Importance of cell elongation for root growth plasticity*

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Abstract:

The study underlines the high plasticity of root systems according to environmental conditions. Cell proliferation and elongation play a central role. The effects of mechanical impediments, temperature, oxygen deficiency, light and water deficit on cell elongation in roots are discussed.

The root system is the target of discontinuous and primary interest of Mrs. Lore KUTSCHERA, the organizer and Honorable President of the International Society of Root Research.

While visiting her laboratory in Gumpenstein (Institut für Alpenländische Landwirtschaft, Irdning) and moving along the corridor walls covered with preparated long manifold - branched root systems, one feels like a traveller through the underground kingdom populated with various roots. At a glance, one can visualize the root extension in soil, the large soil volumes penetrated by the roots of various orders, root interaction and competition for water and solutes and then imagine the intricate life at the below - ground stirey of a plant community.

On the lectures delivered by Lore KUTSCHERA, a great impression is made by numerous photos and pictures of diverse root systems of different plant species in various environments. Especially impressive for me were the slides with the root systems of one and the same plant but grown under contrasting conditions. These root systems differed in their architecture so emphatically that they provided the most spectacular illustration of root growth plasticity.

The plasticity of growth is a unique property of root systems; the above-ground organs are unable to show anything comparable. The plasticity manifests itself in the ability to change the architecture of root system responding to variable soil conditions. These changes in morphological patterns provide a high degree of root adequacy to temperature, oxygen concentration, water content and mineral composition varying with soil depth and, in its turn, depending on climatic, seasonal and local conditions. Main components of root growth plasticity, i.e. root tropisms, root lengthening and root branching, determine the direction, extension and density of the root system.

Here, the growth plasticity of root systems will be considered in terms of cell proliferation and elongation. The primary importance of cell division in apical meristems is the maintenance of long - term longitudinal growth by discontinuous production of new cells capable of starting the elongation. The proliferative activity of apical meristems is supported by the quiescent center representing the reserve of initial cells sufficient to provide the proliferative activity during the whole vegetative period of plant development. The cell proliferation in the primordia of lateral and adventitious roots is of decisive importance for root branching. These meristems are characterized by nearly two times more rapid mitotic cycles then the apical meristems (MACLEOD & THOMPSON 1979).

However, it is cell elongation that underlies root tropisms and root penetration through the soil as well as rapid responses to the changes in the environments. The direction of root growth depends on the combination of gravitropisms, hydrotropism and chemotropism. At present, we know much about gravitropism, but it was L. KUTSCHERA, who attracted our attention to the role of hydrotropisms (KUTSCHERA 1983).

* Dedicated to Professor Lore KUTSCHERA, whose devotion to plants and inexhaustible enthusiasm has made leader in root science.

It is beyond doubt that the major role of cell elongation is a rapid increase in the organ length allowing penetration through soil. A predominant contribution of cell elongation to the lengthening of axial organs during growth initiation and further growth follows from manifold increase of meristematic cells in length, contrary to their only twofold increase in the course of cell proliferation. Cell cycling alone is unable to provide a rapid root extension.

The leading role of cell elongation becomes evident from the very beginning of seed germination. Cell elongation is the primary and obligatory growth process in early germination. Both epigeal and hypogeal germination are characterized by rapid cell expansion providing fast lengthening of axial organs (OBOUCHEVA 1992) and their readiness to respond to many environmental factors. The commencement of cell elongation is regulated independently of initiation of cell division. In the protruding roots, the elongation zone is formed in the embryonic radicle prior to meristem.

Due attention needs to be given to differential responsiveness of cell division and cell expansion to various factors. It is also important to discriminate between direct and indirect effects. A direct effect on cell elongation manifests itself in the change of final cell size within several hours. An indirect effect is delayed and seen as a decelerated root elongation resulting from primary inhibition of cell division and reduced number of cells initiating the extension.

In soil, the root tip encounters impediments to its growth, especially in compact soil. The root responds to such mechanical stress by reducing elongation rate and cell length (WILSON et al. 1977). Cell elongation is the primary growth process to respond to mechanical impediment. Secondary growth modifications involve an increase in diameter and often in number of cells, root thickening and a change in branching pattern.

The effect of temperature must be considered relative to the temperature at which root growth proceeds most rapidly, e.g. 24-29^0 for maize or onion roots. At temperature 30-35^0 C, decreased growth rate resulted from markedly reduced length of fully-developed cells although the cell cycle became shorter. Root growth at lowered temperatures is much lower due to lengthening of the cell division cycle (LOPEZ-SAEZ et al. 1969, GRIF & IVANOV 1995). The effects of low temperature on the cell elongation appear to be ambiguous.

Oxygen deficiency inhibits both cell division and cell elongation (LOPEZ-SAEZ et al. 1969, OBROUCHEVA 1983). With onion roots, a deceleration of cell proliferation was shown to be dramatic at 2-5% O_2 as compared to 10-20% O_2 content, no effect on final cell length was reported. Nonetheless, direct arrest of elongation in roots completely deprived of oxygen was demonstrated. Apparently, cell division is more sensitive to decreasing oxygen concentration than cell elongation.

Light indicates an unfavourable environment for roots that forces the root to curve downwards back into the more favourable soil environment. Rapid cessation of elongation after maize root illumination was described by PILET & NEY (1978), whereas a gradual inhibition of elongation as a result of decelerated cell divisions, was recorded (LARQUE-SAAVEDRA et al. 1975).

Mild water deficit due to an osmotic effect and mimicked by application of polyethylene glycol or mannitol, directly inhibits cell elongation reducing the final cell length (GONZALES BERNALDEZ et al. 1968), but only slightly decelerates cell cycling, especially at low osmotic pressure.

So far it can be said that direct inhibition or acceleration of cell elongation results in a rapidly changed rate of organ extension thus providing an immediate response to external factors. Any event interfering with meristematic activity exerts a delayed effect on organ lengthening, which becomes visible after one mitotic cycle is over and later on. Thereby, one more advantage of cell elongation manifests itself in the readiness for a rapid response. It is obvious, in addition to those studies cited above that cell elongation is an indispensable process for initiation and further root growth.

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