ONTOGENETIC CHANGES IN THE SHOOT PRIMARY VASCULATURE OF *ANAGALLIS ARVENSIS* L.

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ABSTRACT

Ontogenetic changes in the primary vasculature of *Anagallis* shoots are strictly related to phyllotaxis. During the ontogeny of *Anagallis*, whorled and spiral phyllotactic patterns appear alternately in a regular sequence. The initial decussate phyllotaxis is transformed into the spiral Fibonacci, and then further into trimerous pattern. This in turn may change into the spiral Lucas phyllotaxis. Sporadically the immediate transition from the decussate to trimerous phyllotaxis takes place. The vascular system in *Anagallis* is always closed, despite that both whorled and spiral phyllotaxes are present. Also the number of vascular traces diverging to the leaf is constant. In the course of a single phyllotactic transition, there is an increase in the number of vascular sympodia and in the number of leaf traces present in the vascular cylinder. Usually only one single sympodium and one or two traces are added to the system. The immediate addition of two sympodia occurs only during infrequent transition from the decussate to trimerous pattern. The increase in the number of sympodia is most often simultaneous with the phyllotactic transition, however, when the trimerous pattern is transformed into the spiral Lucas, the increase is delayed, sometimes for as much as ten plastochrons. In shoots with changing phyllotaxis, a sector within the vascular cylinder can be distinguished, in which the leaf traces are arranged as if the previous phyllotactic pattern continued, whereas rearrangement of traces takes place at the same level but in the complementary sector. This is in agreement with the concept of discontinuous circumferential changes in the shoot apex being responsible for qualitative transformations of phyllotaxis.

KEY WORDS: *Anagallis arvensis*, shoot primary vasculature, phyllotactic transitions.

INTRODUCTION

The relationships between the shoot primary vasculature and phyllotaxis have been well known and documented (Esau 1965, Beck, Schmid, Rothwell 1982, Romberger, Hejnowicz, Hill 1993). Some authors worked on the vasculature of plants differing in phyllotaxis (Namboodiri, Beck 1968a, 1968b, Puławska 1972, Kwiatkowska 1992). Others studied reorganization of the vascular system associated with changing expression (order) of spiral phyllotactic pattern (Puławska 1965, Larson 1977). However, reorganization of a vascular system accompanying qualitative ontogenetic changes in phyllotaxis has been studied only in a few species, like *Kalanchoe tubiflora* (Jensen 1968) and *Linum usitatissimum* (Giroulami 1953, Meicenheimer 1986).

Anagallis arvensis has been recently recognized as a plant with an unstable phyllotaxis and variable architecture of primary vascular system (Kwiatkowska 1992, 1993, 1994). Phyllotactic patterns in this species appear in a regular ontogenetic sequence. The initial decussate pattern changes into the spiral Fibonacci, this in turn into trimerous pattern. Unfrequently the direct change from the decussate to trimerous phyllotaxis occurs. Usually either spiral Fibonacci or trimerous pattern is the last one in the shoot development. On some axes, however, the trimerous pattern changes once again, always into

the spiral Lucas phyllotaxis. A striking feature of *Anagallis* shoots with spiral pattern is the formation of pseudo-whorls due to the uneven elongation of stem internodes (Kwiatkowska 1993, 1994). Depending on the type of a spiral pattern pseudo-whorls are composed of different number of leaves: two, three (Fibonacci) or four (Lucas), and thus can be easily mistaken for true whorls of trimerous or tetramerous phyllotaxis.

Due to its plasticity *Anagallis* represents a particularly valuable material for the analysis of the reorganization in the pattern of vascular strands associated with phyllotactic transition, but until now this problem has not been studied. De Sloover (1958) studied the *Anagallis* primary vasculature, but only in the decussate shoots. The basic pattern of *Anagallis* vascular system and deviations from this pattern characteristic of shoots with different phyllotaxis have been described (Kwiatkowska 1992), but ontogenetic changes of the vascular system were not analysed. Neither a distinction between true and pseudo-whorls has been made.

The purpose of the present study is to analyse the changes in *Anagallis* primary vascular system in the course of phyllotactic transitions. Also the revision of the relationships between the primary vasculature and phyllotaxis of *Anagallis* shoots will be made with consideration of pseudo- and true whorls.

Fig. 1. Two maps show the outer surface of the split open vascular cylinder (left) and the distribution of leaves on the surface of the shoot (right). Vertical axes indicate the distance from the base of the shoot. The circumference of the vascular cylinder is given below the left map; the angular distances between leaves – below the right one. Sympodia are outlined with solid lines; dashed lines indicate borders between metaxylem bundles. Regions of the vascular cylinder occupied by parenchyma are stippled. Symbols of leaves are given above the levels at which their half traces depart from the vascular cylinder. Leaves of the same whorl have symbols consisting of the successive whorl number and letters a-c. Spirally arranged leaves are numbered in order of their initiation. The older the leaf or the whorl, the smaller its number. On the map of the shoot surface the direction of the ascending ontogenetic helix is indicated by arrows. Part of the shoot with two subsequent transitions: from the decussate (whorls 1 and 2) to spiral Fibonacci phyllotaxis (pseudo-whorl composed of leaves 3-5), and from the latter to trimerous pattern (leaves 6a-c). Above the whorl 2, the number of sympodia increases from four to five due to the branching of the sympodium connected with leaf 5. The further increase takes place above leaf 5, because one of newly formed sympodia splits again. Both branching sympodia occur in the same sector of the vascular cylinder, and are composed of more than two half traces. Also the sympodium connected with leaves 1a and 2a has higher number of traces. The number of half traces within the vascular cylinder changes from eight below the whorl 1, to eleven above this whorl, and then further to twelve, below the whorl 6. Both half traces of leaf 6a as well as those of leaf 6c diverge from the same sympodia, which are composed of three traces instead of two. Half traces of leaves 1a, 1b, 2a and 6a include anastomoses (A). The horizontal line indicates the level of the transverse section shown in Fig. 2.

Fig. 2. Photomicrograph of the transverse section of the shoot shown in Fig. 1. Bar = 0.3 mm. An arrowhead indicates the point where the vascular cylinder was "split" to prepare the map. Sympodia are delimited with arched lines. The section was cut above the last two-leaved whorl before the phyllotactic transition from decussate to spiral Fibonacci pattern. The two sympodia delimited with bold lines are newly formed, due to the sympodium branching.

MATERIAL AND METHODS

The plant material used in the investigation belonged to the form *arvensis* of *Anagallis arvensis* L. (Kornaś 1962). It was collected three times: 1) in October 1988 – on the stubble field in Przeclawice n. Trzebnica (the same batch as used by Kwiatkowska 1992); 2) in August 1990 – in the Botanical Garden of Wrocław University; and 3) in May 1991 – in the glasshouse, where plants were grown from the seeds collected in the Botanical Garden of Wrocław University.

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). Thirty two shoot portions with unchanging phyllotaxis, and thirty six shoots exhibiting phyllotactic transitions were selected for the analysis. Among them there were six shoots with the unchanging decussate pattern; nine with spiral Fibonacci; seven with trimerous; and ten with the spiral Lucas phyllotaxis. Twenty one shoots exhibited the transition from the decussate to the spiral Fibonacci pattern; five – from the latter to trimerous; six from the trimerous to spiral Lucas pattern; and two – directly from the decussate to trimerous.

Maps showing the distribution of metaxylem bundles on the outer surface of the split open vascular cylinder were prepared in the way described earlier (Kwiatkowska 1992). They were paralleled by the maps of leaf spacing on the split open stem surface. Vertical distances between leaves were calculated from the number of serial transverse sections between the points of their attachment. The circumferential spacing of leaves was estimated the same way as in previous works (Kwiatkowska 1992, 1994). Leaf symbols were always the same in both corresponding maps. In spiral phyllotaxis leaves were indicated with the increasing numbers in order of their initiation. In whorled phyllotaxis leaf symbols consisted of numbers of successive whorls and of the letters identifying the members of the same whorl.

Following terminology was adopted in this study: "pseudo-whorl" – a group of leaves attached at similar levels but initiated in a spiral, the term used to differentiate these groups from true whorls (Kwiatkowska 1993, 1994); "half trace" – each of the two metaxylem bundles initially present in the vascular cylinder and then diverging to a leaf at the nodal level (Girolami 1953); "vascular sympodium" – a group of sequentially appearing, interconnected segments of leaf half traces (Meicenheimer 1986, Romberger, Hejnowicz, Hill 1993).

RESULTS

The stem vasculature in *Anagallis* was always closed. Two bundles (half traces) diverging from the vascular cylinder at the nodal level to the single leaf, formed a single trace before they left the stem. Some half traces were composed of two discrete metaxylem bundles, one of them smaller than the other. The smaller ones were referred to as "anastomoses" (Kwiatkowska 1992), and indicated with "A" in figures.

Shoots with various phyllotactic patterns differed in the number of sympodia, the number of leaf half traces present in the vascular cylinder, and the mode of connection between stem and leaf vasculature.

The initial decussate phyllotaxis

In shoots with the decussate leaf arrangement, e.g. at the bottom of the shoot in Fig. 1, four sympodia were always pre-

sent, each composed of two half traces. The two half traces of every leaf diverged from two different neighbouring sympodia. At the nodal level every sympodium was connected with only one leaf.

The advanced spiral Fibonacci pattern and its development from the decussate phyllotaxis

In shoots with well advanced spiral Fibonacci phyllotaxis five sympodia always occurred, as it can be seen in the upper portion of the shoot shown in Fig. 3; or in the lower portion of the shoot in Fig. 4. The number of half traces present in a vascular cylinder varied from nine (Fig. 3) to eleven or twelve (Fig. 4). Both half traces of some leaves diverged from the same sympodium (Fig. 4). Certain sympodia were connected with two neighbouring leaves of a pseudo-whorl (Fig. 3). Some portions of sympodia were composed of more than two half traces, or only of a single trace (Fig. 4).

During the formation of the Fibonacci pattern from the decussate phyllotaxis, the changes in vasculature were apparent both in the last two-leaved whorl before the transition and in the first pseudo-whorl composed of spirally arranged leaves (Figs 1, 3). In the course of the transition the number of sympodia increased from four to five, due to the branching of a sympodium already present in the vascular cylinder (Figs 1-3). The number of half traces present in the branching sympodium was usually higher than two, and this already could be seen below the last two-leaved whorl (Figs 1, 3). Sometimes the same increase was observed in a neighbouring sympodium which was not branching during the transition (Figs 1, 3). Below the last two-leaved whorl the number of half traces present in the vascular cylinder could be then as high as nine (Fig. 3) or even ten or eleven (Fig. 1). Leaves composing the last two-leaved whorl were connected with the stem vasculature in the mode typical of the decussate phyllotaxis. Within the first pseudo-whorl, however, one of the leaves was often supplied with two half traces diverging from the same sympodium (Fig. 3).

The vascular changes in the course of the transition were always sectorial. All symptoms of the change were visible in one sector only: the sympodia with higher number of half traces, the sympodium branching, and leaves atypically connected with the stem vasculature. In Fig. 1 it is the sector including leaves 5 and 3 (visible also in Fig. 2); in Fig. 3 – the sector between leaf 1a – on left, and 1b – on right, including leaf 2. In the complementary sector of the vascular cylinder the arrangement of half traces was always the same as if the decussate pattern continued.

The trimerous phyllotaxis: advanced and developing

In the trimerous phyllotaxis, the number of sympodia was always twice as high as the number of leaves per whorl, similarly like in the decussate pattern (Fig. 6). However, in trimerous phyllotaxis both half traces of some leaves diverged from the same sympodium (Fig. 6), similarly as in the spiral pattern. Also the number of half traces composing sympodia was variable: often one sympodium was composed of three half traces, whereas another sympodium at the same level was composed of a single trace only (Fig. 6).

The trimerous phyllotaxis most often resulted from the transformation of the spiral Fibonacci pattern. In some shoots Fibonacci phyllotaxis persisted long enough for several pseudo-whorls to be formed before the true trimerous whorls appeared (Fig. 4). In others, the spiral pattern changed further so quickly that only one pseudo-whorl could be formed (Fig. 1). The Fibonacci to trimerous pattern transition was always

Fig. 3. Phyllotactic transition from the decussate to spiral Fibonacci pattern. The principles of map construction and the labelling are the same as in Fig. 1. Leaves 1a, 1b compose the last two-leaved whorl before the transition; leaves 2 and 3 – the first pseudo-whorl. During the transition the number of sympodia increases from four to five because of the splitting of the sympodium connected with leaf 4. This sympodium and the neighbouring one are composed of three half traces instead of two. Both half traces of the leaf 2 diverge from the same sympodium. The number of half traces changes from nine below the whorl 1, to ten – above this whorl, and then again to nine below leaves 4-6. Half traces of the two neighbouring leaves 4 and 6 diverge from the same sympodium.

Fig. 4. Transition from spiral Fibonacci to trimerous phyllotaxis. The spiral pattern persists for several plastochrons (leaves 1-6). The last pseudo-whorl formed before the transition (leaves 4-6) resembles a true whorl, since angles between leaves are intermediate between 120° and the Fibonacci divergence. However, the vasculature of this pseudo-whorl is typical of the Fibonacci pattern. Five sympodia and eleven or twelve half traces are present in this portion of the shoot where phyllotaxis is spiral. Half traces of leaves 4, 5, and 6 include anastomoses (A). Both half traces of leaves 3, 5, and 6 diverge from the same sympodia. Some portions of sympodia are composed of a single half trace, like the portion of sympodium connected with leaves 3 and 7c, above leaf 3. The others consist of three traces, like that connected with leaf 6, below this leaf. In the course of the phyllotactic transition the number of sympodia increases from five to six, due to the branching of the sympodium connected with leaf 7a. The number of half traces increases to twelve just below the first true whorl. Both half traces of leaf 7b diverge from the same sympodium. The horizontal line indicates the level of the transverse section shown in Fig. 5.

Fig. 5. Photomicrograph of the transverse section of the shoot shown in Fig. 4. Labelling as in Fig. 2. Bar = 0.3 mm. The section was cut above the last three-leaved pseudo-whorl preceding the phyllotactic transition from the spiral Fibonacci to trimerous pattern. The branching sympodium is indicated with a bold arched line. Some sympodia are composed only of a single trace.

associated with an increase in sympodium number from five to six (Figs 1, 4). Like before, the increase was due to a branching of the existing sympodium (Figs 1, 4, 5). In shoots with a single pseudo-whorl, the split of the sympodium took place always in the same sector of the vascular cylinder, in which the previous branching associated with the transition from the decussate to Fibonacci phyllotaxis occurred (Fig. 1). The number of half traces at the level of the last pseudo-whorl before the transition amounted to eleven (Figs 1, 4), increasing to twelve (Fig. 4), or even temporarily to thirteen (Fig. 1) above the pseudo-whorl. In all cases that have been investigated both half traces of one leaf composing the first true whorl diverged from a single sympodium (Figs 1, 4). This mode of connection between stem and leaf vasculature was characteristic of Fibonacci as well as of trimerous shoots.

In two of all shoots examined, the number of sympodia increased immediately from four to six (Figs 6, 8). These were the only two shoots, where phyllotaxis changed from the decussate to trimerous pattern without an intermediate pseudo-whorl. In the first shoot (Fig. 6) the splitting took place below the first three-leaved whorl. Two neighbouring sympodia that were splitting had higher number of half traces (Figs 6, 7). The total number of metaxylem bundles present in the vascular cylinder changed from nine, below the last two-leaved whorl, to thirteen, and then decreased to twelve. In the other shoot (Fig. 8), the sympodia branching was delayed and occurred at the level of the second three-leaved whorl formed after the transition. Also the number of half traces increased not below but above the last two-leaved whorl. In both the shoots, despite the prominent vascular reorganization, the sector of the vascular cylinder occurred where the arrangement of half traces was like in the decussate phyllotaxis, as if no transition took place.

Spiral Lucas phyllotaxis

The vasculature of shoots with well advanced Lucas phyllotaxis resembled that of shoots with Fibonacci pattern, especially in the mode of vascular connection between stem and leaf: some leaves were connected with two half traces diverging from the same sympodium; also the traces supplying two

neighbouring leaves of the same pseudo-whorl diverged sometimes from the same sympodium (Fig. 9). Usually seven sympodia and thirteen or fourteen half traces occurred (Fig. 9), but the number of sympodia was not always the same. Interestingly, at some levels of the shoot, due to the departure of the entire sympodium from the vascular cylinder the number temporarily decreased to six (Fig. 9). The characteristic number of sympodia reappeared due to the branching of a sympodium neighbouring the departing one.

The spiral Lucas phyllotaxis developed exclusively as the result of the trimerous pattern transformation. Since seven sympodia were characteristic of shoots with the well developed Lucas phyllotaxis, the increase of sympodia number from six to seven was expected in the course of the transition from trimerous to Lucas pattern. It was, however, significantly delayed in most of the examined shoots. Although one sympodium was always branching during the transition, simultaneously all the half traces of the other sympodium were departing from the vascular cylinder terminating its course (Fig. 11). Therefore, leaves appearing after the transition were connected with only six sympodia, sometimes for as long as ten plastochrons (Fig. 11). Afterwards the seven sympodia reappeared, again due to the sympodium branching taking place at such a level of the shoot where no phyllotactic transition occurred (Fig. 11).

The transition was frequently but not always simultaneous with the increase in the number of half traces. Additional traces appeared usually already below the last three-leaved whorl, and the total number of traces equalled thirteen (Fig. 11). Below the first pseudo-whorl formed during the transition, it was often increasing to fourteen (Fig. 11).

In one single shoot, shown in Fig. 9, the change from six to seven sympodia was concurrent with the phyllotactic transition. The increase was accomplished by the branching (Figs 9, 10). However, Lucas phyllotaxis in this shoot was less regular than in other shoots. Some leaves were attached at the levels inconsistent with their sequence along the ontogenetic helix: leaf 8 arises significantly higher than leaf 9, although it is a predecessor of the other on the helix (Fig. 9).

Fig. 6. Immediate transition from the decussate (whorl 1) to trimerous pattern (whorls 2 and 3). The change is accompanied by the increase of sympodium number from four to six. Two sympodia, one connected with leaf 2b and the other with leaf 2c, are branching almost simultaneously. The number of half traces changes from nine below the whorl 1, to thirteen below whorl 2, and then further to twelve above this whorl. Both half traces of leaf 3a diverge from the same sympodium. Some portions of sympodia are composed of a single half trace, like the portion of the sympodium connected with leaf 2a, above the second whorl; whereas the others consist of three traces, as that connected with leaf 3a. The horizontal line indicates the level of the transverse section shown in Fig. 7.

Fig. 7. Photomicrograph of the transverse section of the shoot shown in Fig. 6. Bar = 0.3 mm. The section was cut at the level between the last two-leaved whorl and the first three-leaved whorl. Two branching sympodia are delimited with the bold arched lines. They have both higher than normally number of half traces.

Fig. 8. The transition from the decussate (whorl 1) to trimerous phyllotaxis (whorls 2 and 3). The number of sympodia increases immediately from four to six, however, the increase does not occur until the second whorl of three leaves (3a-c) is formed. The branching sympodia are connected with leaves 3a and 3b. The number of half traces increases earlier: eleven traces are present already below the first three-leaved whorl. The number of traces below the last two-leaved whorl is normal.

DISCUSSION

It has been positively confirmed that *Anagallis arvensis* is especially attractive and suitable in phyllotaxis research because of its variable phyllotactic patterns and relative simplicity of the primary vasculature. The general plan of the vascular system in *Anagallis* is the same despite the changing phyllotaxis: all the leaves are supplied by two half traces, and the system is closed both in whorled and in spiral phyllotaxis, unlikely as in other plant species. Modifications of the system are limited to the differences in the number of sympodia, the number of half traces present in the vascular cylinder, and the mode of connection between stem and leaf vasculature.

The number of sympodia characteristic of *Anagallis* shoots with various phyllotaxes is in agreement with the rules known for other plants (Esau 1965, Namboodiri, Beck 1968a, 1968b, Beck, Schmid, Rothwell 1982). In whorled phyllotaxis the sympodium number is twice as high as the number of leaves per whorl, whereas in spiral phyllotaxis, it is equal to one of the numbers in the parastichy series describing the spiral pattern.

In spiral phyllotaxis the number of leaf half traces which are present in the vascular cylinder is less stable than the number of sympodia. In whorled phyllotaxis it is almost constant. However, even in spiral shoots, the deviations usually do not exceed two half traces being added or subtracted.

The mode of connection between stem and leaf vasculature is uniform only in the decussate shoots. In trimerous and spiral shoots it is variable, and sometimes both leaf half traces diverge from the same sympodium, unlike typically from two neighbouring sympodia. In some spiral shoots two half traces diverge from one sympodium to two different leaves at almost the same level. This is associated with the extreme shortening of the internode separating two neighbouring leaves composing the same pseudo-whorl.

Pseudo-whorls can be distinguished from true whorls on the basis of a decreased number of sympodia below the whorl, and of the two neighbouring leaves of a pseudo-whorl being often supplied with the leaf half traces originating from the same sympodium.

Different kinds of vascular reorganization described in *Anagallis* have a number of features in common, despite the fact

Fig. 9. The transition from the trimerous (whorl 1) to spiral Lucas phyllotaxis (leaves 2-9). It is simultaneous with the increase in a number of sympodia from six to seven. The number increases due to the branching of the sympodium connected with leaf 2. The number of half traces equals thirteen. Within the portion of the shoot where phyllotaxis is spiral, the number of sympodia fluctuates. It is diminished to six when one sympodium departs entirely from the vascular cylinder to leaf 5. Above this leaf, however, the other sympodium, connected with leaf 8, is branching. Both half traces of leaf 9 diverge from the same sympodium. The horizontal line indicates the level of the transverse section shown in Fig. 10. The arrangement of leaves in the shoot portion, where the ontogenetic helix is indicated with a dashed line, is less regular.

Fig. 10. Photomicrograph of the transverse section of the shoot shown in Fig. 9. Bar = 0.3 mm. The section was cut above the last three-leaved whorl before the phyllotactic transition from the trimerous to spiral Lucas pattern. The branching sympodium is delimited with the bold arched line. Three sympodia are composed of only a single half trace.

Fig. 11. Another case of transformation from the trimerous (whorl 1) to spiral Lucas pattern (leaves 2-14). Although the sympodium connected with leaf 3 branches during the transition, the other sympodium departs at the same level from the vascular cylinder, composing two half traces of leaf 2. Therefore, the number of sympodia does not increase earlier than at the level of leaves 12-14, where a sympodium connected with leaf 14 branches. Nevertheless, the number of half traces is already thirteen during the transition. Several sympodia, like those connected with leaf 5 or with leaf 8, are composed of more than two half traces; the others consist only of a single trace (a sympodium connected with leaf 10, above this leaf). Leaves 10 and 11 of the same pseudo-whorl are connected with the same sympodium. Both half traces of leaves 5 and 8 diverge from the same sympodia.

that they accompany various phyllotactic transitions. During all the transitions the number of traces and sympodia increases. In most cases the increase is gradual: a single sympodium and only one or two half traces are added. The immediate increase in sympodium number by two is least common, and was encountered only in two shoots, which on the other hand exhibited the least common transition, directly from decussate to trimerous phyllotaxis. Usually the additional half traces are already visible at the beginning of the transition. The sympodia multiply by means of branching, most often in the shoot portion transient between the two phyllotactic patterns. However, when the trimerous phyllotaxis is transformed into the spiral Lucas pattern, the branching is almost always significantly delayed. The lapse of time between this transition and the branching can be as long as ten plastochrons. This spiral phyllotaxis is the least common of all the patterns encountered in *Anagallis*.

The rearrangement of the vascular system in *Anagallis* is more similar to the same process associated with changes in the expression of a spiral pattern in other species, than to that occurring during the phyllotactic transitions between whorled

and spiral patterns. The first type of changes has been studied for *Actinidia arguta* (Puławska 1965) and *Populus deltoides* (Larson 1977). In both cases the reorganization is accomplished through the change in the number of sympodia. The transitions between whorled and spiral phyllotaxis, as those characteristic of *Anagallis*, have been described for *Kalanchoe tubiflora* (Jensen 1968) and *Linum usitatissimum* (Meicenheimer 1986). In these plants, contrary to the *Anagallis* case, not only the number of sympodia changes, but also the vascular system fluctuates between closed and open, and the change in the number of traces departing to the leaf occurs.

In phyllotactic transitions from the decussate to spiral Fibonacci, and from the decussate to trimerous pattern, the changes in the vascular system of *Anagallis* are clearly sectorial. There is a limited sector within the vascular cylinder where they occur. In the complementary sector the pattern of leaf half traces is exactly the same as previously. Moreover, when two successive transitions, i.e. from the decussate to spiral Fibonacci pattern and from the Fibonacci to trimerous occur within the short time, the vertical borders between the changing and stable sectors are in the same position. The sectorial

character of the vascular reorganization is concurrent with the concept of discontinuous circumferential changes in shoot apex responsible for qualitative changes in phyllotaxis (Zagórska-Marek 1987, 1994, Meicenheimer, Zagórska-Marek 1989). The sectorial character of morphogenetic changes in *Anagallis* was already reported by the author of this work for the circumferential spacing of leaf primordia in shoot apices with changing phyllotaxis (Kwiatkowska 1993). The vascular pattern change in the transitions from spiral Fibonacci to trimerous phyllotaxis, and from the trimerous to spiral Lucas, is more difficult to interpret, because in shoots with these patterns the mode of connection between the stem and leaf vasculature is not uniform.

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ZMIANY ROZWOJOWE PIERWOTNEGO SYSTEMU WASKULARNEGO PĘDÓW *ANAGALLIS ARVENSIS* L.

STRESZCZENIE

Zmiany rozwojowe pierwotnego systemu waskularnego pędów *Anagallis* są ściśle związane ze zmianami wzoru filotaksji. W ontogenezie tego gatunku naprzemiennie występują spiralne i okółkowe wzory ulistnienia. Porządek ich występowania jest następujący: Początkowy wzór, naprzeciwległy, zmienia się we wzór skrętoległy Fibonacciego, a następnie dalej we wzór okółkowy z trzema liśćmi w okółku. Ten z kolei przechodzi we wzór skrętoległy Lucasa. Sporadycznie występuje także bezpośrednia transformacja wzoru okółkowego naprzeciwległego we wzór okółkowy z trzema liśćmi w okółku. System waskularny *Anagallis* jest zawsze zamknięty, mimo że występują zarówno okółkowe jak i spiralne wzory ulistnienia. Liczba śladów odchodzących do każdego liścia jest również stała. W trakcie wszystkich transformacji filotaksji wzrasta liczba sympodiów waskularnych i liczba śladów liściowych przebiegających w cylindrze waskularnym. Wzrost ten jest najczęściej stopniowy: podczas transformacji liczba sympodiów wzrasta jednostkowo, a liczba śladów o jeden lub dwa. Jednorazowe dodanie dwóch sympodiów występuje wyłącznie w trakcie najrzadziej spotykanej transformacji pomiędzy wzorami okółkowymi z dwoma i trzema liśćmi w okółku. Najczęściej wzrost liczby sympodiów jest równoczesny z transformacją, jednak w przypadku zmiany wzoru okółkowego z trzema liśćmi w okółku we wzór skrętoległy Lucasa, wzrost ten jest opóźniony czasami aż o dziesięć plastochronów. Mimo zmieniającej się filotaksji pędów *Anagallis*, w obrębie cylindra waskularnego można wyznaczyć sektor, w którym ułożenie sympodiów waskularnych jest takie, jak gdyby utrzymywany był poprzedni wzór ulistnienia.

SŁOWA KLUCZOWE: *Anagallis arvensis*, pierwotny system waskularny pędu, transformacje filotaksji.