ONTOGENETIC VARIATION OF PHYLLOTAXIS AND APEX GEOMETRY IN VEGETATIVE SHOOTS OF *SEDUM MAXIMUM* (L.) HOFFM.

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ABSTRACT

Phyllotaxis of vegetative shoots of *Sedum maximum* (L.) Hoffm. is variable and unstable. Phyllotactic transitions proceeding either between two whorled, two spiral or a whorled and a spiral pattern occur during shoot ontogeny. A general rule is that in the course of these transitions numbers of contact parastichies increase or much less often diminish. During most common transitions only a single parastichy is added to or subtracted from the already existing contact parastichy pattern. This applies both to the transitions between a spiral and a whorled and to those between two spiral patterns. More parastichies appear only when phyllotaxis changes from one whorled pattern to another. These transitions, however, are the least common in *S. maximum*. Parameters of apex geometry differ significantly in shoots exhibiting different contact parastichy numbers. The sequence of phyllotactic patterns arranged according to an increasing apical dome area or area ratio, as well as decreasing plastochron ratio (both as defined by Richards) is the same as their sequence based on increasing numbers of contact parastichies. This in turn is the sequence of patterns as they appear during shoot ontogeny. The only parameter which remains relatively constant is the area of the youngest leaf primordium. This implies that during phyllotactic transitions in *S. maximum* the area ratio changes mainly due to the increase of the apical dome. It seems that in *S. maximum* this ontogenetic increase of the apical dome, which on the other hand is typical for many plants, somehow differs from these cases where such a change alters only contact parastichy numbers within the same phyllotactic series.

KEY WORDS: Phyllotaxis, phyllotactic transitions, shoot apex, *Sedum maximum*.

INTRODUCTION

Species belonging to the Crassulaceae family are known for their unstable phyllotaxis (Jensen 1968). An intriguing observation in a number of these species, especially those with narrow leaf bases (Rutishauser 1998), is the transition from one phyllotactic pattern to another during ontogeny of an individual shoot. The change is not associated with the switch between developmental phases, which usually introduces a change in primordium identity. A prominent example is *Bryophyllum tubiflorum* Harv. Both its phyllotactic diversity and ontogenetic transitions were described in details by Gómez-Campo (1974). Other investigations, devoted to the genus *Sedum*, have also revealed a significant phyllotactic diversity (Astruc 1949; Deschatres 1954). However, in case of both *B. tubiflorum* and *Sedum* sp., the authors analyzed mainly leaf arrangement in mature shoots, and the arrangement of leaf primordia in apices with changing phyllotaxis was not studied. Moreover, Astruc and Deschatres have focused on the "foliar helices" (Plantefol 1947) rather than the overall contact parastichy (CP) pattern or the angular spacing of leaves.

Studies of phyllotactic transitions occurring during the same developmental phase are limited in number. Exceptions are papers devoted to: *Linum usitatissimum* L. (Williams 1975; Meichenheimer 1987) where phyllotaxis changes during the

vegetative phase of development; *Nerium oleander* L. where phyllotactic transitions occur both in the vegetative and generative phases (Williams et al. 1982); various *Magnolia* species exhibiting phyllotactic transitions in carpel arrangement in gynoecea (Zagórska-Marek 1987, 1994); and finally *Anagallis arvensis* L. in which transitions occur in shoots during the generative phase of development (Kwiatkowska 1995b). On the other hand, papers presenting theoretical approach to phyllotaxis increase in number, but many variables used in models of phyllotaxis have no clearly defined analogues known from nature. There is a growing need for empirical data on intraspecific phyllotactic diversity, and especially on the course of spontaneous phyllotactic transitions analyzed in situ, i.e. in the shoot apical meristem. This would help in determining the intrinsic factors playing important role in phyllotactic pattern formation and regulation.

Theories explaining the mechanism of phyllotaxis usually assume that the apex geometry differs in shoots exhibiting different phyllotactic patterns (Richards 1951; Thomas 1975; Rutishauser 1998). Some authors use parameters such as the plastochron ratio (R) or the phyllotaxis index (Richards 1951; Thomas 1975; Erickson 1981), which describe the rate of leaf primordia production at apex and its transverse growth. These two parameters decrease when numbers of contact parastichies (CPs) increase. It remains true, whether their values are calculated on the basis of ideal (Richards 1951), or Braunian

Figs 1-6. Photomicrographs of transverse sections of *S. maximum* shoots cut at the level of the apical dome. Phyllotactic patterns and pattern transitions most characteristic for *S. maximum* were chosen; other patterns of leaf primordia arrangement are shown in section contours (Figs 7-18). Whorled primordia were given a single number; the younger the whorl, the higher the number. In some cases, a letter was added in order to differentiate between members of one whorl. Spirally arranged primordia were numbered in order of appearance. Bars = 250 μ m.

Fig. 1. A tetracussate apex.

Fig. 2. A shoot with the second accessory spiral pattern (CPs are shown in contours of this micrograph in Fig. 13).

Fig. 3. Transition from decussate primordia arrangement (whorls 1 and 2) to the Fibonacci pattern (primordia 4-9), with a doubled primordium (3b) formed in the transition zone.

Fig. 4. Direct transition from decussate to tetracussate pattern. Two leaf primordia (5a and 5b; 5c and 5d) appear instead of a single one in each space between the last opposite primordia 4a and 4b.

Fig. 5. Fibonacci phyllotaxis (primordia 1-9) is transformed into tricussate (whorls 10 and 11); an arrangement interpreted in Fig. 16.

Fig. 6. Transition from the Fibonacci (primordia 1-10) to Lucas pattern (11-16), CPs shown in Fig. 17.

(Thomas 1975) divergence, or empirically estimated (Meicenheimer 1987; Rutishauser 1998). Also parameters which refer directly to the relationships between the dimensions of apical dome and leaf primordia are sometimes employed. Richards (1951) introduced the "area ratio" (AR) which is the ratio of the area occupied by the apical dome to the area of the youngest leaf primordium, and can be calculated directly from R . Its value increases with CP numbers. In other models of phyllotaxis, such as the proposition of Phyllotactic Triangular Unit (Zagórska-Marek 1987; Meicenheimer and Zagórska-Marek 1989) more attention is paid to the angular dimension of the primordium. This parameter differs in apices with different numbers of CPs. Its changes are supposed to result in ontogenetic transitions of phyllotaxis. The relationship between apical dome and primordium dimension plays a role also in a biophysical model of whorled phyllotaxis proposed by Green, Steele and Rennich (1996). Here the number of leaf primordia per whorl depends both on the intrinsic wavelength of a meristem surface tissue (corresponding to the dimension of a primordium), and on the diameter of the formative annulus.

Although theories addressed above deal with relative dimension of apical dome and leaf primordia, the question remains open: which absolute dimension differs in shoots of the same species exhibiting various phyllotaxis. Is it the change of absolute apical dome area while area of the youngest primordium is constant, or vice versa? An answer to this question would improve our understanding of the mechanism of phyllotactic transitions. However, only scarce empirical data are available to date. One of few examples is the study of *Hippuris* by McCully and Dale (1961). They showed that the number of leaves per whorl depends on the circumference of the apical dome at the level of primordia initiation. The reason for the lack of empirical data may lay in the fact that only a small number of species studied exhibit variable phyllotaxis, and a certain number of patterns occurring with a frequency high enough for statistical comparison.

Sedum maximum (L.) Hoffm. already known for its unstable phyllotaxis (Astruc 1949; Deschatres 1954; Jensen 1968; Florek 1997; Kwiatkowska and Florek-Marwitz 1998), is a valuable species for the kind of comparative analysis mentioned above. Among different species of the genus *Sedum*, this particular one is easily obtainable from natural habitats in central Europe, and is characterized by exceptionally unstable phyllotaxis, often changing during the vegetative phase of shoot development. For these reasons *S. maximum* has been selected in the present investigation. The objectives of this study are: to determine the ontogenetic sequence of phyllotactic patterns in vegetative shoots of *S. maximum*; and to compare parameters characterizing the apex geometry in shoots with different phyllotaxis.

MATERIALS AND METHODS

All the examined material came from two wild populations: one growing near Męcinka in the Kaczawskie Foothills (Western Sudeten Mts.); and another – on the Odra river bank in Wrocław. All mature shoots growing in each location, i.e. about 80 axes, were collected in October 1993 and placed in a freezer. In April 1996 also about 150 axillary vegetative shoots with not yet elongating internodes were collected in these same places. They were all at least six plastochrons old, i.e. after the end of the juvenile phase of development (Astruc 1949).

Peels of stem cortex were prepared from the frozen shoots in the way described by Gómez-Campo (1974). The arrange-

ment of leaf scars on the stem surface was then copied from the outer surface of cortex peels which were earlier pressed and flattened under a glass plate. Their phyllotaxis was determined on the basis of numbers of contact parastichies (CPs) drawn between the closest leaf scars. Chiral configuration of CPs was referred to as "S" when they were ascending clockwise, and "Z" – for those ascending counterclockwise. Since all the mature axes were collected in the two locations, their analysis allowed the estimation of frequencies of various phyllotactic patterns. Also the sequence of patterns during the vegetative phase of shoot development was recognized.

Vegetative shoot buds were fixed in formalin-aceto-alcohol, embedded in paraffin and serially sectioned in the transverse plane (sections 10 μ m thick). Sections were stained with Ehrlich's hematoxylin (Johansen 1940). Their phyllotaxis was determined on the basis of angular leaf primordia spacing (see below) and CP numbers. Three sets of CPs were always recognized. The number of those still easily traced but connecting more distant leaf primordia were given in square brackets.

Ten shoot apices representing each phyllotactic pattern were randomly chosen for further analysis. Images of sections cut at the level where the youngest leaf primordium or whorl of primordia were attached to the apical dome, were recorded using the Silicon Graphics workstation Indy connected to Olympus microscope BX50. The following measurements were performed on these sections: angular distances between leaf primordia; radial distances from the centre of every primordium to the geometrical centre of the apex (Green and Baxter 1987); areas of the apical dome and of the youngest leaf primordium (an average area of the youngest whorl members was calculated in apices with whorled phyllotaxis). Radial distances were used for the calculation of plastochron ratio (R); the areas were used for the area ratio (AR) calculation, both according to Richards (1951). For apices with whorled phyllotaxis R was calculated "per leaf", i.e. as an appropriate root of plastochron ratio calculated "per whorl" (Rutishauser 1998). AR was determined separately for each apex. Two computer programs written by R. Karwowski (Institute of Botany, Wrocław University) for a Silicon Graphics workstation were used: PHYL-3 version of PHYL program described by Matkowski et al. (1998) – for angle measurements and the determination of radial distances; and SURFACE – for area measurements. For the latter, the values presented are based on the mean of three independent measurements. Numerical data concerning divergence angles, areas, AR and R were analyzed with the aid of CSS Statistica 3.1 (Statsoft Inc. 1993, Tulsa). An analysis of variance was performed for every variable. Mean values were tested for a difference with Least Significant Difference test for independent samples. Both tests were performed at $P = 0.05$.

RESULTS

Phyllotactic patterns and ontogenetic transitions in vegetative shoot apices

Six different phyllotactic patterns were found in shoot apices of *S. maximum*: three whorled – decussate (Fig. 7), tricusate (Fig. 8); tetracusate (Fig. 1); and three spiral – Fibonacci; the first (Lucas); and the second accessory pattern. In apices exhibiting Fibonacci phyllotaxis, various numbers of CPs were apparent: 2:3:[5] (Fig. 9); [2]:3:5 (Fig. 10); or 3:5:[8] (Fig. 11). Nevertheless, angular spacing of leaf primordia in all these apices was characterized by the same

Figs 7-12. Contours of transverse sections of *S. maximum* shoot apices exhibiting various phyllotaxes. Borders of procambial or vascular strands are marked with thinner lines. Leaf primordia labeling as in Figs 1-6. Exemplary CPs from every set are marked with different kinds of lines; the less prominent ones always with a dashed line. Bars = 250 μ m.

Fig. 7. A decussate apex.

Fig. 8. A tricussate pattern.

Fig. 9. Fibonacci pattern with 2z:3s:[5z] CPs.

Fig. 10. Fibonacci with [2s]:3z:5s CPs.

Fig. 11. Fibonacci with 3z:5s:[8z] CPs.

Fig. 12. Lucas pattern with 3s:4z:[7s] CPs.

TABLE 1. Frequency of various phyllotactic patterns in *S. maximum*, and angular spacing of leaves in shoot apices exhibiting these patterns (mean $\pm$ s.e.). Frequencies are of final patterns developing in mature vegetative shoots; percentages of all the shoots are given in parentheses. Angular distances in apices with whorled patterns were measured between members of one whorl (A) and between primordia of adjacent whorls (B).

Phyllotactic pattern	Pattern frequency	Angular leaf spacing	Limiting value of divergence
Decussate (A/B)	20 (26%)	$179^\circ \pm 0.8^\circ / 89^\circ \pm 0.6^\circ$	$180^\circ / 90^\circ$
Tricussate (A/B)	18 (24%)	$120^\circ \pm 0.6^\circ / 60^\circ \pm 0.3^\circ$	$120^\circ / 60^\circ$
Tetracussate (A/B)	5 (7%)	$90^\circ \pm 0.4^\circ / 45^\circ \pm 0.3^\circ$	$90^\circ / 45^\circ$
Spiral Fibonacci	26 (34%)		$\sim 137.5^\circ$
2:3:[5]		$139^\circ \pm 1.0^\circ$	
[2]:3:5		$139^\circ \pm 0.7^\circ$	
3:5:[8]		$139^\circ \pm 1.0^\circ$	
Spiral Lucas	7 (9%)		$\sim 99.7^\circ$
3:4:[7]		$101^\circ \pm 0.8^\circ$	
Second accessory	0		$\sim 77.9^\circ$
4:5:[9]		79°	

mean divergence, namely 139° (Table 1). CP numbers in apices with Lucas phyllotaxis were always the same – 3:4:[7] (Fig. 12). The second accessory pattern was represented only in a single apex, with 4:5:[9] CPs (Figs 2, 13).

Some apices appeared to undergo quite recently ontogenetic transitions of phyllotaxis. Transitions from decussate to Fibonacci (2:3) patterns were the most common (Figs 14, 15). Other relatively frequent transitions were: from Fibonacci (3:5) to tricussate (Figs 5, 16); and from Fibonacci (3:5) to Lucas (Figs 6, 17). In few apices, decussate phyllotaxis was transformed directly into tetracussate (Fig. 4) or the tricussate pattern into Lucas (Figs 5, 18).

During the transition from decussate to Fibonacci pattern (Figs 14, 15) the number of CPs increased, i.e. a single parastichy was added to one of the sets of two (2s:2z changes into 2s:3z in both the Figures). In the last decussate pair of leaf primordia preceding the spiral pattern (4a and 4b in Fig. 14; 3a and 3b in Fig. 15) the primordia were not exactly opposite (Table 2). On this side where the circumferential distance between them was larger, two primordia (5 and 7 in Fig. 14; 4 and 6 in Fig. 15) appeared instead of the one, which would be there if the decussate phyllotaxis persisted. In few apices a "double" leaf primordium occurred in this wider sector (3b in Fig. 3). On the other side, in the middle of the smaller sector a single primordium (6 and 5 in Figs 14 and 15, respectively) was always initiated as expected if the decussate pattern continued. Angles between the first three spirally arranged primordia differed from the Fibonacci divergence. The angle between the first two was larger than the ideal Fibonacci angle; that between the second and the third one was smaller; and the next angle – again larger. A close approximation of the

Fibonacci divergence was observed after the fourth plastochron. Still later, higher CPs became apparent in Fibonacci phyllotaxis. For example in Fig. 15, leaf primordium 10 is in a closer contact with primordia 5 and 7 than with 8, i.e. [2s]:3z:5s CP pattern develops from the initial 2s:3z.

In the course of the transition from the Fibonacci (3:5) to tricussate pattern (Figs 5, 16) the number of CPs also increased. Here one parastichy was added to the set of 5 (with Z configuration in Fig. 16), which event immediately transformed them into orthostichies of whorled phyllotaxis. The divergence increased abruptly between the youngest primordium on the spiral and the next one belonging to the first tricussate whorl (as between 9 and 10a in Fig. 16). The angle between younger primordia, arranged in whorls, was fluctuating around 120° typical for the tricussate pattern (Table 2).

The transition from the Fibonacci (3:5) to Lucas (3:4) phyllotaxis (Figs 6 and 17) was the only one during which the number of CPs was decreasing. In the apex shown in Fig. 17 a set of five Z parastichies changes into four, whereas the number of parastichies in the other set (3s in this Figure) is constant. During this transition the configuration of the ontogenetic spiral always altered (from S to Z in this Figure). The change in angular spacing of leaf primordia was abrupt and Lucas divergence was quickly approached (Table 2).

When tricussate phyllotaxis transformed into Lucas, a single parastichy was added to one of the sets of three, i.e. 3:3 CPs changed into 3:4. In the apex shown in Fig. 18 due to such change leaf primordium 7 is already in contact with 3c (a new, fourth parastichy in a set of 3z becomes apparent). During this transition two primordia instead of one arose in one of three sectors between the members of the last whorl,

TABLE 2. Changes in angular spacing of leaf primordia in the course of phyllotactic transitions, and frequencies of various transitions estimated for mature shoots calculated as a percentage of all the transitions observed in mature shoots (followed by a number of shoots in parentheses). Numbers of examined apices are given in square brackets after the transition specification.

Angles between:	Decussate to Fibonacci [9]	Fibonacci to tricussate [8]	Fibonacci to Lucas [4]
The last two leaves of initial pattern	$170^\circ \pm 2.3^\circ$	$133^\circ \pm 2.7^\circ$	$149^\circ \pm 4.1^\circ$
Last of initial and 1 st of new pattern	$118^\circ \pm 5.5^\circ$	$156^\circ \pm 2.4^\circ$	$92^\circ \pm 5.8^\circ$
1 st and 2 nd leaf of new pattern	$158^\circ \pm 5.5^\circ$	$120^\circ \pm 3.9^\circ$	$115^\circ \pm 7.2^\circ$
2 nd and 3 rd	$124^\circ \pm 5.5^\circ$	$126^\circ \pm 4.5^\circ$	$98^\circ \pm 1.4^\circ$
3 rd and 4 th	$152^\circ \pm 4.7^\circ$	$121^\circ \pm 3.2^\circ$	$97^\circ \pm 2.2^\circ$
4 th and 5 th	$134^\circ \pm 1.5^\circ$	$117^\circ \pm 3.7^\circ$	$103^\circ \pm 5.6^\circ$
Transition frequencies ¹	62% (34)	24% (13)	4% (2)

¹Transitions not included in this Table occurred with the following frequencies: from decussate to tetracussate phyllotaxis – 4% (2 shoots); from decussate to tricussate – 4% (2); from tricussate to tetracussate 2% (1).

Figs 13-18. Contours of transverse sections of *S. maximum* shoot apices showing various phyllotactic patterns and phyllotactic transitions. New or disappearing parastichies are marked with thicker lines.

Fig. 13. The second accessory spiral pattern; with 4s:5z:[9s] CPs (the same as in Fig. 2).

Fig. 14. An early stage of the transition from decussate (whorls 1-4) to spiral Fibonacci phyllotaxis (primordia 5-8) with 2s:3z CPs becoming apparent between spirally arranged primordia: 5 and 7 (a parastichy from the set 2s); and 7 and 4b (from set 3z).

Fig. 15. A later stage of the transition shown in Fig. 14. The youngest leaf primordia (7-10) are packed closer than the first spirally arranged ones (4-6). Since primordium 10 is in closer contact with 7 and 5 than with 8, parastichies of higher numbers (3z and 5s) become apparent.

Fig. 16. The transition from Fibonacci to tricussate phyllotaxis (the same as in Fig. 5). In the initial spiral pattern (primordia 1-9) the CPs from sets 3s and 5z are visible. During the transition, one parastichy is added to the more numerous set; then all the six lines extend into orthostichies of tricussate primordia arrangement.

Fig. 17. Fibonacci phyllotaxis (3s:5z; primordia 1-10) transforming into the Lucas pattern (3s:4z; primordia 11-16) due to the disappearance of a parastichy in set 5z (the same as in Fig. 6).

Fig. 18. The initial stage of a transition from the tricussate phyllotaxis (whorls 1-3) to Lucas (primordia 4-7). While the tricussate pattern is transformed, four primordia (4-7) appear around the apical dome instead of three. Two of them (4 and 7) are in the space between 3c and 3a where a single primordium would form if the tricussate pattern persisted.

Figs 19-20. Distribution of leaf scars (dark dots) on the outer surface of flattened cortex peels. Leaves or whorls are numbered in order of initiation (the younger the primordium or whorl, the higher the number). Members of some whorls are also labeled with a letter so that they could be differentiated. Exemplary CPs from every set are drawn with different kinds of lines. New or disappearing parastichies are marked with thicker lines. Bars = 20 mm.

Fig. 19. The decussate leaf arrangement (whorls 1-2) changes into the spiral Fibonacci pattern [1z]:2s(solid line):3z(dashed) (leaves 3-14) and then further into the tricusate pattern (whorls 15-19). The initial fragment of the ontogenetic helix of the spiral pattern is marked with a dotted line. The first transition comprises an increase in the number of Z parastichies (from 2s:2z to 2s:3z); the second – an addition of one parastichy to set 2s.

Fig. 20. A cortex peel was divided into two fragments; leaves 26-28 are repeated in both drawings. Decussate phyllotaxis is transformed into spiral Fibonacci [1z]:2s(solid):3z(dashed) (leaves 2-21), which further changes into spiral Lucas 1s(solid):3z(dashed) (leaves 22-56). The ontogenetic helix in the Fibonacci pattern was marked with a dotted line. During the first transition one Z parastichy is added. During the second – a single parastichy from the set of 2s disappears, whereas the other one from this set becomes the ontogenetic helix of the Lucas pattern. Between spiral Fibonacci and Lucas patterns an intermediate stage can be distinguished (leaves 26-34) where trimerous pseudowhorls (26-28; 29-31; 32-34) are formed.

e.g. primordia 4 and 7 arise between 3a and 3c in this Figure. Within the remaining two sectors, a single primordium was positioned (5 between 3a and 3b; 6 between 3b and 3c) as if in the tricusate pattern.

An unusual transition proceeding directly from decussate to tetracusate pattern was encountered in one apex only (Fig. 4). Here in both circumferential sectors between the last pair of leaves, two primordia are initiated instead of one (5a and 5b; 5c and 5d in spaces between 4a and 4b). This could be interpreted as an increase from 2:2 to 4:4 CPs, which is a doubling of parastichies in each set.

Phyllotactic diversity and ontogenetic sequence of phyllotactic patterns in mature vegetative shoots

All phyllotactic patterns described above, with the only exception of the second accessory spiral pattern, were encountered in mature shoots (Table 1). Only numbers of CPs in mature shoots were lower than those observed in shoot apices. Both Fibonacci and Lucas phyllotaxes were always represented by the same numbers of CPs: Fibonacci – by [1]:2:3 (Figs 19, 20); Lucas – by 1:3:[4] (Fig. 20). Various patterns occurred with different frequencies (Table 1): the Fibonacci phyllotaxis was the most common; decussate and tricusate phyllotaxes occurred with only a little lower frequency; whereas the Lucas and tetracusate patterns were represented in a small number of shoots.

The decussate pattern was initial in almost all examined axes (Figs 19-22). There was one exception (Fig. 23) where even the prophylls had a tricusate arrangement. In about one third of axes, decussate phyllotaxis persisted until the beginning of the generative phase, while in the remaining shoots it was transformed into one of the following patterns: Fibonacci (Figs 19, 20); tricusate (Fig. 21); or tetracusate (Fig. 22). The first transition occurred most often, whereas other two were much less common (Table 2). The direct change from decussate to tricusate pattern was found only in two mature shoots. More commonly, the tricusate phyllotaxis developed from spiral Fibonacci, and the ontogenetic sequence of patterns was as follows: decussate, Fibonacci, and tricusate (Fig. 19). Fibonacci pattern either persisted until the beginning of generative phase or, less often, further transformed into the Lucas pattern (Fig. 20). As in shoot apices, also here the reversal of the ontogenetic helix was observed during this transition (from Z to S in Fig. 20). The least common transition was the direct change from the tricusate to tetracusate pattern, encountered in only one shoot (Fig. 23). In general then, all the transitions proceeding between two whorled patterns were infrequent (Table 2).

In the course of transitions analyzed in mature shoots a change in at least one of CP sets took place. When the decussate pattern was transformed into Fibonacci, 2:2 CPs changed into [1]:2:3, i.e. a single parastichy was added to one of the

Figs 21-23. Distribution of leaf scars on cortex peels; continuation.

Fig. 21. A decussate leaf arrangement is transformed directly into tricussate. The latter, however, is not yet fully developed. In the course of the transition two leaves (15b and 15c) appear in the space between 14a and 14b where a single one would be attached in the decussate pattern.

Fig. 22. Direct transition from the decussate pattern to tetracussate. Pairs of leaves (3a and 3b; 3c and 3d) are attached in each of two spaces between 2a and 2b.

Fig. 23. The tricussate pattern transforms into tetracussate, which however, is less regular than in the shoot from Fig. 22. The last tricussate whorl (21) is asymmetric. Later, two leaves (22b and 22c) appear in the space between 21a and 21b, whereas other leaves from whorl 22 alternate with those from 21. In this particular shoot tricussate phyllotaxis occurred already in the arrangement of prophylls at the base of the stem.

sets of two (to 2z in Figs 19 and 20). Another example of an increase in CP number was the change from [1]:2:3 to 3:3, where one parastichy was added to the set of two in the course of the transition from the Fibonacci to tricussate pattern ([1z]:2s:3z changes into 3s:3z in Fig. 19). Also transitions from one whorled pattern to another; i.e. directly from decussate to tricussate or to tetracussate; and from tricussate to tetracussate; were examples of an increase in CP numbers, but always in both sets of CPs; i.e. from 2:2 to 3:3 (Fig. 21) or to 4:4 (Fig. 22), and from 3:3 to 4:4 (Fig. 23), respectively. The only example of CP number decrease was the subtraction of one parastichy from the set of two in Fibonacci pattern (from 2s in Fig. 20) which led to 1:3 CPs of Lucas phyllotaxis (1s:3z in this Figure).

Apex geometry in various phyllotaxes

Among the examined parameters characterizing apex geometry, the area of the dome and the plastochron ratio (R) showed the highest number of statistically significant differences between various phyllotactic patterns (Table 3). The

sequence of patterns arranged in the order of increasing dome area or decreasing R was the same as that of patterns arranged according to increasing CP numbers. It also generally concurred with the sequence of patterns observed during the ontogeny of vegetative shoots (Fig. 24). Decussate apices were characterized by the smallest dome area and the highest R, both significantly different from all the other apices, whereas domes of tetracussate apices were the largest and their R was the smallest of all. The area of an apex with 4:5 CPs was still larger and R the same as in tetracussate apices, but the single occurrence of this pattern did not allow any statistical comparison. Apices with the two lower CP numbers of the Fibonacci pattern did not differ significantly one from the other either in dome area or in R. In these two groups of apices, however, the same three sets of CPs (2, 3, 5) were apparent, and the only difference was in sets which were estimated to be the most prominent. Also, apices with the highest CPs of Fibonacci phyllotaxis were the same as those with Lucas pattern. These two patterns in turn differed only by a single parastichy in the more numerous set.

TABLE 3. Parameters of shoot apex geometry for various phyllotactic patterns, empirically estimated for *S. maximum*. Differences between values of the same column marked with different superscripts are significant at $P < 0.05$ level of LSD test. The last column presents AR_{theor} , calculated on the basis of empirical R according to Richards (1951) equation: $AR = (2\ln R)^{-1}$.

CP numbers	R	Apical dome area ($10^3 \mu m^2$)	Primordium area ($10^3 \mu m^2$)	AR	AR_{theor}
2:2:[4]	1.31 ± 0.03 ^a	8.2 ± 0.9 ^a	9.1 ± 1.8 ^{ab}	1.09 ± 0.16 ^a	1.85
2:3:[5]	1.21 ± 0.01 ^{bc}	13.4 ± 1.2 ^{bc}	6.2 ± 0.7 ^{bcd}	2.28 ± 0.22 ^b	2.62
[2]:3:5	1.18 ± 0.01 ^{bcd}	15.5 ± 1.2 ^{bcd}	4.7 ± 0.4 ^{cd}	3.40 ± 0.21 ^c	3.02
3:3:[6]	1.18 ± 0.01 ^{cde}	21.1 ± 2.1 ^{def}	6.4 ± 0.6 ^{bcd}	3.31 ± 0.11 ^c	3.02
3:4:[7]	1.15 ± 0.01 ^{cde}	20.0 ± 2.5 ^{cdef}	5.4 ± 0.5 ^{cd}	3.70 ± 0.25 ^c	3.58
3:5:[8]	1.15 ± 0.01 ^{de}	21.5 ± 1.4 ^{def}	4.9 ± 0.4 ^{cd}	4.46 ± 0.25 ^d	3.58
4:4:[8]	1.12 ± 0.01 ^{de}	26.9 ± 2.0 ^g	7.9 ± 0.9 ^{abc}	3.59 ± 0.25 ^c	4.41
4:5:[9]	1.12	30.3	5.1	5.97	4.41

Fig. 24. Areas of apical dome (hatched boxes) and of the youngest leaf primordium (empty boxes) in $10^3 \mu\text{m}^2$, plotted against increasing CP (or orthostichy) numbers. The average (innermost square), a standard error (outer rectangle) and a standard deviation (outermost bars) are given for every pattern. Arrows below the graph show the direction of ontogenetic transitions of phyllotaxis encountered in *S. maximum*. Dotted lines point out the least common transitions (frequency no larger than 4%).

For the area ratio (AR), the number of significant differences was lower, but the sequence of patterns arranged according to increasing AR was the same as that with increasing dome area. The smallest number of significant differences was encountered in areas of the youngest leaf primordium. These areas in fact were generally fluctuating around the same value in all the apices, and only those of decussate and tetracussate shoots were significantly larger than others.

DISCUSSION

Unlike in previous works devoted to phyllotaxis of *S. maximum*, in the present paper transitions of phyllotaxis are analyzed both in apices and in mature shoots. Moreover, empirical data on apex geometry in various phyllotactic patterns are presented. All transitions described in this paper, whether they were shifts between two spiral, two whorled, or spiral and whorled patterns, can be explained in terms of dislocations in crystal-like lattice of CPs. These are local disturbances of the CP pattern leading to the appearance of new parastichies or disappearance of already existing ones. This interpretation has been introduced by Zagórska-Marek (1985, 1987) and thoroughly illustrated in *Abies balsamea* (L.) Mill. (Zagórska-Marek 1985), various *Magnolia* species (Zagórska-Marek 1987, 1994), lycopods (Gola 1996), cacti (Gola 1997), and sunflower (Couder 1998). In *S. maximum*, a general rule is that most often only a single parastichy is added or sometimes subtracted from the already existing CP pattern. Therefore the sequence of phyllotactic patterns appearing during the shoot ontogeny is to some extent predictable. Exceptions to this rule are transitions proceeding directly from one whorled pattern to another. In all these cases, not one but more parastichies are added to the existing sets: one to each set during decussate to tricussate transition, or even two in an extreme case of the transition from the decussate to tetracussate pattern, where numbers of CPs double. Transitions from

one whorled pattern to another, however, from decussate to tetracussate in particular, were found to be the least common in *S. maximum*. All these facts are in agreement with the postulate that CP pattern itself may play a crucial role in defining the position of primordia initiation at the apex, and therefore is a more natural parameter for describing phyllotaxis than the divergence angle or the ontogenetic spiral(s) (Zagórska-Marek 1987, 1994).

It has been well documented that in many plant species the size of the shoot apex is increasing during ontogeny (Richards 1951; Gregory and Romberger 1972; Rutishauser 1998). In shoots of plants in which spiral phyllotaxis develops either after few decussate leaves or immediately after the cotyledons or prophylls, increase in dome dimension is usually accompanied by an increase in CP numbers **within the same phyllotactic series**. Such is the case of *Linum usitatissimum* (Williams 1975; Meicenheimer 1987; Rutishauser 1998), and *Picea abies* Karst. (Gregory and Romberger 1972). This implies that in *S. maximum* the increase in size of the apical dome is somewhat different – it causes qualitative transitions occurring **between different patterns**. According to (Zagórska-Marek 1987; Meicenheimer and Zagórska-Marek 1989) the first type of transition could be explained by continuous changes in the circumferential component of apical dome growth, while the second – by discontinuous changes. The discontinuous growth rate changes, causing a total increase in apical dome in *S. maximum*, might be supported by the fact that the decussate to Fibonacci transition is preceded by the formation of an asymmetric whorl of primordia. Similar tendency could be seen in an apex where another whorled pattern, tricussate, changes into spiral Lucas (compare spaces between primordia of the last whorl in Fig. 18).

This interpretation is also consistent with Green's postulate on the existence of intrinsic wavelength characteristic for the meristem surface tissue (Green et al. 1996): despite differences in the apical dome area (corresponding to the formative annulus dimension), the size of a leaf primordium (an intrinsic

sic wavelength) remains relatively constant. These conclusions could come only from a comparison of various phyllotactic patterns in shoots of one plant species and all in the same developmental phase. This makes a *S. maximum* case exceptional.

The phyllotactic diversity in *S. maximum* reported in the present paper generally concurs with the results obtained by Astruc (1949) and Deschatres (1954). The main difference is in a frequency of the tetracussate pattern which, following Astruc, was encountered in a few fasciated shoots of *S. maximum* exclusively. This paper reports a pattern new for *S. maximum* (the second accessory spiral phyllotaxis) which was found in a single shoot apex only. Both Astruc (1949) and Deschatres (1954) paid much attention to the problem of phyllotactic transitions in *S. maximum*. However, they performed this analysis mostly on mature shoots, and encountered only some of the transitions described in the present paper. None of these authors mentioned the change from Fibonacci to tricussate phyllotaxis. Also a direct transition from decussate to tetracussate pattern was reported for other *Sedum* species only (Deschatres 1954).

S. maximum phyllotaxis resembles to some extent that of *B. tubiflorum*, another member of the Crassulaceae family (Jensen 1968, Gómez-Campo 1974). The two species have most patterns in common (decussate, tricussate, tetracussate, as well as spiral Fibonacci and Lucas), but the course of some phyllotactic transitions differs. In *S. maximum* the change from decussate to tetracussate pattern is direct: two leaf primordia develop instead of a single one of the decussate pattern. The type of transition is the same as that described for *Nerium oleander* by Williams et al. (1982). In *B. tubiflorum* tetracussate phyllotaxis arises differently, due to the gradual "compression" of successive decussate ("pseudobijugate") whorls. Another difference between *B. tubiflorum* and *S. maximum* transitions can be found in the course of the transition from Fibonacci to Lucas pattern. According to Gómez-Campo results, in *B. tubiflorum* imperfect tricussate whorls ("imperfect trios") intermediate between the two patterns. They may in fact be pseudowhorls rather than true whorls, because despite their appearance the configuration of the ontogenetic helix in Lucas pattern is always opposite to that of Fibonacci (Gómez-Campo 1974). Numbers of shoots with altered and not altered configuration of the helix should be equal if true tricussate pattern occurred, whereas the transition from the Fibonacci pattern to Lucas accompanied by a reversal of the ontogenetic helix, has been shown to be theoretically more probable than that with unchanging configuration (Zagórska-Marek 1985). Moreover, few "imperfect trios" (pseudowhorls) could be seen in Fig. 20 of *S. maximum* although the CP pattern in this part of the shoot clearly indicates spiral phyllotaxis. In a number of plant species, like *Peperomia verticillata* (L.) A. Dietr. and *Anagallis arvensis* L., pseudowhorls develop in all shoots with spirally arranged leaves (Schoute 1925; Kwiatkowska 1995b, 1999).

Differences in apex geometry parameters between shoots exhibiting various phyllotactic patterns are concurrent with the theoretical models like that of Richards (1951) and Thomas (1975). The higher the CP numbers are, the lower is R and the higher – AR. However, empirical R values for *S. maximum* are generally lower than theoretical R calculated either for the ideal (see Richards 1951) or for the Braunian (Thomas 1975) divergences. Nevertheless, they usually fall within the range of empirical values reported for other plant species by Rutishauser (1998). Also empirical AR values obtained for *S. maximum* approach the theoretical values calculated on the

basis of empirical R according to Richards equation (Table 3). The differences between empirical and calculated AR most probably result from plastochron changes in apex and primordium area, which may also influence R from which AR was calculated. This is justified especially for apices exhibiting low CP numbers (Richards 1951). The decrease of R in the course of phyllotactic transition observed in *S. maximum* implies an acceleration in leaf primordia production, while increase in AR – closer packing of primordia around the apical dome. This is consistent with the fact that transitions are most often accompanied by an increase in the numbers of CPs. A similar tendency was reported for *B. tubiflorum* (Rutishauser 1998, calculated from data of Gómez-Campo, 1974), as well as for *Linum usitatissimum* (Meicenheimer 1987).

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ONTOGENETYCZNA ZMIENNOŚĆ FILOTAKSJ I GEOMETRII WIERZCHOŁKA WEGETATYWNYCH PĘDÓW *SEDUM MAXIMUM* (L.) HOFFM.

STRESZCZENIE

Filotaksja pędów wegetatywnych *Sedum maximum* (L.) Hoffm. jest zróżnicowana i niestabilna. W ontogenezie pędu często pojawiają się transformacje filotaksji przebiegające pomiędzy wzorami okółkowym i spiralnym, dwoma wzorami spiralnymi, lub rzadziej – pomiędzy dwoma wzorami okółkowymi. W trakcie transformacji liczba parastych kontaktowych zmienia się. Najczęściej pojawia się wówczas jedna dodatkowa parastycha, lub rzadziej – jedna parastycha znika. Dzieje się tak zarówno w trakcie transformacji zachodzących pomiędzy wzorami okółkowym i spiralnym, jak też pomiędzy dwoma wzorami spiralnymi. Liczby parastych kontaktowych ulegają większym zmianom tylko w trakcie transformacji jednego wzoru okółkowego w drugi, które są jednak dużo rzadziej spotykane. Parametry opisujące geometrię merystemu apikalnego pędów o odmiennych wzorach ulistnienia istotnie się różnią. Uporządkowanie wzorów zgodne z rosnącą powierzchnią czaszy merystemu i stosunkiem powierzchni czaszy do zawiązków liści, bądź też malejącym stosunkiem plastochronowym, jest takie samo jak sekwencja wzorów o rosnących liczbach parastych kontaktowych. Ta z kolei to kolejność pojawiania się wzorów w ontogenezie pędu. Jedynym parametrem, który pozostaje względnie stabilny jest powierzchnia zawiązka najmłodszego liścia. Oznacza to, że w trakcie transformacji filotaksji u *S. maximum* względne wymiary czaszy merystemu i zawiązków zmieniają się na skutek wzrostu powierzchni czaszy. Wydaje się, że u gatunku tego powiększanie się czaszy, typowo występujące w ontogenezie pędów innych roślin, przebiega w sposób wyjątkowy. Powoduje to jakościowe zmiany filotaksji, a nie występujące zwykle u innych gatunków zmiany liczb parastych kontaktowych w obrębie tego samego ciągu filotaktycznego.

SŁOWA KLUCZOWE: filotaksja, transformacje filotaksji, wierzchołek pędu, *Sedum maximum*.