 7:10. All of them are exceedingly rare.

There remains quite a substantial number of unexplained irregular patterns (Tab. 1, Tab. 2). In more than half of these difficult cones, one set of parastichies is quite readable while the opposite set is not. Sometimes a single parastichy may be seen to disappear or to be added to an already established pattern, disturbing and deforming the course of parastichies (Fig. S4). Usually, it is quite impossible to classify such irregular patterns (Fig. S5). Very rarely, the resulting phyllotactic transition from one pattern to another pattern can be deciphered in such cases (Fig. 4).

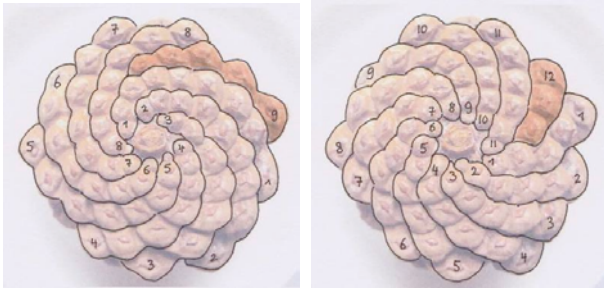


Fig. 4 *Pinus nigra* – an unusual irregular cone, starting at the cone base (center) with 8 parastichies clockwise and 11 parastichies counter-clockwise. Two parastichies (colored) are added later on in opposite directions. At the edge of the cone, the pattern reads 9:12 instead of 8:11. The numbers here mark the parastichies, not the individual scales. The scales themselves cannot be numbered to an uniform pattern.

Discussion

Phyllotactic diversity in conifers was observed and published almost 200 years ago. When studying *Picea abies* cones, Alexander Braun [6] noted in 1831 that a small minority did not show the main Fibonacci sequence, but other patterns; most often the sequences 1, 3, 4, ... (first accessory) and 2, 4, 6, ... (bijugy of the main Fibonacci). His early observation of the most frequent aberrant patterns was confirmed by later researchers. The largest quantitative study was made by Beata Zagórska-Marek [7] in 1985 with 3200 vegetative shoots of 155 *Abies balsamea* trees. Her most frequent aberrants were the same two sequences 1, 3, 4, ... (first accessory) and 2, 4, 6, ... (bijugy). Rolf Rutishauser with his coauthors (unpublished data) studied 2055 *Picea abies* cones from an unknown number of trees. Again, his most frequent aberrant sequences were bijugy and first accessory, found in 71 cones. In 1994, Roger Jean [1] pooled the data

from 12 750 observations on more than 650 species, not all of them conifers, and found bijugy the most frequent aberrant sequence, followed by the first accessory. In 1998, Iliya Vakarelow [8] studied both vegetative shoots and cones of conifers. In *Pinus mugo*, he found an influence of altitude on the phyllotaxis of the shoots but not on that of the cones, and a very much higher frequency of aberrant patterns in shoots than in cones, especially in high altitudes.

The aim of this study was to find as many different aberrant patterns as possible in cones from one single conifer, and to compare the yield of one single genet with the existing theories [1] or with the results of Beata Zagórska-Marek's large quantitative study based upon pooled genetic material from *Abies balsamea* shoots [7]. With a single tree one can study neither intra- or interspecific differences nor environmental influences. At the same time, in this case the genetic uniformity is ensured to study phenotypic plasticity effects, and cones have an important sampling advantage: one can pick up practically all cones of a tree, whereas with vegetative shoots of larger conifers, one is limited to the accessible parts which might not represent the overall distribution of patterns. The results presented in this work show that the genetic information of one single *Pinus nigra* tree is sufficient to produce almost the same range of phyllotactic patterns as a very large number of conifer trees pooled together.

The statistical analysis of even a quite respectable harvest presents some difficulties. Suppose that in a sample of 6000 cones, a rare pattern occurs with a theoretical incidence of 1:6000. Then the probability to find just one single cone with this unusual pattern is only 37%. The chance to find no cone of this same pattern is almost equal, followed by a probability of about 19% to find two such cones in a 6000 cone sample. Thus, even with a sample of 6000 cones, statistically significant differences are not to be expected for very rare patterns. On the other hand, the consistently large m/n deviation of the "almost-never-reported" patterns is quite suggestive. What we can observe is at least a conspicuous trend from highest to lowest pattern frequencies if we range them according to the deviation of their m/n quotient from 0.618 (Tab. 1, Tab. 2). Quite decidedly, an ideal study would encompass several thousand cones per tree, from a considerable number of trees of the same and of other species, all in different environments and in different seasons, all trees separately analyzed: a task which is quite beyond the capacity of one single collector.

Hypotheses about the reasons for the empirically stated order of spiral pattern frequency have been made before. In computer simulations, based on the geometric model of phyllotaxis, the main Fibonacci pattern, its bijugy and the first accessory (Lucas) pattern appeared to be developmentally the most stable, which may explain their prevalence in nature [4]. Roger V. Jean's entropy-based model in turn may be sorely contradicted by the existence of the 7:10 and 8:11 patterns found at first in balsam fir's vegetative shoots [7], later in magnolia flowers [2] and now also in the cones of *Pinus nigra* analyzed in the present study. According to the model these patterns shouldn't exist [1], but otherwise, the order of frequency of cone patterns corresponds quite well with it. Roger Jean's model and this study have the following identical results: (i) the three most frequent aberrant

patterns are (in descending order) the sequences 2, 4, 6, ... (bijugy), 1, 3, 4, ... (first accessory) and 3, 6, 9, ... (trijugy); (ii) multijugate patterns are found in descending frequency from bijugy down to trijugy down to tetrajugy patterns (Fig. S1), and so on; (iii) accessory patterns are found in descending frequency from the sequences 1, 3, 4, ... (first accessory) down to 1, 4, 5, ... (second accessory) down to 1, 5, 6, ... (third accessory; Fig. S2), and so on.

If we assume a correlation of pattern frequency with the deviation of their m/n quotient from the golden ratio: how would it agree with actual hypotheses about pattern formation? In recent models of phyllotaxis employing the concepts of inhibitory fields or auxin fluxes not much is being said about the reasons for empirically detectable differences in pattern frequency [9–11].

The fertile concept that spiral patterns are determined by the ratio of primordium size to the meristem size (P/M ratio) [2,5,12] seems to be promising in future attempts to study phyllotactic diversity. Pattern transitions are thought to result from change of available space for the primordia on the shoot apical meristem (SAM) during ontogeny [4]. Many transitions have been described in *Abies balsamea* shoots [7] and in *Magnolia* flowers [2], and strikingly similar patterns have been created with computer models [4,12] when changing the ratio between primordia size and meristem circumference. Aberrant patterns might be seen as adaptation to an unusual P/M ratio right from the start. Primordia and meristem size are thought to be genetically determined

[4,5,12] but might also be influenced by environment [8]. The P/M ratio can vary in both directions: primordia can be too small or too big in relation to meristem size. Therefore, in adaptation to altered P/M ratios, m/n quotients would have to show deviations in both directions from the standard value. And so they do, as some patterns have positive, other patterns have negative deviations from 0.618 (Tab. 1, Tab. 2).

As a consequence, the m/n hypothesis would seem to be limited to the species where the main Fibonacci sequence is found in a great majority. Species or genets with other standard patterns than the main Fibonacci sequence exist [2,3,13], and on the phyllotactic grid, their aberrant patterns should be expected in clusters around their own standard pattern, with rarest patterns at the edge of the cluster. Further studies are certainly needed.

The correlation between the frequency of spiral patterns in conifers and the deviation of their m/n quotient from the golden ratio is a hypothesis which has not been considered before in phyllotactic literature. It is a much simpler mathematical description of phyllotactic diversity than Roger Jean's entropy model [1]. It might be an interesting alternative: for Fibonacci phyllotaxis, it has its important majority of results in common but does not forbid certain patterns to exist (e.g. 7:10 or 8:11) which have been found in nature [2]. Moreover, it accepts the existence of even more exotic patterns (e.g. the 6, 13, 19, ... sequence in *Picea abies* [14], or the 9:13 *Pinus nigra* pattern in this study) which were not foreseen, and therefore not even discussed, by Roger Jean.

Acknowledgments

This paper is dedicated to the memory of Peter Peisl, the inspiring biology teacher of my school days in Zürich almost 60 years ago. When we met again some three years ago, he started to teach me phyllotaxis with the same didactic enthusiasm. Happily, he lived just long enough to enjoy the considerable variety of cone patterns and the unexpected mathematical results. He died on June 2, 2015; he will be unforgettable to his students. I am grateful to Rolf Rutishauser for many helpful suggestions and for his friendly encouragement; and to my son Martin Fierz for mathematical support and for preparing the manuscript for online submission. This study was done out of private interest and was not funded by anyone.

Competing interests

No competing interests have been declared.

Supplementary material

The following supplementary material for this article is available online at <http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.2015.025/0>:

1. Fig. S1: multijugate Fibonacci patterns in cones of *Pinus nigra*.
2. Fig. S2: monojugate Fibonacci-type patterns in cones of *Pinus nigra*.
3. Fig. S3: monojugate Fibonacci-type patterns in cones of *Pinus nigra*.
4. Fig. S4: some unclassifiable patterns.
5. Fig. S5: the most puzzling irregular cone of our whole series.

References

1. Jean RV. Phyllotaxis: a systemic study in plant morphogenesis. Cambridge: Cambridge University Press; 1994. <http://dx.doi.org/10.1017/CBO9780511666933>
2. Zagórska-Marek B. Phyllotactic diversity in *Magnolia* flowers. Acta Soc Bot Pol. 1994;63(2):117–137. <http://dx.doi.org/10.5586/asbp.1994.017>
3. Gola E. Phyllotaxis diversity in *Lycopodium clavatum* L. and *Lycopodium annotinum* L. Acta Soc Bot Pol. 1996;65(3–4):235–247. <http://dx.doi.org/10.5586/asbp.1996.036>
4. Szpak M, Zagórska-Marek B. Phyllotaxis instability – exploring the depths of first available space. Acta Soc Bot Pol. 2011;80(4):279–284. <http://dx.doi.org/10.5586/asbp.2011.043>
5. Wiss D, Zagórska-Marek B. Geometric patterns of the apical meristem and the quality of phyllotactic patterns in *Magnolia* flowers. Acta Soc Bot Pol. 2012;81(3):203–216. <http://dx.doi.org/10.5586/asbp.2012.029>
6. Braun A. Vergleichende Untersuchung über die Ordnung der Schuppen an den Tannenzapfen als Einleitung zur Untersuchung der Blattstellung überhaupt. Bonn: Thormann; 1831. <http://dx.doi.org/10.5962/bhl.title.69200>
7. Zagórska-Marek B. Phyllotactic patterns and transitions in *Abies balsamea*. Can J Bot 1985;63(10):1844–1854. <http://dx.doi.org/10.1139/b85-259>
8. Vakarelov II. Changes in phyllotactic pattern structure in *Pinus* L. due to changes in altitude. In: Jean RV, Barabé D, editors. Symmetry in plants. Singapore: World Scient. Press; 1998. p. 213–230. http://dx.doi.org/10.1142/9789814261074_0009
9. Reinhardt D, Pesce ER, Stieger P, Mandel T, Baltensperger K, Bennett M, et al. Regulation of phyllotaxis by polar auxin transport. Nature. 2003;426:255–260. <http://dx.doi.org/10.1038/nature02081>
10. Traas J. Phyllotaxis. Development. 2013;140:249–253. <http://dx.doi.org/10.1242/dev.074740>
11. Besnard F, Refahi Y, Morin V, Marteaux B, Brunoud G, Chambrier P, et al. Cytokinin signalling inhibitory fields provide robustness to phyllotaxis. Nature. 2014;505:417–421. <http://dx.doi.org/10.1038/nature12791>
12. Zagórska-Marek B, Szpak M. Virtual phyllotaxis and real plant model cases. Funct Plant Biol. 2008;35(10):1025–1033. <http://dx.doi.org/10.1071/FP08076>
13. Gola E. Phyllotactic spectra in cacti: *Mammillaria* species and some genera from Rebutia group. Acta Soc Bot Pol. 1997;66(3–4):237–257. <http://dx.doi.org/10.1071/FP08076>
14. Rutishauser R. Plastochrone ratio and leaf arc as parameters of a quantitative phyllotaxis analysis in vascular plants. In: Jean RV, Barabé D, editors. Symmetry in plants. Singapore: World Scient. Press; 1998. p. 171–212. http://dx.doi.org/10.1142/9789814261074_0009