ONTOGENETIC CHANGES OF PHYLLOTAXIS IN *ANAGALLIS ARVENSIS* L.

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ABSTRACT

During the ontogeny of *Anagallis* spontaneous changes of phyllotaxis appear in a regular sequence. The initial decussate pattern is followed by spiral Fibonacci phyllotaxis, this in turn, by a trimerous pattern, and finally Lucas spiral phyllotaxis is formed. In the course of the first and most common phyllotactic transition, from the decussate to spiral Fibonacci pattern, changes in primordia arrangement occur only within a limited sector of the apex circumference. In the complementary sector, primordia emerge as if the decussate phyllotaxis continued. It is likely that similar circumferential discontinuity accounts for further transitions. The common ontogenetic sequence of patterns in *Anagallis* is such that, theoretically, each transition requires minimal changes in shoot apex geometry. Although the meristem in *Anagallis* is able to produce primordia either in whorls or spirally, the elongated shoots of this plant seem to have leaves exclusively in whorls. It appeared that in shoots with an initially spiral pattern, leaves can be clustered in pseudo-whorls due to the uneven internode elongation. Pseudo-whorls are composed usually of three (Fibonacci) or four (Lucas) leaves of successive nodes. The number of leaves in a pseudo-whorl equals the number of leaves positioned on one revolution of the ontogenetic helix, which is different in these two spiral patterns. In shoot apices with whorled phyllotaxis, the leaf and flower primordia of a whorl are of different size. On elongated shoots, flower buds emerging in the axils of leaves of one whorl also differ in size.

KEY WORDS: *Anagallis arvensis*, phyllotactic patterns, phyllotactic transitions.

INTRODUCTION

Ontogenetic changes in phyllotaxis, i.e. phyllotactic transitions, are characteristic of many plants. In some species phyllotaxis is transformed only once during ontogeny. It can be a change from the decussate to the spiral Fibonacci pattern, as in *Linum usitatissimum* L. (Williams 1975, Meicenheimer 1987), or from bijugate to Fibonacci pattern as in *Epilobium hirsutum* L. (Meicenheimer 1982). There are also plants where phyllotaxis changes more than once during ontogeny, and several spiral and whorled patterns may occur in a sequence. Phyllotactic transitions are often concurrent with the beginning of the floral phase of development, as in *Epilobium* (Meicenheimer 1982). However, in some species such as *Juniperus chinensis* L. (Meicenheimer, Zagórska-Marek 1989), *Abies balsamea* (L.) Mill. (Zagórska-Marek 1985), or *Hippuris vulgaris* L. (McCully, Dale 1961), phyllotaxis is independent of flowering, even though it may change quite frequently along the axis of the vegetative shoots. A very interesting case is found in *Bryophyllum tubiflorum* Harv. (Gómez-Campo 1974), where phyllotaxis changes a few times during the vegetative phase, but always returns to the initial decussate pattern just before flowering. A new example of phyllotactic transitions appears to be *Anagallis arvensis* L. in which phyllotaxis may also vary significantly (Meicenheimer, Zagórska-Marek 1989, Kwiatkowska 1992). The initial leaf

arrangement in this species is always decussate, and most of the investigators who have studied this plant concentrated on shoots exhibiting this phyllotaxis. Vaughan (1955) examined the growth of vegetative and reproductive shoot apices; De Sloover (1958) studied the differentiation of the primary vascular system of decussate shoots. Green, Havelange, and Bernier (1991) documented the development of the surface of apical meristems of *Anagallis* in vegetative and reproductive ontogenetic phases, but again only of decussate shoots. Trippi and Brulfert (1973) working on senescence, noticed the change from two- to three-leaved nodes at the beginning of flowering in *Anagallis*, but did not study the phyllotaxis. The vasculature of *Anagallis* was examined earlier by the author of this work in relation to the number of leaves per node, but with no consideration of phyllotactic transitions (Kwiatkowska 1992).

When it was discovered that the phyllotaxis of *Anagallis* is not stable, and various patterns appear during its ontogeny, it became clear that the plant may provide valuable material for studies on the phenomenon of variability and ontogenetic changes in phyllotaxis. The purpose of this work is the analysis of phyllotactic patterns and phyllotactic transitions in *Anagallis*. Both shoot apices and elongated (mature) shoots were examined, so that the ontogenetic sequence of phyllotactic patterns could be determined.

MATERIALS AND METHODS

Anagallis arvensis is a caulescent annual herb. During the vegetative phase of its ontogeny, axillary meristems produce lateral shoots, whereas in the reproductive phase, they develop into single flowers. Therefore, the axial growth of the shoot is not restrained during flowering. The only difference in meristem activity in the two phases is that the flower primordia enlarge more rapidly and become prominent earlier than the primordia of lateral shoots (Vaughan 1955, Green, Havelange, Bernier 1991).

All plant material used in the present study belonged to the form *arvensis* of *Anagallis arvensis* L. (Kornaś 1962). It was collected at three different locations: 1) from the stubble field in Przecławice n. Trzebnica treated with the glyphosate herbicide "Round-up" (Monsanto) - in October of 1988 (the same batch as used by Kwiatkowska 1992); 2) from the beds of the Botanical Garden of Wrocław University - during July to August of 1990; and 3) from a population grown in the glasshouse from seeds collected in the Botanical Garden of Wrocław University - in May of 1991. All the plants were in the flowering stage.

Shoot apices were fixed in formalin-aceto-alcohol for scanning electron microscopy (SEM). Specimens were dehydrated in ethanol, dried (critical drying point) with carbon dioxide, dissected and coated with gold (Postek et al. 1980). Micrographs of apices in a top view were prepared using the Stereoscan 150 (SEM Cambridge Instruments).

Elongated shoots were fixed in formalin-aceto-alcohol or in chrom-aceto-formalin and embedded in paraffin. Serial transverse sections, 10 µm thick, were stained with either Ehrlich's hematoxylin, or safranin and fast green (Johansen 1940).

Phyllotaxis was determined both on micrographs of shoot apices and on serial transverse sections. The angles between the leaves or leaf primordia, and a mean divergence angle in the case of spiral phyllotaxis, were calculated. The geometric center of the apex area was determined as in Green and Baxter (1987). It is a rule in *Anagallis* that bigger flower primordia emerge in the axils of bigger leaf primordia. Thus, in some apices where the older leaf-primordia had to be dissected, the position of the flower primordium was used in measurements instead of the position of the supporting leaf. For apices with spiral phyllotaxis the direction of the ontogenetic spiral was noted as S - ascending clockwise, or Z - ascending counterclockwise. The order of leaf primordia initiation was estimated on the basis of their size. Phyllotaxis of about 100 apices was examined.

In serial transverse sections of shoots, the center of concentric circles drawn to fit the stem circumference and the outline of the vascular cylinder, was taken as the vertex of angles between leaves (Williams 1975). Each side of an angle passed between the two vascular traces of a leaf (Kwiatkowska 1992). In order to measure the angles between leaves attached at different levels, a sufficient number of successive sections was analysed. The transparent section drawings were arranged in such a way that the outlines of the stem circumference and the vascular bundles of one section exactly overlapped those of the other. Serial sections of about 70 shoots were examined.

RESULTS

Phyllotactic patterns encountered in *Anagallis* were either whorled, with two or three members in one whorl, or spiral

belonging to Fibonacci or Lucas series. Despite this diversity the mature shoot fragments seemed to exhibit whorled patterns exclusively. It appeared that in shoots with spiral phyllotaxis (Fig. 1), the groups of two to four leaves clustered together represented not true whorls but "pseudo-whorls", because they formed due to uneven elongation of internodes. Vertical distances between leaves of a pseudo-whorl were very small, and only the detailed analysis of their circumferential and vertical spacing allowed the distinction between pseudo- and true whorls.

Fig. 1. A shoot of *Anagallis arvensis* with spiral Fibonacci phyllotaxis. Due to uneven elongation of internodes leaves are clustered in pseudo-whorls, indicated by arrows. Bar = 1 cm.

The sequence of phyllotactic patterns in *Anagallis* shoot ontogeny appeared to be nonrandom and very regular.

Decussate phyllotaxis

This was the initial pattern in all shoots. Flower buds emerging in axils of opposite leaves were always unequal, although the mature leaves of the whorl were identical in size. Buds of successive whorls formed two clear helices, each one connecting either larger or smaller members of these whorls. In shoot apices exhibiting this phyllotaxis, leaf primordia of a given whorl were always of different size. For instance, in Fig. 2, primordium P2a is visible, whereas P2b is not yet apparent; in Fig. 3, P2a is bigger than P2b. The same was true of the flower primordia (B1a and B1b in Figs. 2, 3).

Spiral Fibonacci phyllotaxis

In some shoots the decussate phyllotaxis was followed by the spiral Fibonacci pattern. The course of this transition, very similar in all the cases (Figs. 4, 5), was as follows: the primordia of the last pair before the transition were never precisely opposite and differed in size (B2a and B2b in Fig. 4; P1a and P1b in Fig. 5). The successive primordia were spirally arranged, with the angles between them approximating 137°; the Fibonacci divergence. The first of these primordia emerged always in the space above the wider of the two angles between primordia of the last pair (P3 between B2a and B2b in Fig. 4; B2 between P1a and P1b in Fig. 5), shifted towards the bigger of them (towards B2a in Fig. 4). The next primordium (P4 in Fig. 4; B3 in Fig. 5) was initiated in the middle

Figs 2-7. SEM micrographs of shoot apices of *Anagallis arvensis*. In spiral phyllotaxis leaf primordia (P) and flower primordia (B) are numbered increasingly in order of their initiation. In whorled phyllotaxis successively higher numbers are given to primordia of successively younger whorls. Letters a-c added to the symbols of whorls facilitate recognition of the members of one whorl. Bars = 50 μm. Fig. 2. An apex with the decussate phyllotaxis. Flower primordia B1a and B1b differ in size. Fig. 3. Another apex with decussate phyllotaxis. Flower primordia of the first whorl (B1a and B1b) are unequal, as are leaf primordia of the second whorl (P2a and P2b). Fig. 4. An apex at the transition from the decussate to the spiral Fibonacci pattern. Flower primordia B1a and B1b, B2a and B2b are opposite. Leaf primordium P4 is located as if the decussate phyllotaxis continued, whereas on the opposite side of the apex two primordia, one older than the other (P3 and P5), appear instead of one. Primordium P3 and successive primordia are arranged along an S ontogenetic spiral. Fig. 5. An apex with spiral Fibonacci phyllotaxis (ontogenetic spiral Z). The decussate phyllotaxis which preceded the spiral pattern, can be still recognized in the position of the bases of primordia P1a and P1b. B3 is in an appropriate position for a member of the next whorl if the decussate pattern continued. On the opposite side, however, there are two primordia, B2 and P4, instead of one. Together with P5, P6, and P7 they all form a Z ontogenetic spiral. Fig. 6. An apex with spiral Fibonacci phyllotaxis (ontogenetic spiral S). On approximately one revolution of the ontogenetic spiral there are three primordia (as B2, P3, and P4). Later, they may possibly form a pseudo-whorl due to uneven elongation of internodes. Fig. 7. Another apex with Fibonacci phyllotaxis (ontogenetic spiral Z).

of the smaller angle, as if the decussate pattern continued. The direction of the ontogenetic spiral developing in the course of the transition was either S (Fig. 4), or Z (Fig. 5).

In shoot apices with the Fibonacci pattern well advanced, the differences in primordia size were prominent, and the ontogenetic spiral could be easily traced, as either S (Fig. 6) or Z (Fig. 7).

On elongated shoots with spiral Fibonacci phyllotaxis the leaves were always in pseudo-whorls. They most often consisted of three (Fig. 1), or sometimes – two leaves.

In a few shoot apices the arrangement of leaf primordia was less regular. It looked to be intermediate between trimerous and spiral. Triads of successive leaf primordia formed distinct clusters, as in the case of P4-6 and B1-3 in Fig. 8. The differences in size of primordia from the same cluster were greater than in apices with trimerous phyllotaxis, and the mean angle between successive primordia approximated the Fibonacci divergence.

In other apices with less regular phyllotaxis (Fig. 9), no clusters were prominent, but the angles between successive primordia varied and some of them distinctly differed from the Fibonacci divergence. Nevertheless, as in the previous case, leaf primordia were all of different size and spirally arranged, with the mean of angles measured along the ontogenetic spiral close to the Fibonacci divergence.

Trimerous phyllotaxis

Sometimes Fibonacci pattern was further transformed, and if so, always into the trimerous phyllotaxis. This transition was documented only in serial sections of elongated shoots. It has not been found in shoot apices analysed in the SEM. Only in a very few cases did the trimerous pattern appear immediately after decussate phyllotaxis. During this peculiar and rare transition, two leaves of the first trimerous whorl emerged as if in the decussate pattern, however, there was also one more leaf at the slightly higher level, above one of the members of the last pair.

In elongated shoots exhibiting trimerous phyllotaxis, flower buds emerging in axils of leaves of a single whorl were always of different size, as in the decussate shoots. The arrangement of the bigger buds of consecutive whorls was also helical. In shoot apices, leaf or flower primordia of one whorl were not equal. Sometimes two primordia of one whorl had a similar size, whereas the third one was distinctly different despite that they all emerged at the same level (Fig. 10). In other apices all the members of one whorl differed (Fig. 11). The biggest leaf primordium of the younger whorl, appeared always on the same side of the apex as the biggest flower primordium of the older whorl (in Fig. 10 both P2a and B1a are the biggest primordia within their whorls).

Spiral Lucas phyllotaxis

Usually trimerous or spiral Fibonacci phyllotaxis was last in the development of the shoot. A few instances have been found where the trimerous pattern was transformed further into the Lucas spiral phyllotaxis. This transition was found in elongated shoots and analysed on serial sections only. Leaves of the last whorl before the transition were usually arranged asymmetrically. The leaves situated above, i.e. belonging to the transition zone, were positioned at different levels, with the angles between them decreasing to c. 100°, thus approximating the Lucas divergence.

On elongated shoots with spiral Lucas phyllotaxis, pseudo-whorls usually consisted of four, sometimes of three or two leaves. In apices with this pattern, the consecutive primordia

along the ontogenetic spiral often did not differ very much in size (Fig. 12). The S (Fig. 12) and Z (Figs. 13) configurations of ontogenetic spirals were both encountered.

In a few shoots the reversal of Lucas pattern to trimerous phyllotaxis was noted. Otherwise it was the last pattern in shoot development.

DISCUSSION

It is clear that, contrary to the previous reports, not only whorled but also spiral phyllotaxis is present in *Anagallis*. The formation of pseudo-whorls in shoots with spiral phyllotaxis, seen with the SEM, is responsible for their appearance so closely resembling the shoots with leaves in true whorls. For both spiral phyllotactic patterns observed in *Anagallis*, the number of leaves in a pseudo-whorl equals the number of leaves positioned on approximately one revolution of the ontogenetic helix. There are usually three leaves in the Fibonacci and four leaves in the Lucas pattern. Formation of pseudo-whorls is known also for other plants, like *Eloidea* sp., *Myriophyllum heterophyllum* Michx. (England, Tolbert 1964), and a number of species listed by Schoute (1936).

Phyllotactic diversity encountered in *Anagallis* is not common in other species. Vegetative shoots of *Nerium oleander* L. exhibit various whorled, but no spiral patterns (Williams, Metcalf, Gust 1982). A single transition from the decussate to spiral pattern is known to occur in *Linum usitatissimum* L. (Williams 1975). Sequential transitions have been described in *Bryophyllum tubiflorum* Harv. (Gómez-Campo 1974). They resemble to some extent these of *Anagallis*. In *Bryophyllum* shoots, the initial decussate pattern is replaced by a pseudobijugate one, changing subsequently into the spiral Fibonacci pattern. The latter changes into imperfect trimerous, and finally trimerous phyllotaxis appears (Gómez-Campo 1974). Sometimes an imperfect trimerous pattern is transformed into the spiral leaf arrangement, which resembles Lucas phyllotaxis. In the Lucas pattern the direction of the ontogenetic helix is opposite to that existing in the preceding Fibonacci pattern. This is as in *Abies balsamea* (L.) Mill., where such a transition predominantly occurred with a reversal of the ontogenetic helix (Zagórska-Marek 1985). The question arises, what happens at the apex to facilitate such transitions?

Thorough SEM analysis of *Anagallis* apices showed that in the course of the phyllotactic transition from the decussate to the spiral Fibonacci pattern, a peculiar retention of leaf spacing pattern occurs in a sector of apex circumference, where leaf primordia are arranged as if the decussate phyllotaxis had continued. In the complementary sector, two primordia emerge instead of one, and the pattern changes. This is in agreement with the concept of discontinuous phyllotactic transitions (Zagórska-Marek 1987, 1994). Moreover, the ontogenetic sequence of phyllotactic patterns in *Anagallis* concurs with this concept. It can be calculated from the phyllotactic grid (Zagórska-Marek 1994), that every phyllotactic transition in this sequence requires theoretically the smallest changes both in the ratio of apex circumference to primordia size, and in the position (inclination) of the shoot axis (Fig. 14). The direct transition from the decussate to trimerous phyllotaxis was very rare, observed only on a few axes. Theoretically each of the two consecutive transitions, i.e. first from decussate to spiral Fibonacci, and then from the latter to trimerous pattern, requires smaller geometric changes than the direct transition from the decussate to trimerous phyllotaxis. In *Anagallis*, the peculiar order of phyllotactic transitions can be in-

Figs 8-13. SEM micrographs of shoot apices of *Anagallis arvensis*. Labelling as in Figs. 2-7. Bars = 50 μ m. Fig. 8. An apex with less regular Fibonacci phyllotaxis (ontogenetic spiral S). All primordia are of different size and spirally arranged, clusters of three primordia (P1-3; P4-6) are formed. They will later form pseudo-whorls. Fig. 9. An apex with less regular Fibonacci phyllotaxis (ontogenetic spiral S) and no obvious clustering of primordia. Angles between successive primordia fluctuate, but the mean angle approximates the Fibonacci divergence. Fig. 10. An apex with trimerous phyllotaxis. Flower primordium B1a is the biggest of the first whorl; the size of B1b is similar to B1c. Within the second whorl, primordium P2a is again the biggest and located on the same side of the apex as B1a; P2b and P2c are similar. Fig. 11. Another apex with trimerous phyllotaxis. Primordia within each of three subsequent whorls are unequal. The biggest primordia B1a, B2a, and P3a emerge on the same side of the apex. Fig. 12. An apex exhibiting Lucas phyllotaxis (ontogenetic spiral S). Four successive primordia are clustered – they are positioned on approximately one revolution of the ontogenetic spiral, and will probably form later a pseudo-whorl in elongated shoot. Flower primordia B3 and B4, as well as leaf primordia P7 and P8 are similar in size. Fig. 13. Another apex with Lucas phyllotaxis (ontogenetic spiral Z).

terpreted as the result of a constant ontogenetic increase in the apex circumference, or progressive decrease in primordia size. It is because theoretically the ratio of apex circumference to primordia size, in *Anagallis* ontogenetic sequence of patterns, constantly increases. The only exception is an infrequent reversal to trimerous phyllotaxis from the Lucas spiral pattern.

Fig. 14. Phyllotactic grid – a diagram of orthogonal lines symbolizing unrolled contact parastichies, based on Zagórska-Marek (1987, 1994). Intersections of lines indicate points of leaf attachment. Numbers given below intersections are the numbers of contact parastichy pairs. They characterize the phyllotaxis of a shoot, as seen on its split open surface in which the shoot circumference equals the distance between the point of intersection marked with dash (left) and the point with the selected pair of numbers. Arrows show phyllotactic transitions encountered in *Anagallis*. They result from the smallest of all possible changes in the circumference of the shoot relative to the leaf size. The change of the grid inclination to the axis of the system is also minimal in each case. The dashed line shows an un-frequent transition, leading directly from the decussate to trimerous phyllotaxis.

A less regular arrangement of primordia in some apices with Fibonacci phyllotaxis may be interpreted as an example of the transition from spiral Fibonacci to a trimerous pattern, often observed on elongated shoots. Another possibility is an undefined disturbance of the process of leaf initiation.

In apices with whorled phyllotactic patterns (including decussate), the size of leaf and flower primordia composing one whorl was not uniform. It is not known whether this was the effect of non-simultaneous initiation of primordia of one whorl, or of unequal rates of their growth. In some species with whorled phyllotaxis, like *Euphorbia lathyris* L. (Soma 1958), *Vinca major* L. (Jesuthasan, Green 1988), or *Nerium oleander* L. (Williams, Metcalf, Gust 1982), members of a given whorl are uniform in size. In others however, as in *Anagallis*, the differences between primordia emerging at the same level can be noted. These are: *Rauwolfia vomitoria* Afzl. (Mia 1960), *Herniaria hirsuta* L., and *Honckenya pe-*

ploides (L.) Ehrh. (Rutishauser 1981). In *Anagallis* the formation of unequal flower primordia is probably related to the characteristic helical arrangement of unequal flower buds in axils of mature leaves, because the bigger members of successive whorls emerge always on the same side of the apex. The differences in size of buds on decussate shoots of *Anagallis* were noted by Ballard (1969). He traced two separate helices: one connecting the advanced, the second – the retarded buds. The formation of unequal buds in axils of leaves composing one whorl is known as anisoclady (Loiseau, after Cutter 1972, Rutishauser 1981). Cutter (1972) investigated the anisoclady of *Alternanthera philoxeroides* (Mart.) Griseb. and *Hygrophila* sp. She found physiological interactions between the buds.

In general, *Anagallis* shows a tendency of forming whorls even in the case of spiral leaf initiation. Pseudo-whorls present on shoots with spiral phyllotaxis are very similar to whorls of trimerous or tetramerous shoots. On the other hand, clearly whorled shoots of this plant show some features of the spiral pattern. These are: prominent differences in size of leaf primordia comprising one whorl, and helical anisoclady of the shoots with leaves arranged in whorls.

The present study on phyllotaxis of *Anagallis* explains non-uniform structure of the primary vascular system in stem segments with three- and four-leafed whorls (Kwiatkowska 1992). Instability of vasculature in the stem segments with three-leafed whorls, which was the greatest of all patterns, could be the result of their non-uniform origin, i.e. from either trimerous (true whorls) or spiral Fibonacci phyllotaxis (pseudo-whorls). Also, irregularities in the number of vascular bundles, and the vertical displacement of leaves within non-decussate whorls, could be interpreted as the result of leaf arrangement spiral rather than whorled.

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LITERATURE CITED

- BALLARD L.A.T., 1969. *Anagallis arvensis* L. In: The Induction of Flowering. Evans L.T. (ed.). Macmillan Comp. of Australia, pp. 376-392.
- CUTTER E.G., 1972. Regulation of branching in decussate species with unequal lateral buds. *Ann. Bot.* 36: 207-220.
- DE SLOOVER J., 1958. Recherches sur l'histogénèse des tissus conducteurs. II. Le sens longitudinal de la différenciation du procambium, du xylème et du phloème chez *Coleus*, *Anagallis* et *Taxus*. *Cellule* 59: 55-202.
- ENGLAND W.H., TOLBERT R.J., 1964. A seasonal study of the vegetative shoot apex of *Myriophyllum heterophyllum*. *Amer. J. Bot.* 51: 349-353.
- GÓMEZ-CAMPO C., 1974. Phyllotactic patterns in *Bryophyllum tubiflorum* Harv. *Bot. Gaz.* 135: 49-58.
- GREEN P.B., BAXTER D.R., 1987. Phyllotactic patterns: characterization by geometrical activity at the formative region. *J. theor. Biol.* 128: 387-395.

- GREEN P.B., HAVELANGE A., BERNIER G., 1991. Floral morphogenesis in *Anagallis*: SEM sequences from individual growing meristem before, during, and after the transition to flowering. *Planta* 185: 502-512.
- JESUTHASAN S., GREEN P.B., 1988. On the mechanism of decussate phyllotaxis: biophysical studies on the tunica layer of *Vinca major*. *Amer. J. Bot.* 76: 1152-1166.
- JOHANSEN D.A., 1940. *Plant Microtechnique*. McGraw-Hill, New York, London.
- KORNAŚ J., 1962. Rodzaj *Anagallis* L. w Polsce. *Fragm. Flor. et Geobot.* 8: 131-138.
- KWIATKOWSKA D., 1992. The relationships between the primary vascular system and phyllotactic patterns of *Anagallis arvensis* L. (*Primulaceae*). *Amer. J. Bot.* 79: 904-913.
- McCULLY M.E., DALE H.M., 1961. Variations in leaf number in *Hippuris*. A study of whorled phyllotaxis. *Can. J. Bot.* 39: 611-625.
- MEICENHEIMER R.D., 1982. Change in *Epilobium* phyllotaxy during reproductive transition. *Amer. J. Bot.* 69: 1108-1118.
- MEICENHEIMER R.D., 1987. Role of stem growth in *Linum usitatissimum* leaf trace pattern. *Amer. J. Bot.* 74: 857-867.
- MEICENHEIMER R.D., ZAGÓRSKA-MAREK B., 1989. Consideration of the geometry of the phyllotactic triangular unit and discontinuous phyllotactic transitions. *J. theor. Biol.* 139: 359-368.
- MIA A.J., 1960. Structure of the shoot apex of *Rauwolfia vomitoria*. *Bot. Gaz.* 122: 121-124.
- POSTEK M.T., HOWARD K.S., JOHNSON A.H., McMICHAEL K.L., 1980. *Scanning Electron Microscopy. A Student's Handbook*. M.T. Postek, Jr. and Ladol Research Industries.
- RUTISHAUSER R., 1981. Blattstellung und Sprossentwicklung bei Blütenpflanzen. *Dissertationes Botanicae* B. 62.
- SCHOUTE J.C., 1936. On whorled phyllotaxis. III. True and false whorls. *Rec. Trav. Bot. néerl.* 33: 670-687.
- SOMA K., 1958. Morphogenesis of the shoot apex of *Euphorbia lathyris* L. *Journ. of Faculty of Science, Univ. of Tokyo S. III* 7: 199-256.
- TRIPPI V.S., BRULFERT J., 1973. Organization of the morphophysiological unit in *Anagallis arvensis* and its relation with the perpetuation mechanism and senescence. *Amer. J. Bot.* 60: 641-647.
- VAUGHAN J.G., 1955. The morphology and growth of the vegetative and reproductive apices of *Arabidopsis thaliana* (L.) Hey., *Capsella bursa-pastoris* (L.) Medic. and *Anagallis arvensis* L. *Journ. Linn. Soc. Bot.* 55: 279-301.
- WILLIAMS R.F., 1975. *The Shoot Apex and Leaf Growth*. Cambridge University Press, New York.
- WILLIAMS R.F., METCALF R.A., GUST L.W., 1982. The genesis of form in oleander (*Nerium oleander* L.). *Aust. J. Bot.* 30: 677-687.
- ZAGÓRSKA-MAREK B., 1985. Phyllotactic patterns and transitions in *Abies balsamea*. *Can. J. Bot.* 63: 1844-1854.
- ZAGÓRSKA-MAREK B., 1987. Phyllotactic triangular unit; phyllotactic transitions as the consequence of the apical wedge disclinations in a crystal-like pattern of the units. *Acta Soc. Bot. Pol.* 56: 229-255.
- ZAGÓRSKA-MAREK B., 1994. Phyllotactic diversity in *Magnolia* flowers. *Acta Soc. Bot. Pol.* 63: 117-137.

ZMIANY ROZWOJOWE FILOTAKSJII *ANAGALLIS ARVENSIS* L.

STRESZCZENIE

W ontogenezie *Anagallis* występują w regularnej sekwencji spontaniczne zmiany wzoru ulistnienia. Początkowa filotaksja naprzeciwległa zmienia się w skrętoległą Fibonacciego, która z kolei ulega transformacji we wzór okółkowy z trzema liśćmi w okółku. Jako ostatnia pojawić się może filotaksja skrętoległa Lucasa. W trakcie pierwszej i jednocześnie najbardziej rozpowszechnionej transformacji filotaksji naprzeciwległej we wzór skrętoległy Fibonacciego zmiany układu zawiązków liści występują wyłącznie w obrębie ograniczonego sektora obwodu wierzchołka pędu. Natomiast w sektorze dopełniającym układ zawiązków jest taki, jaki byłby w filotaksji naprzeciwległej. Przypuszczalnie, podobna nieciągłość obwodowa jest odpowiedzialna za pozostałe transformacje filotaksji. Kolejność pojawiania się różnych wzorów ulistnienia w ontogenezie *Anagallis* jest taka, że każda transformacja filotaksji wymaga teoretycznie minimalnej zmiany geometrii wierzchołka. Chociaż merystemy apikalne *Anagallis* inicjują zawiązki zarówno w układzie okółkowym jak i skrętoległym, wydłużające się odcinki pędów tego gatunku wydają się być ulistnione wyłącznie okółkowo. Jest tak, ponieważ mimo skrętoległego ułożenia zawiązków liściowych w strefie wierzchołkowej, w wydłużających się odcinkach pędu liście skupione są w pozorne okółki, które powstają wskutek nierównego wydłużania międzywęźli. W skład pozornych okółków wchodzi zwykle trzy (w filotaksji Fibonacciego) lub cztery liście (we wzorze Lucasa). Liczba liści w pozornym okółku jest więc równa liczbie liści leżących na jednym obrocie helisy ontogenetycznej, która jest różna dla wspomnianych wzorów filotaksji skrętoległej. Na wierzchołkach o filotaksji okółkowej zawiązki liści tworzące ten sam okółek są różnych rozmiarów. To samo dotyczy zawiązków kwiatów z jednego okółka. Pąki kwiatowe wyrastające z kątów liści budujących dany okółek w wydłużającym się odcinku pędu również różnią się rozmiarami.

SŁOWA KLUCZOWE: *Anagallis arvensis*, wzory filotaksji, transformacje filotaksji.