PHYLLOTAXIS OF VEGETATIVE SHOOTS OF *ANAGALLIS ARVENSIS* L. TREATED IN VITRO WITH 6-BENZYLAMINOPURINE

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ABSTRACT

Application of 6-benzylaminopurine (BA), a synthetic cytokinin, to the growth medium in vitro stimulates the formation of adventitious shoots on stem explants of *Anagallis arvensis*. They regenerate from dedifferentiating epidermal cells of stem internodes. The process starts from periclinal and anticlinal divisions in a few of neighbouring cells. The amount of adventitious shoots increases with an increasing BA concentration. The BA treatment also affects phyllotaxis, but only of adventitious shoots, and not of normal lateral shoots developing in leaf axils. Leaf arrangement on adventitious shoots is always variable, even on the control medium. Generally, patterns observed in case of in vitro shoots do not differ from those reported earlier for intact *A. arvensis* plants. BA treatment also leads to the teratologic development, i.e. fasciation and the formation of abnormally shaped leaves, but again in adventitious rather than in normally developing shoots. We postulate that the variability of phyllotaxis characteristic for adventitious shoots and their response to BA treatment, result from the fact that their apical meristems develop de novo from initially unorganised meristematic centres, whereas meristems of normally developing lateral shoots are well organised from the time of their initiation.

KEY WORDS: *Anagallis arvensis*; phyllotaxis; in vitro culture; BA treatment, axillary and adventitious shoots.

INTRODUCTION

The influence of plant growth regulators on phyllotaxis is known from a number of experimental studies in which regulators were applied directly on an intact plant (e.g. Mingo-Castel et al. 1984). The result of the treatment depends on the kind of a regulator, the plant species, and on the initial phyllotactic pattern. Gibberellins applied to shoots with spiral Fibonacci phyllotaxis induce an increase in the divergence angle in *Hedera helix* (Marc and Hackett 1991), or an acceleration of primordia production in *Xanthium* (Maksymowych and Erickson 1977). In shoots of *Euphorbia lathyris* with initially decussate pattern, gibberellins cause the transition to spiral phyllotaxis (Mingo-Castel et al. 1984). Auxin treatment has variable effects depending on the type of regulator used. Indole-acetic acid causes a temporary disruption of phyllotaxis regularity in *Tropaeolum majus* (Ball 1944), *Dryopteris austriaca* (Wardlaw 1957), and *Lupinus albus* (Varnell and Vasil 1978). The treatment with 2,4-dichlorophenoxyacetic acid changes the distichous phyllotaxis of *Phaseolus vulgaris* into various whorled patterns, or into an aberrant leaf arrangement (Soma 1968). Auxin antagonists or transport inhibitors increase the divergence angle, causing the change of spiral Fibonacci phyllotaxis into distichous pattern in *Chrysanthemum* (Schwabe 1971). In *Epilobium* the similar treatment induces the transition from bijugate to spiral Fibo-

nacci phyllotaxis (Meichenheimer 1981). An application of cytokinins results in an increase in whorled pattern merosity in shoots of *Euphorbia lathyris* (Mingo-Castel et al. 1984), or an acceleration of the rate of primordia initiation in *Chenopodium rubrum* (Seidlová and Krekule 1977). These experiments differ in the method of the growth regulator application. It ranges from a direct application of a regulator in a lanolin paste on the shoot apex (e.g. Ball 1944, Varnell and Vasil 1978) or on a leaf primordium (Seidlová and Krekule 1977, Meichenheimer 1981), to spraying of a whole plant with the solution containing a regulator (Mingo-Castel et al. 1984).

Phyllotaxis of plants cultured in vitro has not been investigated, although in most of the in vitro experiments the growth regulators are added to the medium. This mode of application poses a number of problems, e.g. with the estimation of what amount of the compound reaches the shoot apex. However, when a regulator is applied in the growth medium, an interesting question on the relationship between the origin of shoots and phyllotaxis can be addressed: does a regulator affect the shoot apex, or does it rather cause the formation of shoots in an abnormal way, which may in turn result in altered phyllotaxis? Also, the application of growth regulators to in vitro culture medium allows a precise estimation of their concentrations, and thus improves the replicability of these experiments. This can not be obtained when regulators are applied in a lanolin paste or by spraying.

In the present investigation we examine the influence of 6-benzylaminopurine (BA), a synthetic cytokinin, on phyllotaxis. The regulator is applied in the growth medium. We analyse its effect on normally developing and regenerating shoots, and compare the chemically induced variation in phyllotaxis with that spontaneously occurring in intact plants. *Anagallis arvensis* was selected for this study because BA is already known to induce adventitious shoot formation in stem explants of this species (Bajaj and Mäder 1974, Kwiatkowska 1997b), and because phyllotaxis of potted *A. arvensis* is spontaneously variable (Kwiatkowska 1995). Four different patterns occur on its shoots: decussate, tricussate, spiral Fibonacci, and spiral Lucas. The first one is dominant in the vegetative and less so in the generative phase of shoot development, whereas the occurrence of the other three patterns is limited to the generative phase. Among the three, spiral Fibonacci is the most common pattern, and spiral Lucas – the least (Kwiatkowska 1995).

MATERIALS AND METHODS

The *in vitro* culture was established from one potted plant obtained through sowing seeds of a weed growing in the Botanical Garden of Wrocław University. Shoot tips were cut off from the plant numerous lateral branches, at the level of the youngest elongating internode. They were submerged in 96% ethanol, disinfected in 0.025% HgCl_2 and placed on the full-strength modified Murashige and Skoog (1962) medium (MS). Lateral axes developing in leaf axils of these explants were propagated on MS by means of stem explants composed either of nodes with upper and lower portions of consecutive internodes (each c. 3 mm long) or of shoot tips. The same type of explants was used for the experiments.

In experiment A, explants were cultured on the following media: MS as a control; and MS supplemented with 0.05; 0.1; 0.2; 0.4; or 0.8 mg dm^{-3} BA (24 explants on each medium). All explants except the controls were transferred to MS after two weeks of culture in order to decrease the number of necroses caused by high BA doses. The data on shoot phyllotaxis were collected after nine weeks (see below).

In experiment B, which was repeated twice, the doses of BA were reduced. Stem explants were cultured on MS as a control medium, and MS supplemented with 0.1 or 0.2 mg dm^{-3} BA (30 explants per medium). One explant from each medium was collected after the first and the second week of culture in order to examine the process of adventitious shoot formation. Five weeks later, ten explants were taken from every medium for an analysis in which the numbers of normally developing and adventitious shoots were determined with the aid of stereomicroscope. The remaining explants were cultured for the next five weeks to collect material for the analysis of phyllotaxis. All the cultures were kept in a phytotrone in a short photoperiod (12-h a day) in order to keep plants in the vegetative phase of development. The illumination was $24 \mu\text{M m}^{-2} \text{s}^{-1}$; temperature – $24 \pm 3^\circ\text{C}$. All the media contained 3% of sucrose and 0.8% of agar; pH was always adjusted to 5.8.

At the end of each experiment, all the shoots were examined with the aid of stereomicroscope (c. 3 000 shoots from experiment A; 2 000 – from experiment B); and some were documented with the Scalar videolupe connected to a Silicon Graphics workstation "Indy". Leaf arrangement was examined in whole shoots so that stable whorled, spiral, and aberrant phyllotactic patterns, as well as fasciations could be recog-

nised. Some axes representing the different types of phyllotaxis were sectioned transversally (see below) to determine the leaf primordia arrangement in the apical shoot region.

Terminal shoot portions, 5 mm long, collected at the end of experiment A (10 shoots per medium), and stem explants collected at the beginning of experiment B were fixed in formalin-aceto-alcohol, embedded in paraffin and serially sectioned in the transverse plane (sections 6 μm thick). Sections were stained with Ehrlich's hematoxylin (Johansen 1940). This material was studied with the aid of an Olympus light microscope BX 50.

RESULTS

BA had a toxic influence on *A. arvensis* stem explants. Their viability rapidly decreased with increasing BA concentrations (Fig. 1), and more than half of explants were killed by necrosis on the media with the concentration higher than 0.2 mg dm^{-3} (experiment A). Therefore in the experiment B the concentrations were reduced.

Fig. 1. Viability of stem explants of *A. arvensis* growing on media with various BA concentrations (experiment A, nine weeks of culture).

Fig. 2. A fragment of stem internode with numerous adventitious shoots (experiment B, two weeks of culture, MS + 0.2 mg dm^{-3} BA). L – a leaf-like structure; D – a shoot with presumably decussate leaf arrangement. Bar = 0.5 mm.

Figs 3-6. Photomicrographs of transverse sections of stem explant internodes showing consecutive stages of the adventitious shoot regeneration (experiment B). V – vascular tissue. Bars = 50 μ m.

Fig. 3. A meristematic centre (*) in the stem epidermis. Two epidermal cells started to divide periclinally (one week of culture, control).

Fig. 4. Two leaf primordia-like structures developed on the flanks of the meristematic centre (*) (two weeks of culture, control).

Fig. 5. An adventitious shoot with the first leaf primordia larger than in Fig. 4, emerging on both sides of the apical dome (*). No vascular connections between the shoot and the explant vascular cylinder (V) are visible (two weeks of culture, control).

Fig. 6. An adventitious shoot with primary vascular system already connected with the explant vascular cylinder. Three leaf primordia (1a-c) surround the apical dome (*) (two weeks of culture, MS + 0.2 mg dm⁻³ BA).

Two different modes of shoot formation from explants were observed. Some shoots developed as normal lateral branches in leaf axils. They are further referred to as "axillary". Sometimes their number was higher than one shoot per leaf axil, especially in BA treated explants, but this phenomenon is also observed in potted plants. The remaining shoots were adventitious (Fig. 2). They regenerated from dedifferentiating epidermal cells of stem internodes. The regeneration started from periclinal and anticlinal divisions in a few neighbouring cells (Fig. 3). This resulted in the formation of a nodular meristematic centre, on the flanks of which the first leaf primordia developed (Fig. 4). Vascular connections between adventitious shoots and the stem explant vascular cylinder were observed not until several leaf primordia were already initiated (compare Figs 4, 5, and 6). Sometimes instead of adventitious shoots the leaf-like structures with determinate axial growth were formed directly from the meristematic centres (Fig. 7).

The percentage of adventitious axes among all the shoots collected after seven weeks of culture (experiment B) depended directly on BA concentration in the growth medium: the higher was the concentration, the higher their percentage (Fig. 8). In explants treated with 0.2 mg dm⁻³ BA the majority of axes were adventitious.

Adventitious shoots were often teratologic. Some of them were band-shaped (Fig. 9) and represented a typical fasciation of Gorter (1965). In others, fused leaves (Fig. 10) were observed, or the shape of some leaves was abnormal (Fig. 13). In the material collected after seven weeks from the experiment B (0-0.2 mg dm⁻³ BA), the highest percentage of adventitious axes was teratologic on the control medium (Table 1), and the BA treatment significantly reduced this number. However, at the medium containing 0.2 mg dm⁻³ BA the percentage of teratologic shoots was higher than at this with 0.1 mg dm⁻³. At the same time, axillary shoots were virtually not

Fig. 7. A photomicrograph of a leaf-like structure growing from an explant surface, prepared with the aid of videolupe (experiment B, two weeks of culture, MS + 0.2 mg dm⁻³ BA). Bar = 0.5 mm.

Fig. 8. Percentages of adventitious shoots among all the axes, plotted against the BA concentration in the medium (experiment B, seven weeks of culture).

Fig. 9. A fasciated adventitious shoot (experiment B, seven weeks of culture, MS + 0.2 mg dm⁻³ BA). Bar = 0.5 mm.

Fig. 10. A transverse section of an apex exhibiting irregular leaf primordia arrangement, approximating tetracussate phyllotaxis. Leaf primordia are labelled with numbers; the younger the whorl, the higher the number. Letters added to numbers differentiate between members of one whorl. Primordia 1b-d are fused at margins (*). Members of whorl 2 alternate with members of whorl 1 and their arrangement within a whorl is fairly regular (experiment A, nine weeks of culture, MS + 0.4 mg dm⁻³ BA). Bar = 100 µm.

fasciated and did not exhibit any other teratomas, also on media containing BA (Table 1).

All shoots (i.e. axillary and adventitious), excluding teratologic ones, were classified by their phyllotaxis into two groups: shoots with stable decussate phyllotaxis (Fig. 14), i.e. those with regularly decussate leaf arrangement along the whole axis; and shoots with various nondecussate leaf arrangements. The latter group included shoots with unstable phyllotaxis, e.g. changing from the tricussate into decussate pattern (Fig. 12) or from the spiral into tricussate; as well as those with stable tricussate (Fig. 15) or spiral Fibonacci phyllotaxis (Figs 11, 16).

TABLE 1. Percentages of shoots with various phyllotaxes and of teratologic shoots among adventitious and axillary shoots growing on media with various BA concentrations (experiment B, seven weeks of culture). A number of shoots examined follows the specification of BA concentration in parentheses.

Type of shoots	BA concentration [mg dm ⁻³]		
	control (94)	0.1 (174)	0.2 (118)
Axillary shoots:			
Stable decussate	95	92	92
Nondecussate	5	7	8
Teratologic	0	1	0
Adventitious:			
Stable decussate	11	51	44
Nondecussate	33	31	29
Teratologic	56	18	27
All the axes:			
Stable decussate	78	73	54
Nondecussate	11	18	25
Teratologic	11	9	21

Figs 11-13. Adventitious shoots exhibiting various patterns of leaf arrangement (experiment B, seven weeks of culture, MS + 0.2 mg dm⁻³ BA). Bars = 0.5 mm.

Fig. 11. A shoot with spiral Fibonacci phyllotaxis and evenly elongated internodes.

Fig. 12. Tricusate leaf arrangement (lower whorl) is transformed into decussate (upper whorl).

Fig. 13. A shoot with irregular phyllotaxis and abnormally shaped leaves (*).

After seven weeks of culture, the percentage of adventitious shoots with nondecussate leaf arrangement was high and almost constant for BA ranging from 0 to 0.2 mg dm⁻³. In contrast, phyllotaxis of axillary shoots was predominantly decussate despite various BA concentrations (Table 1). This was true even in the case of shoots developing in leaf axils of nondecussate adventitious shoots, as they were usually decussate. Also fasciated shoots sometimes split into axes with almost regular decussate leaf arrangement. However, since the number of adventitious axes was correlated with BA doses (Fig. 8), the percentage of nondecussate shoots among all the shoots examined was increasing with increasing BA concentrations (Table 1).

In the material collected a few weeks later, i.e. at the end of both experiments, the number of shoots with nondecussate phyllotaxis was correlated with the BA dose: it was higher on media with elevated BA concentration (Figs 17, 18). Teratologic shoots also rapidly grew in number with increasing BA concentrations in both experiments (Figs 17, 18). Since in BA treated plants the majority of axes were adventitious, these data presumably apply mostly to adventitious shoots.

DISCUSSION

The results show that phyllotactic variability in *in vitro* cultured vegetative shoots of *A. arvensis* changes with the addition of BA to the culture medium. BA action, however, is in-

direct. It leads in the first place to the formation of adventitious shoots, the phyllotaxis of which is always more variable than that of normally initiated axillary axes. Acting simultaneously on both, BA affects phyllotaxis of adventitious but not of axillary shoots. An increase in the regulator dose leads to a rapid increase in the percentage of adventitious shoots with nondecussate phyllotaxis. Another effect of BA on this type of shoots is an induction of teratologic development (Mowszowicz 1972), like fasciation or abnormally shaped leaves. Although the highest percentage of teratologic adventitious axes was observed on the control medium, an increase in the BA dose led to an increase in the percentage of teratomas. BA also caused the formation of leaf-like structures with determinate axial growth, which are somewhat similar to those formed on callus cultures, e.g. of *Quercus rubra* (Seckinger et al. 1979).

Phyllotaxis of axillary axes has been only slightly affected by the BA concentrations used, and fasciation of these shoots was extremely rare. This stability of phyllotaxis is unlike in *P. verticillata* cultured *in vitro* (Kwiatkowska 1999). The same doses of BA (0-0.2 mg dm⁻³) applied to normal, not adventitious, shoots of this species cause the increase in contact parastichy numbers of the spiral Fibonacci pattern, and the occurrence of a higher percentage of shoots with whorled phyllotaxis. However, the two species differ in the dominant phyllotactic pattern in intact plants, which is spiral Fibonacci in *P. verticillata*, with only some shoots exhibiting whorled phyllotaxis, and decussate in *A. arvensis*. Nevertheless, in *Eu-*

Figs 14-16. Photomicrographs of transverse sections of apices of *A. arvensis* shoots growing on various kinds of media and exhibiting different phyllotactic patterns (experiment A, nine weeks of culture). Labelling of whorled primordia as in Fig. 10. Spirally arranged primordia are numbered in order of their initiation. Bars = 100 μ m.
 Fig. 14. A shoot apex with decussate phyllotaxis (control).
 Fig. 15. A tricussate pattern (MS + 0.05 mg dm⁻³ BA).
 Fig. 16. Shoot apex exhibiting spiral Fibonacci phyllotaxis (MS + 0.05 mg dm⁻³ BA).

Fig. 17. Experiment A: percentages of teratologic axes and of shoots exhibiting various phyllotactic patterns plotted against the BA concentration in the medium (nine weeks of culture).

Fig. 18. Experiment B: percentages of teratologic axes and of shoots exhibiting various phyllotactic patterns plotted against the BA concentration in the medium (12 weeks of culture, mean values of two repetitions).

phorbia lathyris initially decussate phyllotaxis of shoots sprayed with the same growth regulator changes into bijugate (helical leaf arrangement with two leaves per node) or whorled patterns with the number of leaves per whorl higher than two (Mingo-Castel et al. 1984). Apparently then a normally initiated shoot apical meristem of *A. arvensis*, although spontaneously changing its phyllotaxis in intact plants, is relatively resistant to exogenous BA. A similar situation is known for *Lupinus albus* where no changes in phyllotaxis were observed after the treatment with kinetin (Varnell and Vasil 1978).

We postulate that the differences in phyllotaxis and in the BA effect on adventitious and axillary shoots result from various modes of their formation. First of all, adventitious shoots develop de novo from initially unorganised meristematic centres, which may possibly differ in size. Thus the phyllotactic pattern generated by an apex which is just "self-organising" and of variable dimensions, can as a rule be unstable and nondecussate, regardless of the BA treatment. Also, the arrangement of the first leaf primordia initiated is affected neither by a supporting leaf as it is in the case of prophylls, nor by an already organised primary vasculature, which is sometimes postulated to play an important role in a mechanism of phyllotaxis (Larson 1977). A significance of

the lack of these two factors is manifested by the high percentage of nondecussate and teratologic adventitious axes formed also on control explants. Secondly, adventitious shoot meristems being de novo organised are responding to BA treatment. The addition of BA to the growth medium somehow facilitates the normal development (a decrease in the percentage of teratologic shoots), but a gradual increase in both nondecussate and teratologic shoot percentages accompanies an increase in BA doses. In contrast, apical meristems of axillary axes are well organised structures from the moment of their initiation. This is presumably the reason for their stable and uniform phyllotaxis as well as for their resistance to BA.

The direct regeneration of adventitious shoots from epidermal or subepidermal cell layers of cytokinin treated stem explants of *A. arvensis* was described already by Bajaj and Mäder (1974), and what we observed generally concurs with their description. A similar process was reported for other species, e.g. *Linum usitatissimum* (Link and Eggers 1946), *Begonia rex* (Chlyah and Tran Thanh Van 1975), or *Muscari botryoides* (Kromer and Kukulczanka 1992). However, in the majority of these investigations, virtually no attention was paid to phyllotaxis. One of few exceptions is the study of *Nautilocalyx lynchii* (Venverloo et al. 1983). Although its adventitious shoots not necessarily exhibit decussate leaf arrangement from the beginning of ontogeny, their phyllotaxis always finally changes into the decussate pattern typical of this species. In *A. arvensis* nondecussate phyllotaxis of a low number of adventitious shoots also changes into decussate, but the number of shoots in which either tricussate or spiral Fibonacci pattern persists, is higher. Since both Fibonacci and tricussate patterns are relatively common in potted *A. arvensis* (Kwiatkowska 1995, 1997a), it seems to be a rule that non-teratologic in vitro shoots of this species attain one of phyllotactic patterns typical for intact plants.

Low contact parastichy numbers and the apical dome small in comparison with leaf primordia may account for the fact that no pseudowhorls are formed on cultured in vitro *A. arvensis* shoots with spiral phyllotaxis. Pseudowhorls are groups of successively initiated leaves between which no internodes develop. Adjacent groups are separated with full length internodes. Formation of pseudowhorls is typical for all the shoots of potted *A. arvensis* plants exhibiting spiral phyllotactic patterns (Kwiatkowska 1997a). The number of leaves forming a pseudowhorl has been shown to be closely related to the number of leaf primordia packed around the apical dome (Kwiatkowska 1999). In spiral meristems of in vitro cultured *A. arvensis* the youngest leaf primordium is so large in comparison with the apical dome that there is enough space for only a single primordium at a given level.

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FILOTAKSJA WEGETATYWNYCH PĘDÓW *ANAGALLIS ARVENSIS* L.
TRAKTOWANYCH IN VITRO 6-BENZYLAMINOPURYNĄ

STRESZCZENIE

Dodatek syntetycznej cytokininy, 6-benzylaminopuryny (BA), do pożywki w kulturze in vitro stymuluje tworzenie pędów przybyszowych na eksplantatach pędowych *Anagallis arvensis*. Pędy przybyszowe powstają na skutek odróżnicowania a następnie peryklinalnych i antyklinalnych podziałów komórek epidermy. Liczba regenerujących pędów wzrasta wraz z rosnącym stężeniem BA w pożywce. BA ma również wpływ na filotaksję przede wszystkim pędów przybyszowych i w znacznie mniejszym stopniu pędów bocznych, rozwijających się w sposób typowy w pachwinach liści. Ponadto, filotaksja pędów przybyszowych jest zmienna nawet na pożywce kontrolnej. Generalnie jednak wzory ulistnienia występujące na pędach rosnących w warunkach in vitro są takie same jak te, które opisano wcześniej dla roślin *A. arvensis* hodowanych w doniczkach. BA powoduje również tworzenie form teratologicznych, jak fascjacje i liście o nietypowych kształtach, znowu jednak dotyczy to przede wszystkim pędów przybyszowych. Autorki postulują, że zmienność filotaksji pędów przybyszowych i ich podatność na działanie BA, wynika z faktu, że ich merystemy apikalne tworzone są de novo z początkowo nieorganizowanych centrów merystematycznych, podczas gdy merystemy normalnie rozwijających się pędów bocznych są zorganizowanymi strukturami już w momencie ich inicjacji.

SŁOWA KLUCZOWE: *Anagallis arvensis*, filotaksja, kultura in vitro, BA, pędy przybyszowe i boczne.