ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. XLVII, nr 3
1978

Auxin and plant morphogenesis — a model of regulation

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(Received: April 13, 1978)

Abstract

In the presented model cells of the plant body form a spatial medium in which three-dimensional morphogenic waves of auxin are propagated. Points in the same phase of oscillation form isophasic surfaces and the vectors of wave propagation form a three-dimensional vector field. The vectors in the case of local inhomogeneities of the medium deviate from organ polarity, providing positional information recognized by cells. Models of functioning of such a supracellular oscillatory system in regulation of tissue differentiation, tropic responses and plant form are discussed.

INTRODUCTION

The amount of auxin efflux to agar from a series of successive short sections of stem segments including the cambial region of large trees (*Pinus silvestris* L.) oscillates forming a wave-like pattern (Zajączkowski, Wodzicki 1978). The observed pattern has been discussed as a two-dimensional moving wave in which the tangentially neighbouring cells are in the same phase of oscillation. It has been postulated that the cambial cells recognize the direction of the vectors of wave propagation and by localized growth and asymmetric divisions adjust their possition to these directions. Basic principles of a model of regulation of plant morphogenesis by such a system, taking into account the effects of three-dimensional auxin waves are proposed in this article.

MODEL

1. The three-dimensional wave

Auxin basipetal transport in tree stems takes place mainly in the cambial region. Some auxin transport also occurs in differentiating xylem and phloem (Nix and Wodzicki 1974). Cells of all these tissues form a spatial medium in which the earlier observed waves of auxin (Zajączkowski, Wodzicki 1978) should be considered in a three-dimensional aspect. In such three-dimensional waves, points in the same phase of oscillation form surfaces of equal phases. If the wave passes along tissue consisting of structurally different cells, the isophasic surfaces must be bent. The boundary effects produce additional bending at the margins of the tissues in which auxin is translocated. If we assume that these effects on both sides of the cambium are not identical, the theoretical wave fronts in radial stem sections must follow curved lines as in the model presented in Fig. 1 A-C. The vectors of wave propagation are always orthogonal to surfaces of equal phase and in this model there is only one envelope in the whole stem (in the layer of cambial initials) in which the vectors seen in radial stem section form continuous lines. Boundary effects produce an increasing shift of the wave phase with increasing distance from the cambium (increasing angle between the cambial envelope and the vectors of wave propagation). This is substantiated by experiments in which 60×20×5 mm blocks of pine stem tissues (comprising phloem, cambial zone, and 2 mm of xylem) were divided in to 5 mm sections for investigation of natural auxin efflux to agar (as described by Zajączkowski, Wodzicki 1978). Immediately after cutting, the sections were separated into the phloem and xylem sides, and placed with their basal ends on agar plates for 15 minutes. The results of bioassays (Fig. 2 A-C) revealed differences in wave phases between the two types of tissues. In the earliest performed experiment (Fig. 2 A) the waves were intermittently synchronous and asynchronized progressing from the basal end. This result as illustrated by the model (Fig. 2 D, E) suggests a possibility of oscillation of the direction of vectors of wave propagation and that the amplitude of the oscillation decreases with the distance from the cambium.

2. Regulation

Divergence of the vectors of wave propagation from the direction of major polar transport of auxin in the organ seems to play an important role in the system regulating morphogenesis of the plant.

a) Tissue

The mechanism of such control at the tissue level may be discussed using the example of some morphogenic processes involved in secondary xylem differentiation. It is seen (Fig. 3 A) that the greatest divergence of the vector of wave propagation from the zones of major polar transport — in this case, the cambial envelope — is reached at the boundary of maturing and mature xylem. At this site an envelope of autolysing axial tracheids forms. It is possible that breakdown of vacuolar membranes, which initiates the processes of autolysis (Wodzicki, Brown 1973), occurs at some critical angle of vector divergence from the cambial envelope. The same critical angles may be attained at different distances from the cambium depending on the shape of the isophasic surfaces of the wave (Fig. 3 B, C). This could explain seasonal variation of the width of the zone of maturing xylem (Wodzicki 1971).

As new xylem cells are produced, the position of already differentiating cells become more distant from the cambium and the whole vector field adjust to the changing position of the cambial envelope. It is possible that earlier stages of differentiation of axial tracheids are under the control of vectors of auxin wave propagation.

The effect of the diverging vectors of auxin wave propagation may be to control the helical orientation of cellulose fibrils in the secondary wall with respect to the cell axis. Sudden changes of orientation of microfibrils in the successive cell wall layers S_1, S_2, S_3 (Frey-Wyssling 1959; Wardrop 1964a) may result from the increasing structural complexity of the cellular medium in which the wave is propagated. In the case of nonhomogeneity of the medium local refraction of the vectors may be expected. For example, such refractions probably occur at the cytoplasm cell wall interface. Circular deposition of fibrils in the secondary wall, which occurs when bordered pits are formed around primary pit-fields permeated by plasmodesmata (Liese 1965; Schmid 1965), may be a manifestation of local turbulence of the vectors of wave propagation.

Involvement of the vectors of auxin wave propagation in morphogenesis, also allows an explanation of the initiation of vessel members, which in the secondary structure of Angiosperms form systems of continuous vessels over long distances. The diffusion-reaction theory of Turing (1952) was invoked by Wardlaw (1965) to explain the control mechanism determining vascular bundles initiation. The elegant experiments of Wetmore and Sorokin (1955) and Wetmore and Rier (1963) in which xylem differentiation was induced in tissue culture, seem to provide evidence of such regulation. However, according to Crick (1970, 1971), the diffusion control system cannot operate at distances greater than a few millimeters. Our proposal of control by vectors of auxin wave propagation overcomes this limitation. Assuming that in the system proposed by Turing some inhomogeneities occur (e.g. changes in the amplitude of auxin wave fronts) then those inhomogeneities may be propagated together with the wave fronts and may operate as a control mechanism over long distances. By the same mechanism the pattern of tissue differentiation initiated below the apical meristems (as discussed by Romberger 1963) may be propagated along the organ axis.

PLATE I

Fig. 1. Theoretical distribution of auxin wave fronts (thick solid lines) and vectors of wave propagation in the stem secondary structure. Three-dimensional drawing of stem segment (A), and small piece of tissue at greater magnification (B), and radial view (C). Small arrows — vectors of wave propagation in the cambial envelope. Trajectories orthogonal to auxin wave fronts as seen in the radial cross-sections represent change of angles between the cambial envelope and the vectors of auxin wave propagation at various distances from cambium.

Fig. 2. Natural auxin efflux from xylem (solid lines) and phloem (dotted lines) sides of successive (about 5 mm long) sections cut from 60-mm stem blocks collected on September 16 — (A), September 23 — (B), and September 30 — (C). Three-dimensional model of amplitudes and wave fronts illustrating the experimental results — (D). Theoretical distribution of wave fronts (thick solid lines) and vectors of wave propagation (small arrows) — (E); in case of moving waves the pattern is translocated along the stem

Fig. 3. Initiation of final phase of axial tracheids maturation (autolysis) in stem secondary xylem — the model of control by vectors of auxin wave propagation. A — inclination of the vectors of auxin wave propagation (a) in the cambial region and differentiating secondary tissues as seen in radial (b) and transverse (c) cross section. The breakdown of cytoplasm occurs at some critical angle (α) between the vector of auxin wave propagation and cell axis. (B) and (C) — model of regulation of early- and latewood formation. Ph_C — conducting phloem; Ph_D — dividing phloem; C_I — cambial initial; X_D — dividing xylem; X_G — enlarging xylem; X_M — maturing xylem; X_T — mature xylem tracheids (according to Wilson et al. 1966), Ph_R — phloem ray; X_R — xylem ray.

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b) Plant body

The postulated ability of cells to recognize the direction of auxin wave propagation and cell adjustment to wave vectors may provide a basis for control of tropisms and coordinated plant growth.

It should be noted that the polarity of each organ and the vectors of auxin wave propagation are parallel to the zones of major polar transport of auxin. In this concept the organ axis is close to that of its polarity (Fig. 4). In an ideal case these two axes coincide and the isophasic surfaces of auxin wave propagation are locally perpendicular to them. It is suggested that in an organ exposed to unilateral illumination, gravity, or mechanical force etc. the vectors of wave propagation deviate from the axis of organ polarity. This produces asymmetric growth bringing the organ to a position in which the vectors again coincide with organ polarity. Fig. 4 illustrates this type of regulation in the case of phototropic and geotropic responses. All known mechanisms of tropic responses proposed by various authors may be considered as operating by deviation of the vectors of auxin wave propagation depending upon the kind of stimulus and organ (or tissue) involved.

PLATE I

FIG. 1

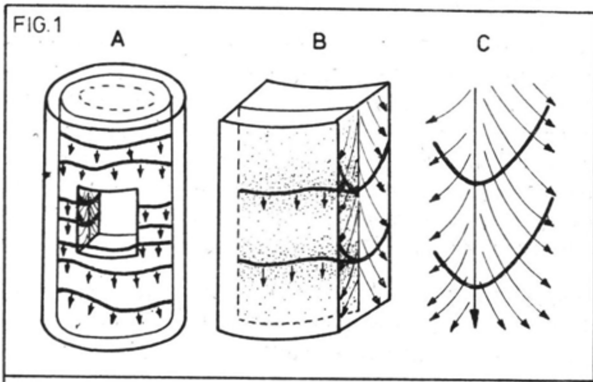


FIG. 2

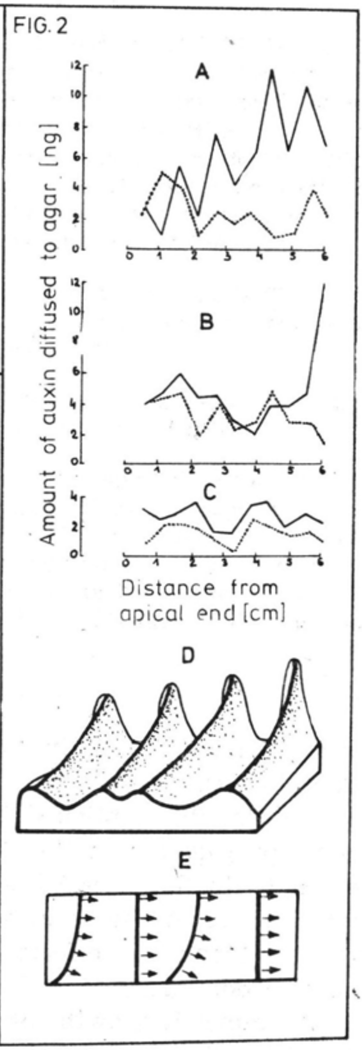
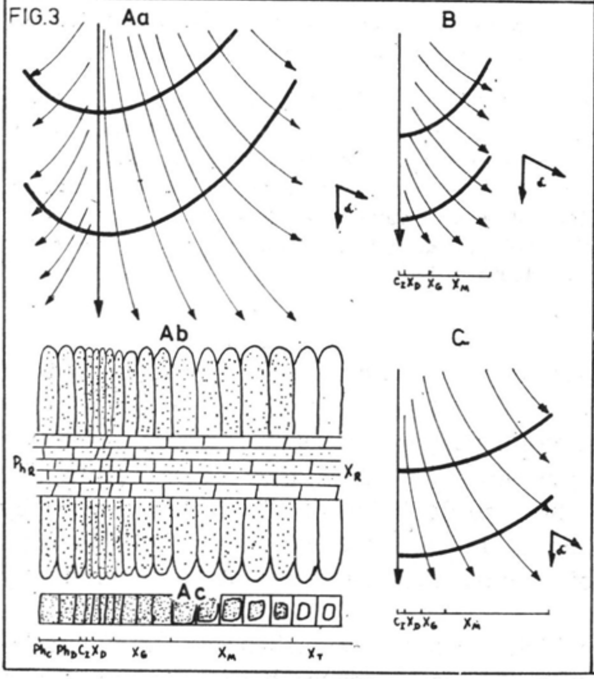


FIG. 3



There is voluminous literature concerning the role of auxin in the control of plant branching and apical dominance. The fronts of auxin waves interfere at nodes (or branching regions) which results in a difference between the wave-lengths at the two sides of the forks. Thus, surfaces with equal phases of waves (and vectors of wave propagation) in both axes are resultants of this interference as in the simplified model presented in Fig. 5 A. Elastic coupling of the waves results in propagation of these deviations along the organ axes in a direction opposite to that of auxin active transport, decreasing gradually owing to a dumping effect. Equal deviating effects in both axes produce dichotomy (Fig. 5 B). Domination of the deviating effects of one axis results in other types of branching which in extreme cases may completely inhibit the propaga-

PLATE II

Fig. 4—7. Models of regulation of plant morphogenesis by vectors of auxin wave propagation (small arrows). Broken lines are theoretical tangentials to isophasic surfaces of auxin waves in the zones of major polar transport of auxin in the organs, prior to any adjustment arising from interference of wave fronts or/and effects of other stimuli. Dotted lines are theoretical tangentials to isophasic surfaces in the organs, but still before the organs have adjusted themselves to new vectors of wave propagation. Dot-and-dash lines are theoretical tangentials to isophasic adjusted themselves to new vectors of wave propagation.

Fig. 4. Tropic responses in the regions of apical meristems. A — shoot phototropism, B — root geotropism; organs before morphogenic response (a) and after adjustment (b). Long arrows — vectors of stimuli.

Fig. 5. Effect of interaction of auxin wave fronts between two organs at branching region. Domination of main stem (A), and codomination (B).

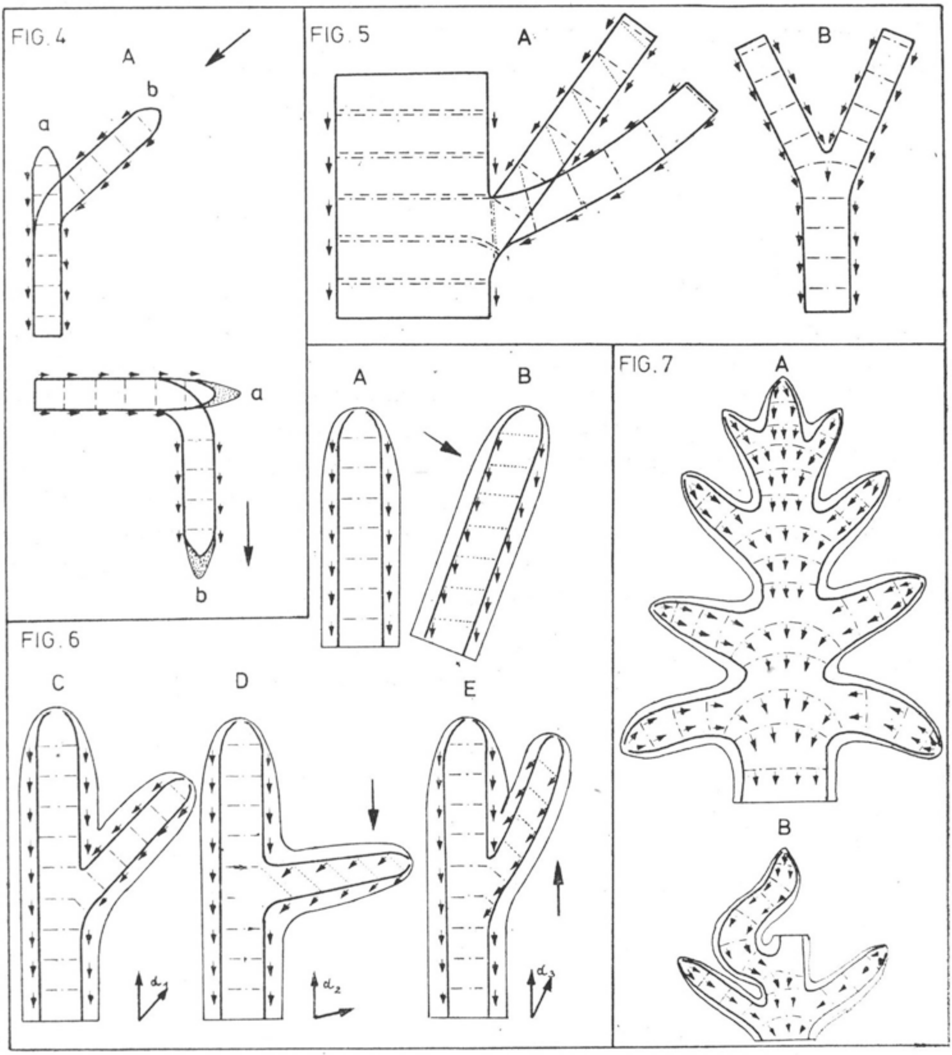
Fig. 6. Geotropic responses in the cambial region of the main shoot (A, B), and lateral branch (C, D, E). Organs adjusted to geotropic stimulus and each other (A, C) — no reaction wood is formed; organs displaced from their adjusted (neutral) position (B, D, E) — reaction wood forms. Long arrows-direction of displacement.
Fig. 7. Theoretical field of vectors of auxin wave propagation in aerial part of a plant with continuous cambial envelope. Main stem intact (A) and regenerated after decapitation (B).

tion of auxin waves in the lateral axes and result in suppression of lateral buds.

As already mentioned in previous paragraphs, the vectors of auxin wave propagation in the organs are also affected by other agents. For example, in the lateral branches the deviation of the vectors caused by interference of the main stem decreases with increasing distance from the node and the effects of gravity and moments of force gradually become dominant.

Asymmetric growth (by which the above described system of regulation involving vectors of wave functions) occurs both in primary and secondary structures. Young plant organs accomodate themselves to deviating vectors by unequal rates of cell division and/or cell extension growth of tissues on opposite sides of the organ. Parts of organs with secondary structure usually adjust the organ position by localized formation of reaction wood (Wardrop 1964b, 1965). The latter case is briefly discussed in the model of compression-wood formation in Gymnosperms (Fig. 6). Inclination of the main stem from the vertical position induces deviation of the vectors of auxin wave propagation toward the direction of gravity extending outside the cambial envelope on the lower side of the stem, which induces compression wood formation. In the lateral branches the vectors of auxin wave propagation always deviate by some characteristic angle from the direction of gravity owing to the

PLATE II



deflecting effect of waves in the main stem, and reaction wood does not form. The increase of this angle (e.g. by branch weight) results in deviating extension of vectors outside the cambial envelope on the lower side of the branch, inducing compression wood. If the branch is bent upward, the deviation of the vectors outside the cambial envelope occurs on the upper side of the branch, where in this case compression wood is formed. This mechanism of recognition of organ position with respect both to gravity and to other plant organs, may function as a biological pendulum although operating on a principle different from that of the micropendulum-statolith concept described by Larsen (1957, 1959). Coordinated growth of various plant parts, which determines the final form of the plant body, is regulated by vectors of propagation of the system of auxin waves in all axes. This vector field tends toward a state of least energy, a simple example of which is illustrated in Fig. 7 A. An analogous model explaining a case of restoration of the main stem, as is sometimes observed in decapitated young trees, is seen in Fig. 7 B.

CONCLUDING REMARKS

Three-dimensional morphogenic waves are formed in cellular media probably owing to synchronization of oscillatory processes originating in individual cells, and their regulatory functioning may require some minimum mass of tissue. This minimum mass requirement for cell differentiation seems to be manifested in tissue cultures (Steward et al. 1958). Spatial relationships involving tensile and compressive forces resulting from mutual cell growth may modify the direction of vectors of morphogenic waves and induce specific differentiation of cells. Experiments, in which externally applied pressure stimulated differentiation of vascular tissues (Brown 1964), support this hypothesis.

Oscillatory processes in cells to which the formation of auxin waves can be related have been but little studied in this aspect. Some authors correlated waves of auxin basipetal transport with the direction and velocity of movement of electric potential differences in the tissue (Newman 1963; Goldsmith 1967; Hertel and Flory 1968). Furthermore several authors measured the effect of auxin upon H^+ — ion transport across the cell membranes (Polevoy 1972; Cleland 1975; Marrè 1977). Maybe some system of feedback inhibition operates at this level. Some support of this concept seems to be provided by experiments in which the effects of electromagnetic fields upon cell differentiation were demonstrated (Dunlop and Schmidt 1964, 1965, 1969). This interesting question is open for further studies. However, no matter what kind of specific mechanisms cooperate in auxin wave formation, the fact of their coupling to basipetal polar transport of this hormone allows the above described system of regulation to function.

The roles of various growth regulators (such as abscisic acid, gibberellins, and cytokinins) in apical dominance, tropic reactions, and tissue differentiation are seen in the proposed model of plant morphogenesis primarily by the effects of these regulators upon auxin waves propagation. All these substances, irrespective of their specific function, are known to affect at least auxin polar transport (Goldsmith 1969; Thimann 1972). Thus, the exceptional position of auxin among all other growth regulators is attributed to its polar transport as discussed earlier by Leopold (1961) and Thimann (1972).

Our suggested mechanism of regulation of plant morphogenesis introduces a principle of morphogenic wave propagation similar to that proposed previously by Goodwin and Cohen (1969) and Hejnowicz (1975). In the Goodwin-Cohen model the positional information is determined by a phase shift between morphogenic waves of different velocities. In Hejnowicz's model the changing phases of oscillations within the morphogenic map give topographic information. The difference between these models and the mechanism of regulation proposed here is that positional information is ascribed to vectors of morphogenic wave propagation and that the deflection of these vectors from the axes of polarity of biological units is recognized by the responding cells. Such a system forms a three-dimensional vector field which behaves similarly to other physical fields (discussed by Feynman et al. 1964); in the case of local space inhomogeneities such field may exhibit local turbulences and aberrations capable of influencing growth and differentiation processes bringing to reality genetically programmed morphological patterns.

Acknowledgments

This work was supported in part by a grant from the U.S. Department of Agriculture (No. FG-Po 317).

The authors are indebted to Mrs. Alina B. Wodzicki for her generous cooperation in doing experiments. Special thanks the authors owe to Dr. John A. Romberger for critical reading of the paper before submission to the journal.

BIBLIOGRAPHY

Brown C. L., 1964. The influence of external pressure on the differentiation of cells and tissues cultured in vitro. [In:] The Formation of Wood in Forest Trees (ed. M. H. Zimmermann) pp. 389-404. Academic Press, New York.

Cleland R. E., 1975. Auxin-induced hydrogen ion excretion: correlation with growth, and control by external pH and water stress, Planta 127: 233-242.

Crick F. H. C., 1970. Diffusion in embryogenesis, Nature Lond. 225: 420-422.

Crick F. H. C., 1971. The scale of pattern formation. — In Control Mechanisms of Growth and Differentiation (Symposia of the Society for Experimental Biology vol. 25) pp. 429-438. University Press, Cambridge.

Dunlop D. W., Schmidt B. L., 1964. Biomagnetics. I. Anomalous development of the root of *Narcissus tazetta* L., Phytomorphology 14: 333-342.

Dunlop D. W., Schmidt B. L., 1965. Biomagnetics. II. Anomalies found in the root of *Allium cepa* L., Phytomorphology 15: 400-414.

Dunlop D. W., Schmidt B. L., 1969. Sensitivity of some plant material to magnetic fields. [In:] Biological Effects of Magnetic Fields (ed. M. F. Barnothy) pp. 147-170. New York: Plenum Press.

Feynman R. P., Leighton R. B., Sands M., 1964. The Feynman Lectures on Physics. Vol. II. Chapter: The "underlying unity" of nature. Addison-Wesley Publishing Co. Inc., Reading, Mass.

Frey-Wyssling A., 1959. Die Pflanzliche Zellwand. Springer-Verlag, Berlin, Göttingen, Heidelberg.

Goldsmith M. H. M., 1967. Movement of pulses of labelled auxin in corn coleoptiles, Plant Physiol. 42: 258-263.

Goldsmith M. H. M., 1969. Transport of plant growth regulators. [In:] Physiology of Plant Growth and Development. (ed. M. B. Wilkins) pp. 127-162. McGraw-Hill, London.

Goodwin B. C., Cohen M. H., 1969. A phase-shift model for the spatial and temporal organization of developing systems, J. Theor. Biol. 25: 49-107.

Hejnowicz Z., 1975. A model for morphogenetic map and clock, J. Theor. Biol. 54: 345-362.

Hertel R., Flory R., 1968. Auxin movement in corn coleoptiles, Planta 82: 123-144.

Larsen P., 1957. The development of geotropic and spontaneous curvatures in roots, Physiol. Plant. 10: 127-163.

Larsen P., 1959. The physical phase of gravitational stimulation. Abstr. 9th Internat. Bot. Congr. Montreal, 2: 216.

Leopold A. C., 1961. The transport of auxin. [In:] Encyclopedia of Plant Physiology (ed. W. Ruhland) vol. XIV pp. 671-682. Springer-Verlag, Berlin, Göttingen, Heidelberg.

Liese W., 1965. The fine structure of bordered pits in softwoods. [In:] Cellular Ultrastructure of Woody Plants (ed. W. A. Côté) pp. 271-290. Syracuse University Press.

Marrè E., 1977. Effects of fusicoccin and hormones on plant cell membrane activities: observations and hypothesis. [In:] Regulation of Cell Membrane Activities in Plants (eds. E. Marrè and O. Ciferri) pp 185-202, Elsevier North--Holland Biomedical Press, Amsterdam.

Newman I. A., 1963. Electric potential and auxin translocation in *Avena*, Aust. J. Biol. Sci. 16: 629-649.

Nix L. E., Wodzicki T. J., 1974. The radial distribution and metabolism of IAA — ^{14}C in *Pinus echinata* stems in relation to wood formation. Canad. J. Bot. 52: 1349-1355.

Polevoy V. V., 1972. Physiology and biochemistry of auxin action on the growth of plant cells (in Russian). In Mekhanyzmy Reghulyatornykh Processov, Trudy peterghofskogho byologhicheskogho instituta No. 21, pp. 191-207, Izdatyelstvo Leningradskogho Universiteta.

Romberger J. A., 1963. Meristems, growth, and development in woody plants. Technical Bulletin No. 1293. U.S. Department of Agriculture, Forest Service.

Schmid R., 1965. The fine structure of pits in hardwoods. [In:] Cellular Ultrastructure of Woody Plants (ed. W. A. Côté) pp. 291-304. Syracuse University Press.

Steward F. C., Mapes M. O., Mears K., 1958. Growth and organized development of cultured cells. II. Organization in cultures grown from freely suspended cells. Am. J. Bot. 45: 705-708.

Thimann K. V., 1972. The natural plant hormones. [In:] Plant Physiology, A Treatise (ed. F. C. Steward) Vol. VI B pp. 3-332.

Turing A. M., 1952. The chemical basis of morphogenesis. Philos. Trans. Roy. Soc. B 237: 37-72.

Wardlaw C. W., 1965. Organization and evolution in plants. Longmans, Green and Co LTD. London.

Wardrop A. B., 1964a. The structure and formation of the cell wall in xylem. [In:] The Formation of Wood in Forest Trees (ed. M. H. Zimmermann) pp. 87-134. Academic Press, New York.

Wardrop A. B., 1964b. The reaction anatomy of arborescent angiosperms. [In:] The Formation of Wood in Forest Trees (ed. M. H. Zimmermann) pp. 405-456. Academic Press, New York.

Wardrop A. B., 1965. The formation and function of reaction wood. [In:] Cellular Ultrastructure of Woody Plants (ed. W. A. Côté) pp. 371-390. Syracuse University Press.

Wetmore R. H., Rier J. P., 1963. Experimental induction of vascular tissues in callus of angiosperms. Amer. J. Bot. 50: 418-430.

Wetmore R. H., Sorokin S., 1955. On the differentiation of xylem. J. Arnold Arboretum, Harvard Univ. 36: 305-317.

Wilson B. F., Wodzicki T. J., Zahner R., 1966. Differentiation of cambial derivatives: proposed terminology. Forest. Sci. 12: 438-440.

Wodzicki T. J., 1971. Mechanism of xylem differentiation in *Pinus silvestris* L. J. Exp. Bot. 22: 670-686.

Wodzicki T. J., Brown C. L., 1973. Organization and breakdown of the protoplast during maturation of pine tracheids, Amer. J. Bot. 60: 631-640.

Zajączkowski S., Wodzicki T. J., 1978. On the question of stem polarity with respect to auxin transport, Physiol. Plant. 44: 122-126.

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Auksyna a morfogeneza drewna — model regulacji

Streszczenie

W pracy przedstawiono teoretyczny model mechanizmu hormonalnej regulacji morfogenezy roślin, w którym decydującą rolę spełnia oscylacyjno-falowy charakter polarnego transportu auksyny.

Na podstawie badań własnych i danych z literatury zaproponowano, że fala auksyny przemieszcza się w trójwymiarowej przestrzeni tkankowej ciała rośliny. Punkty znajdujące się w tej samej fazie oscylacji tworzą powierzchnie izofazowe, a prostopadłe do nich wektory propagacji fal trójwymiarowe pole wektorowe. Komórki posiadają zdolność rozpoznawania wektorów i reagowania procesami wzrostowymi na zmiany pola wektorowego związanego z transportem auksyny. W warunkach lokalnych niejednorodności środowiska tkankowego następuje ugięcie frontów fal i wektorów propagacji stwarzając w ten sposób „informację pozycyjną" rozpoznawaną przez komórki.

Opracowany model wyjaśnia, w jaki sposób zjawiska oscylacyjno-falowe związane z transportem auksyny mogą być odpowiedzialne za regulację funkcjonalnego różnicowania tkanek, kierunkowego wzrostu organów oraz koordynację procesów wzrostowych na poziomie organizmu. Nadrzędną rolę w omawianym mechanizmie spełniają tkanki regionów merystematycznych roślin. Rola innych regulatorów wzrostu rozpatrywana jest w aspekcie ich modulującego działania na polarny transport auksyny.