INTRODUCTION

Speaking of an organism as a whole, we imply that it is an integral system. The integrity of the organism is the capacity of its parts to coordinate their functions in the course of individual development and when interacting with the environment. The attribute of integrity was improved over the course of biological evolution, and the progress in the differentiation of organisms (the specialization of their parts) occurs in parallel with the elaboration of the unifying systems providing for the integrity.

Some people believe that higher plants are less differentiated than animals and plant parts possess considerable autonomy. This is not quite true. None of the isolated plant organs can persist for a long time if they do not regenerate the missing parts of the whole organism.

In higher plants, there are up to 80 specialized cell types, tens of particular tissues, 15 to 25 organs, and 11 systems providing such functions as aerial nutrition (mostly leaves), soil nutrition (roots), respiration, long-distance transport, excretion, plant movement and support, vegetative and sexual propagation, defense, and hormonal and electrophysiological regulation [1]. All these parts and functional systems in the whole plant organism switch over interactively in the course of successive phases and stages of plant ontogeny and contribute to plant adaptation to changing environmental conditions.

M. Kh. Chailakhyan specially emphasized the importance of the problem of integrity. In his monograph Tselostnost’ rasitel’nogo organisma (The Integrity of Plant Organism) published in 1955, Chailakhyan was the first to unravel this fundamental issue of general biology as applied to higher plants. In this book [2], in the papers to succeed this book [3, 4], and in his summarizing monograph Regulyatsiya tsveteniya vysshikh rastenii (Regulation of Flowering in Higher Plants) [5], particularly in the chapter on integrity in plant development, Chailakhyan listed several phenomena related to plant integrity: anatomical and morphological entirety.
polarity, trophic and hormonal interactions among plant parts, and excitability. The latter is the ability of an organism as a whole to efficiently respond to external and internal stimuli. Referring to Ivanovskii [6], Chailakhyan enumerated four successive phases of excitability: (1) the recognition of the external stimulus by a receptor organ, (2) the development of specific metabolites, (3) the translocation of these metabolites to other organs, and (4) the physiological and morphological responses of these organs [5]. As early as 1956 [3] Chailakhyan proclaimed that organ interaction in the course of plant growth and development employs these four phases of excitability. In their numerous and conclusive experiments, Chailakhyan and his associates demonstrated that an adequate photoperiod is recognized by the leaves, where a specific hormonal signal is synthesized; the signal is transported to shoot apical meristems and induces the flower development and the transition to reproduction [5]. Similar processes lead to tuber initiation on the stolon [7]. The experiments proved that sex differentiation in dioecious plants depends on the hormonal interaction of leaves and roots [8].

The studies by Schmalhausen [9] on the interaction of differentiation and integration processes, by Dostal [10] on organ correlations, by Sabinin [11, 12] and Kursanov [13, 14] on metabolic and trophic interactions between shoots and roots, by Gunar [15] and Opritov [16, 17] on plant excitability, and by Mokronosov [18, 19] on source–sink relations were instrumental for developing the concept of plant integrity. Chailakhyan wrote: “The notion of the organism as an integral whole is one of the major principles of studying living Nature. However thoroughly the researchers are engaged in the study of a particular aspect of structure and physiology and however deeply they are involved in unravelling the mysterious puzzles of life using such models as isolated organs, tissues, cells, protoplasts, and organelles, all scientists must invest their data and hypotheses into the integral pattern of the living organism” [5].

Yet the mechanisms of integration in plants have not been properly elucidated, and the general systematic theory of plant integrity has not been developed. In animals and humans, the coordinating activity of the neurohumoral system is the basic mechanism providing for their integrity, with the neural (electrophysiological) control coupled with the endocrine (hormonal) system playing the leading role.

This review attempts to be a concise description of the universal integration system in plants; the description is illustrated by the experimental data, which exemplify the regulatory controls operating in plants.

**BASIC CONCEPTS AND MECHANISMS OF PLANT INTEGRATION SYSTEM**

When unicellular organisms evolved, *intracellular control systems* developed, such as genic (the synthesis of proteins, enzymes in particular), metabolic (the control of enzyme activities), and membrane systems (barrier, transport, energy generating, receptor and other functions). As multicellular organisms evolved and differentiated, the mechanisms for the interactions among cells, tissues, and organs emerged and became more and more elaborated. These *intercellular control systems*, in the broadest sense of the term, include trophic, hormonal, and electrophysiological (local and propagating electric potentials) systems. Intracellular control systems are closely interactive. Similar interactions are found at the intercellular level, and the intracellular control systems are governed by the signals generated by the intercellular systems [1, 20–23].

The trophic interactions of plant tissues and organs have been studied in detail. They include the translocation of assimilates from the leaves into the heterotrophic tissues and organs and also the transport of water, mineral salts, and specific metabolites from the roots into the underground and aboveground shoots [12, 14, 19].

Plant hormonal regulation comprises the synthesis; transport; immobilization and release; degradation; the actions and interactions of such well-known phytohormones as auxin (IAA), cytokinins (zeatin, isopentenyladenine, and their derivatives), gibberellins, abscisins (ABA, etc.), ethylene; and other natural growth regulators, such as brassinosteroids, jasmonates (jasmonic acid and its derivatives), oligosaccharins, etc. [21, 24–26]. The organization of the hormonal control has not been studied systematically. In animals, such a system is built hierarchically, and with plants, a similar principle must hold.

IAA and cytokinins are apparently the major agents of the plant hormonal system. When plant tissues are cultured *in vitro*, no other phytohormones are usually added. IAA and cytokinins are produced in the centralized way, in the shoot and root apices, respectively. These hormones induce cell division, growth, and differentiation and switch on two major genetic programs: the development of shoots and roots [22, 27]. The positive feedback interactions of two phytohormones provide the progressive development of the whole plant. IAA induces the development of root initials, thus enhancing the cytokinin synthesis by the roots; in turn, due to the elevated level of cytokinins, new metameres are initiated in the shoot apex. We can, therefore, define these hormones as participants in the *central hormonal system*, with IAA playing the leading role. Unlike other phytohormones, IAA affects bioelectrogenesis [22, 28]: the hormone induces BEPs and MPs, brings about cell polarization, and moves in polar directions via the living cells of conducting bundles in the oscillating regime at the rate of 0.5–1.5 cm/h. The low rate of IAA movement is the bottleneck of the hormonal system; it is an additional proof of the principal role of this hormone. Meanwhile, other phytohormones, such as abscisins and ethylene, called stress hormones, are synthesized in all plant tissues and organs. Mutants deficient in ABA or ethylene do not manifest morphoge-
netic abnormalities under optimum conditions, but are unable to survive under extreme conditions. We therefore define such phytohormonal systems as adaptive.

The electrophysiological control system comprises BEP gradients and oscillations, as well as the propagating electric potentials (action potentials and variation potentials) [16, 17, 29–32]. Plants are usually devoid of the permanent centers that generate electric potentials, and the latter arise everywhere under stress conditions.

In animals, the electrophysiological and hormonal systems are in close interaction. Some evidence suggests that similar interactions can be found in plants as well. As already mentioned above, IAA generates slow bioelectric waves. The gradients of electric potentials affect IAA transport [33]. The electric potentials propagating from the sites of the local application of a stress agent have been shown to shift the hormonal balance in remote parts of the plant [34, 35]. The problem of the functional interaction of the hormonal and electrophysiological systems in plants has been posed, and vast experimentation will solve this problem.

The intracellular and intercellular control systems listed above establish the basis of the organism level of regulation and integration. In animals, it is the central nervous system, which functions to control and integrate all physiological systems for particular tasks. To consider the plant as an integral organism rather than a colony of cells, one must first answer the question as to whether or not plants comprise centralized control organs. Darwin was the first to suggest that such organs exist as exemplified by shoot and root apices [36].

In his experiments, Darwin demonstrated that shoot and root apices are sensory zones that specifically recognize the effects of environmental factors, such as light, gravitation, mechanical pressure, etc., and send the signals dominant the growth and movements in shoots and roots. This concept was lost in present-day plant physiology; however, in my opinion, it remains true. To support this concept, we may refer to the evidence of the specific hormonal signals generated in shoot and root apices, the well-known phenomenon of apical dominance, when the apical bud inhibits the development of auxiliary buds and the root apex represses the lateral root formation, as well as many other facts (see [1, 21–23]). The general cybernetic theory postulates that a special block to command and coordinate the activities of a complex differentiated system is necessary; in this context, the concept that shoot and root apices are such commanding organs seems persuading enough. We will further define these organs as the dominant (control) centers [1, 20–23].

The dominant center in the shoots of vegetating higher plants comprises the shoot apex, the initiating and developing leaves, buds, and internodes; the dominant center in root includes its apex, root cap, and the zones of growth and differentiation. Higher plants have two types of dominant centers, because they dwell simultaneously in two environments, that is, soil and atmosphere. Shoot movements (elongation, leaf unfolding, and tropisms) aim at the optimization of aerial nutrition, whereas root elongation and tropisms aid better water and nutrient absorption. Shoot and root apices are the first to encounter a new environmental situation. We can, therefore, compare the behavior of the distal root part to that of the head of an earthworm, the sensor and dominant center of its body.

Thus, the shoot and root dominant centers are the organs commanding the whole plant to accomplish its major strategic tasks: to develop all of its parts and to optimize its nutrition-using sensory mechanisms and efficient movement activity. These centers are the growing tissues of high and prolonged morphogenetic activities, which produce the specific hormones of local and distant action. The dominant centers manifest high attracting activities, that is, they are sinks for trophic factors and physiologically active compounds; they comprise the sensory zones and the receptors for phytohormones. By using the hormonal signals and competing for nutrients, the dominant centers produce diverse control effects on the functional activities of tissues and organs in the whole plant. Among the dominant centers, we find the apices of various vegetative shoots, the distal root parts, and the developing flowers, fruits, tubers, and taproots. The fact that there are the primary and auxiliary shoots with the apical buds of various orders and the primary and lateral roots with their apices implies the rigorous hierarchic interactions between the dominant centers of various orders. The mechanism of such interaction apparently involving hormonal, electrophysiological, and trophic factors has not been studied sufficiently, and we will discuss it in more detail in our next paper.

The existing evidence suggests that the integrating function of the dominant centers is accomplished by developing polarity, canalized connections, regulatory controls, and oscillations [1, 20–23]. At the level of the organism, polarity, that is, the biophysical, biochemical, and physiological gradients, is one of the ways towards integrity, because the polar changes affect the entire field. However, the addressed distribution of signals by canalized connections, that is, through such conducting tissues as phloem and xylem, originating in the shoot and root apical meristems, provides much more efficient integration. Via the conducting tissues, nutrients [14] and phytohormones [21, 26] are translocated and electric impulses propagated [16]. The polar IAA transport along the living phloem cells [37] is accomplished in an oscillating regime [38, 39] due to slow BEP waves [21, 32]. This apparently helps to synchronize the transport, metabolic, and morphogenetic
processes in the adjacent tissues. If this suggestion stands true, the IAA-dependent BEP oscillations should be seen as the plant pacemaker tool.

The regulatory controls [1, 20–23] highly essential for plant integrity consist of the following components: (1) the sensory zones, where the external signals are recognized by the receptor cell and transduced; (2) the tissues, which accomplish the long-distance transport of the endogenous signals (the communication channels); (3) the effector tissues and organs, which respond to these signals with efficient (adaptive) changes in the functional activities; and (4) the feedback mechanisms (Fig. 1).

As already mentioned, the shoot and root dominant centers comprise the greatest number of sensory zones. The shoot apex reacts to the gravitation field, light direction, and its spectrum. Thus, in the distal part of the etiolated maize seedling comprising the coleoptile, primary leaves, shoot apex, coleoptilar node, and intercalary mesocotyl meristem, the subepidermal coleoptile cells recognize the gravitation [40], the apical coleoptile cells recognize unilateral blue light [41], and the intercalary mesocotyl meristem [42] and leaf tissues [43] recognize R (Fig. 2). The root tip recognizes the gravitation, light, mechanical pressure, as well as the moisture and nutrient gradients [41].

Reception and transduction of the external signals by sensory cells leads to the generation of endogenous receptor signals, such as phytohormones and BEPs. The cells of conducting bundles translocate the endogenous signals. When the latter arrive at the effector cells, the signals are recognized and transduced into efficient functional responses. At all successive steps of this informational pathway of recognizing, transducing, and translating signals, the negative feedback loops must exist to correct the efficient adaptive responses, and, therefore, we may consider such a pathway as a regulatory control.

A similar model of the regulatory control can be extended to other parts of the plant organism comprising sensory zones different from the dominant centers. Like in animals, the sensory zones can be located in various regions of the plant. Thus, the leaves perceive the photoperiodic signals and translate this information to the central meristem of the shoot apices to induce flowering or to the distal part of stolons to initiate tuber formation [5].

This model of the regulatory control looks rather schematic, because relevant experimental evidence for plants is very scarce. In our laboratory, we attempted to study the regulatory control using as a model the photomorphogenetic processes that occur under the influence of R.

**PHOTOMORPHOGENESIS AS A MODEL OF THE REGULATORY CONTROL**

In etiolated maize seedlings, R is known to dramatically inhibit mesocotyl growth, which primarily depends on IAA transport from the coleoptile [44, 45]. Indeed, the content of free IAA in the mesocotyl growth zone (10 mm below the node) decreased following the R treatment [46, 47]. Interpretations of this phenomenon vary: some researchers believe that the phytochrome-mediated effect of R results in lower rates of IAA synthesis or transport [46], and another group has reported an increase in the conjugated IAA content in this zone [48].

For our study, we used three-day-old etiolated seedlings of maize (*Zea mays*) hybrid Moldavskii 215. The seedlings were grown on a 0.1-strong Knop solution at 26°C in complete darkness. The coleoptile, leaf, mesocotyl, and root of the three-day-old seedlings reached average lengths of 14 ± 0.5, 13 ± 0.5, 38 ± 2.0, and 69 ± 2.9 mm, respectively. Segments including the 5-mm-long basal part of the coleoptile with the primary leaves, the coleoptilar node, and the 5-mm-long upper (growing) part of mesocotyl were used in the experiments. Batches of 12 segments were held in the vertical position 2-mm-deep in solutions of IAA, kinetin, GA (each 1 mg/l), and their mixture; distilled water was the control treatment. All these operations were carried out under dim green light. R irradiation (640–690 nm, 34 J/(m² s)) was carried out at 26°C, while the untreated segments were kept in darkness at the same temperature. The lengths of the segments were assessed at the beginning of the experiment and following 5, 24, and 48 h, using a Microfot 5P01 device for reading microfilms (Russia), at 16× magnification. The experiments were replicated eight times. The figures present mean arithmetic values and their standard errors.

In darkness, the mesocotyl elongated much more rapidly than the coleoptile and leaf, whereas R inhibited twofold the mesocotyl growth without any significant effect on the growth of the coleoptile and leaf (Fig. 3). Within the following 19-h-interval, the mesocotyl growth under R also slowed down when compared to the dark control, while the growth of the coleoptile and
leaf enhanced. On the second day of the experiment, the leaf growth enhanced dramatically compared to the dark control.

When treated with IAA, the mesocotyl growth rate during the initial 5 h under R became as high as in darkness (Fig. 3), that is, IAA alleviated the inhibitory effect of R on the mesocotyl growth. We therefore conclude that R irradiation decreased the IAA content in the mesocotyl growth zone [49]. Within the initial 5 h, kinetin and GA did not considerably affect the mesocotyl growth under light and in darkness. The effect of the mixture of hormones depended mostly on the IAA component (the data are not shown). Previously, we demonstrated [50] that R did not affect the growth of the isolated mesocotyl segments within the 3-h-long exposure. These data corroborate the published evidence that relates to the R-induced inhibition of the mesocotyl growth to the inhibition of IAA transport from the coleoptile to the mesocotyl [45, 46].

To determine the contents of phytohormones in the organs of the three-day-old etiolated maize seedlings irradiated with R for 30 min and kept in darkness, we used the immunoenzyme method [51, 52] and the already published protocol for phytohormone extraction, purification, and fractionation [53, 54]. Gibberelin activity was evaluated as GA equivalents using a highly sensitive biotest (the growth of the maize seedling leaf base). The contents of free IAA, zeatin + zeatin riboside, and ABA and their alcohol-soluble conjugates were assayed in the coleoptile, leaf, coleoptilar node, mesocotyl (10 mm below the node), and root (10-mm-long distal end). After R irradiation for 30 min, the contents of free IAA, zeatin + zeatin riboside, gibberellins, and ABA in the coleoptilar node considerably decreased (by 36, 38, 39, and 25%, respectively). Meanwhile, the contents of free IAA, zeatin + zeatin riboside, and gibberellins in the coleoptile increased by 32, 40, and 61%, respectively (Fig. 4). In contrast, the contents of alcohol-soluble IAA conjugates did not change in the coleoptilar node and slightly increased in the coleoptile by 29% (data not shown). These data support the idea that R inhibited IAA transport from the coleoptile to the node. In addition to IAA, R decreased the content of other phytohormones in the node. It is noteworthy that R evoked a dramatic increase in the content of free gibberellins (by 165%) in the leaves and roots [54].

Apart from the phytohormone analysis, we followed the R effects on BEP in the coleoptilar node and adjoining zone (1 mm) of the mesocotyl intercalary meristem.
measures with EVL-1MZ extracellular silver chloride electrodes (Russia) coupled to a pH-340 direct-current amplifier using the techniques described previously [55]. The segments were held in the vertical positions, with their apical ends upward. The whole segment before the experiment (for one hour) and its basal end during the experiment were kept in 0.1 mM CaCl₂ solution. The segments were prepared and mounted, and BEPs were measured initially (during the first hour of the experiment) under dim green light. Irradiation with R induced dramatic electronegative changes in the node region comprising the intercalary meristem. Then, two minutes later, an electropositive BEP wave developed and reached its maximum at the 35th minute (Fig. 5). Our previous experiments showed that R did not produce an electrophysiological response in the middle part of the coleoptile [32]. We, therefore, interpret the oscillations in the potential difference shown in Fig. 5 as the BEP changes in the node with the adjacent mesocotyl intercalary meristem. These data and the previously published evidence [56] led us to the conclusion that R generates an electropositive BEP wave in the zone of the coleoptilar node and the adjoining tissues.

The next series of experiments focused on the effects of an externally applied potential difference on the mesocotyl growth in the three-day-old etiolated maize seedlings [57]. The rate of elongation was recorded with a 6MKh1S mechanotron (an angular converter of linear displacement, Russia) along with an impedance-matching transformer and recording potentiometer KSP-4 [58]. Segments comprising the coleoptile, coleoptilar node, and mesocotyl were loaded vertically into a special Plexiglas cell (Fig. 6c). A soft rubber ring was slipped on the basal part of the coleoptile to fix a plastic funnel, and the wider end of the latter propped against the mechanotron probe. The potential difference between the coleoptile tip and the node was generated by platinum electrodes, which contacted with cotton-wool plugs attached to the shoot surface. The filter paper in the cell and the cotton wool were moistened with a 0.1-strong Knop solution. An ISE-01 electronic stimulator (Russia) fed the appliance, which produced a potential difference of 4, 6 or 15 V at a current of 3–12 mA. With the anode at the node, the mesocotyl growth was inhibited following a lag-phase of 1–1.5 min, and the extent of inhibition was proportional to the applied potential. In reverse polarity, the cathode was in contact with the node that promoted the mesocotyl growth (Figs. 6a, 6b). It follows that the electropositive changes in the node and adjacent intercalary meristem inhibited the mesocotyl growth. We have already mentioned that R irradiation of the segments or the intact etiolated maize seedlings induced electropositive changes in the node with the adjoining intercalary meristem (Fig. 5). These changes were accompanied by a decrease in the phytohormone content (Fig. 4) and the inhibition of the mesocotyl growth (Fig. 3).

To interpret the effects of the potential difference, both endogenous and externally applied, on plant-tis-

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**Fig. 4.** The contents of free IAA (Z + ZR) zeatin plus zeatin riboside, (GA) gibberellins, and ABA in various tissues of the three-day-old etiolated maize seedling (filled column) following 30-min incubation in darkness or (open column) after irradiation with R [54].

**Fig. 5.** The effect of R on the BEP changes in the zone of the coleoptilar node of the segment of the three-day-old etiolated maize seedling (unpublished data obtained with the participation of K.B. Frolov). During the initial 60 min, BEP was measured under weak green light. (co) Coleoptile; (pl) primary leaves; (cn) coleoptilar node; (me) mesocotyl, (EP) measuring electrode.
sue growth, we employ the phenomenon of electroosmosis. The nature of this phenomenon lies in the movement, from the positive to negative pole, of an electrolyte solution in capillary or capillary–porous bodies the solid phase of which carries fixed negative charges and a counter-ion layer, when a potential difference is applied [59]. In plant tissues, the conducting vessels are capillaries, and intercellular and apoplast spaces are capillary–porous bodies. Our experiments with carrot root disks [60] and maize mesocotyl segments (Fig. 7) unquestionably demonstrated the phenomenon of electroosmosis. Figure 7 shows that with a potential difference of 10 and 15 V applied (the corresponding currents were 37 and 50 \( \mu \)A), the electrolyte solution moved through the mesocotyl segment toward the negative pole. In reverse polarity, the direction of the liquid movement was the opposite. These experiments imply that when the node zone including the mesocotyl intercalary meristem is charged positively in reference to the coleoptile tip, the solutions in the conducting vessels and the apoplast move acropetally and deplete the node zone with the adjoining intercalary meristem of IAA and other phytohormones. The direction of the water movement itself is also essential as the shoot tissues are under moisture deficit. Such a situation may hinder cell division and elongation in the mesocotyl growth zone [61], while the coleoptile growth temporarily enhances due to the enrichment with phytohormones and water.

Based on the ideas stated above, we suggest the following model for the contour regulating the effect of \( R \) on etiolated maize seedlings. The maximum phytochrome contents reported in the maize seedlings that were grown in the dark were found in the mesocotyl intercalary meristem [42] and leaves [43]. Therefore, these tissues are the \( R \) sensory zones (see Fig. 2). \( R \) reception by the intercalary meristematic cells results in the generation of an electropositive BEP, which we define as the receptor potential. The transformation of the light (R) signal into the receptor electric potential is probably related to an increase in the cytoplasmic calcium concentration [62] followed by \( Ca^{2+} \) ion exchange for protons across the tonoplast. The resulting acidification of the cytoplasm activates \( H^+ \)-ATPase in the plasmalemma; by pumping \( H^+ \) ions out, ATPase induces MP hyperpolarization, which is recorded by the external electrode as BEP electropositation. Such a mechanism for the generation of the electropositive BEP wave was put forward and verified in our laboratory when we investigated the IAA effects on competent cells [63, 64]. I believe that the electropositivation of the zone of mesocotyl intercalary meristem and node involves the electroosmotic mechanism, which restrains IAA transport from the coleoptile to the mesocotyl growth zone. As a result, cell division and elongation in this zone are dramatically arrested. BEPs, osmotic phenomena, mechanical tissue tensions, and the competition for nutrients and phytohormones work as the feedback factors in the regulatory control (see
The development of new functionally active sites is the major factor that triggered the feedback mechanism. As seen in Fig. 4, the 30-min R irradiation of the primary leaves of the etiolated maize seedlings dramatically increased the gibberellin activity and in this way promoted rapid leaf growth.

A similar mechanism regulating the root behavior must exist in the root apex under the conditions of gravitropic induction. Konigs [65] reported that the root deviation from the vertical position induced a transverse electric polarization in the root cap columella. Such polarization can modify the direction of IAA transport and in this way, result in asymmetric cell elongation in the root growth zone and produce a gravitropic bending.

The experimental data and the published evidence presented above were combined in a comprehensive model of the regulation and integration in plants shown in Fig. 8. This model combines two concepts, namely hormonal regulation and source–sink relations. The model is still tentative and schematic; it does not cover such items as the functions of some phytohormones (gibberellins, ABA, ethylene), some electrophysiological phenomena, and the driving forces of the long-distance transport. Yet this model can serve as the basis for the further discussion of the mechanisms of plant integrity and promote research in this field.

UKHTOMSKII’S PRINCIPLE OF THE DOMINANT AS APPLIED TO HIGHER PLANTS

The animal and plant organism can switch from one particular activity to another and concentrate all of its functional systems on this new activity. Many such examples are found among plants. Thus, all the resources of a seedling grown in the dark (e.g., in soil) are focused on axial elongation. In this way, a plant guided by the gravitation field grows to the light by the shortest way possible. As shown above, a light signal induces drastic changes in the seedling behavior: the stem elongation is restrained, the leaves start unfolding and expanding, and the photosynthetic apparatus is developed and brought to action. From this point on, the functional activity of the whole plant is focused on photosynthesis.

To explain the mechanism that focuses all the functional systems of the organism on the particular activity, Ukhtomskii advanced the principle of the dominant [66]: a specific signal evokes a particular constellation of nerve centers, and their coordinated activities control the exact activity of the organism. Such steady activation (excitation) of the particular nerve centers inhibits other nerve centers. Ukhtomskii called such transient constellation of activated centers “a dominant organ.” He commented that the principle of the dominant can be applied to the control via not only the electric impulses generated by the nervous system, but via the

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**Fig. 7.** The effect of the electric field on the transport of electrolyte solution (0.01 M KCl) across the mesocotyl segment of the four-day-old etiolated maize seedling (unpublished data obtained with the participation of T.E. Bilova).

(a) A typical experiment demonstrating the changes in the liquid volume in (I) the right and (II) left measuring capillaries when the voltage was switched on, (0) switched off, changed (values at the curves are volts), and (+ or –) when the polarity was reversed. (b) The basic scheme of the appliance to measure electroosmosis in the segments of plant axial organs. (1) 10-mm-long mesocotyl segment; (2) connecting rubber couplings; (3) vials with 0.01 M KCl; (4) measuring capillaries; (5) nonpolarizing electrodes (Cu/CuSO₄–agar).
humoral (hormonal) mechanisms, particularly in embryogenesis, as well (see [67]).

I believe that plant behavior is also governed according to Ukhtomskii’s principle of the dominant. In a vegetating plant, the actively growing tip of the primary shoot evoked by the gravitation field and the illumination gradient maintains the strategic task of the whole plant: to move (grow) towards the light. At the same time, the apical bud inhibits the neighboring auxiliary buds (the phenomenon of apical dominance). A similar mechanism of moving along the vectors of gravitation and/or water and mineral nutrients governs the root behavior. The interaction of two activated (dominant) centers, that is, the shoot apex and the distal part of the root, employs the hormonal signals and trophic factors and molds the behavior pattern of the vegetating plant as a whole. When the environmental changes are regular, e.g., with the arrival of a short-day photoperiod, an adequate signal coming from the leaves to the distal part of potato stolons invokes the active (excited) state in the competent zones of these stolons. A new constellation of the dominant centers—the distal regions of stolons and roots—evokes a new behavioral pattern. It is evident that the developing potato tubers become the focus of the coordinated activities of the whole plant.

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