ISSN 1062-3604, Russian Journal of Developmental Biology, 2018, Vol. 49, No. 2, pp. 79–86. © Pleiades Publishing, Inc., 2018.
Original Russian Text © E.I. Bystrova, N.V. Zhukovskaya, V.B. Ivanov, 2018, published in Ontogenez, 2018, Vol. 49, No. 2.

DEVELOPMENTAL BIOLOGY OF PLANTS

Dependence of Root Cell Growth and Division on Root Diameter

E. I. Bystrova, N. V. Zhukovskaya*, and V. B. Ivanov**

Timiryazev Institute of Plant Physiology, Russian Academy of Sciences, Moscow, 127276 Russia

**e-mail: zhukovskayanv@rambler.ru*

***e-mail: ivanov_vb@mail.ru*

Received May 18, 2017

Abstract—Primary roots of 98 species from different families of monocotyledonous and dicotyledonous plants and adventitious roots obtained from bulbs and rhizomes of 24 monocot species were studied. Root growth rate, root diameter, length of the meristem and elongation zones, number of meristematic cells in a file of cortical cells, and length of fully elongated cells were evaluated in each species after the onset of steady growth. The mitotic cycle duration and relative cell elongation rate were calculated. In all species, the meristem length was approximately equal to two root diameters. When comparing different species, the rate of root growth increased with a larger root diameter. This was due to an increase in the number of meristematic cells in a row and, to a lesser degree, to a greater length of fully elongated cells. The duration of the mitotic cycle and the relative cell elongation rate did not correlate with the root diameter. It is suggested that the meristem size depends on the level of nutrient inflow from upper tissues, and is thereby controlled during further growth.

Keywords: correlation, dicots, monocots, root diameter, root growth, root meristem

DOI: 10.1134/S1062360418020029

INTRODUCTION

The growing part of the root consists of the meristem, where the cells proliferate, and the elongation zone, where they rapidly grow and achieve their final length. The border between the zones is clearly seen on longitudinal sections of roots or upon microscopic observations of ultrathin roots, because, when cells start elongation, their length sharply increases with the distance from the root tip. This is an outcome of a jump in a relative cell growth rate but not of a mere cessation of their division (Ivanov, 2011). It is the initial site of sharp cell elongation that is usually defined as the border between the zones. This approach is applied to many works (Dello Ioio et al., 2007), but certain roots may have a district where the cells no longer divide but yet do not grow at a high relative rate. In this case, a transient zone between the meristem and the elongation zone is considered. It is distinct in *Arabidopsis* roots (Verbelen et al., 2006). However, in thicker roots of some species (for example, *Vicia faba* L. and *Allium cepa* L.), cells may still continue to divide at the beginning of the elongation zone (Ivanov and Dubrovsky, 2013). In the present work, the starting point of sharp elongation of cells is defined as the boundary between the meristem and the elongation zone.

Roots of different species differ considerably by length and diameter (Kutschera et al., 1982, 1992). This is evident as early as in seedlings and is not related to peculiarities of secondary thickening of roots. In one root system, in the course of branching of the first, second, and consequent root orders, a consecutive thinning occurs that entails an enlarged specific root area and more intense consumption of water and ions.

How cell growth and division in the growing part of the root depend on its diameter has hardly been studied thus far. The present work deals with these aspects and comprises measurements of root diameters and determination of the parameters characterizing cell growth and division in roots of different plant species.

MATERIALS AND METHODS

The investigation was carried out on primary roots of seedlings of 35 plant species belonging to the monocotyledon class, of 63 dicotyledonous species, and of adventitious roots of 24 monocotyledonous species derived upon bulb and rhizome germination. In addition, the first-order lateral roots in 11 species and the second-order lateral roots in two species were examined. In the tested species, the radial enlargement of roots finished at the beginning of the elongation zone; we did not study the root secondary thickening, which occurs far later and not in all species. Seeds germinated in Petri dishes at 23 ± 2°C in the dark on filter paper moistened with tap water were kept under room conditions. Bulbs and rhizomes were planted in darkened glass vessels with the conditioned tap water, so that a base of a bulb or rhizome was 0.5 cm submerged.

Tips of stationary growing roots, as long as 1.0–1.5 cm, were fixed in 70% ethanol. Before the fixation, thicker roots were cut lengthwise with a razor blade. After the fixation, thin roots were rinsed in distilled water and transferred to 50% glycerol. The thicker roots or their longitudinal slices were clarified according to (Malamy and Benfey, 1997) and then were put into 50% glycerol. In temporary mounts, root diameter at the start of the elongation zone (D), length of the meristem (L_m) and of the elongation zone (L_e), length of meristematic cells (l_m) and of cells that completed their growth (l_e) in a row of cortex cells were measured with an eyepiece micrometer under an Olympus CX-41 microscope. Root growth rate (V) was calculated as $V = \Delta L/\Delta t$, where ΔL is an augmentation of the root length after time Δt (24 h in our experiments). Seed weight (P) was also measured for the tested species.

On the basis of the evaluated parameters, the number of meristematic cells in a row in the cortex $N_m = L_m/l_m$, the relative elongation rate of cortex cells $K_e = V/L_e$, and the cell division cycle duration $T = \ln 2 N_m l_e/V$ were calculated using the specified formulae. In addition, the ratio L_m/D was calculated.

Data on DNA content (C_{val}) were taken from the database of Kew Botanical Gardens (http://data.kew.org/cvalues/).

For each species, sixteen roots (eight roots per replicate) were analyzed, and then the mean values were obtained. To estimate linkages between root diameter and the above-listed parameters of root growth (and seed weight), correlation coefficients (r) were calculated. The data were processed using Excel.

RESULTS

Variations of Root Diameter across Different Species and Its Dependence on Seed Weight, DNA Content (Normalized to Haploid Chromosome Number), and Size of Meristematic Cells

Tables 1a and 1b represent the values of root diameter, meristem length, and L_m/D ratio in roots of different species.

The diameter of the primary root varied from 97 to 970 μm in monocots and from 109 to 1117 μm in dicots. It varied from 278 to 1420 μm in the adventitious roots of monocot species. Consequently, the three examined plant groups did not differ significantly in this index.

We revealed correlations between root diameter and measured and calculated growth parameters and also seed weight and DNA content normalized to haploid chromosome number (Table 2).

The diameter of seedling root positively correlated with the seed weight ($r = 0.78$ at $n = 35$ in monocots and $r = 0.7$ at $n = 63$ in dicots). In monocots, the root diameter weakly correlated with the DNA content normalized to haploid chromosome number ($r = 0.23$ in seedling roots and $r = 0.18$ in adventitious roots). In dicots, this correlation was also small ($r = 0.29$). The correlations of root diameter and length of meristematic cells of monocotiledons were $r = 0.39$ (seedling roots) and $r = 0.41$ (adventitious roots); it was $r = 0.67$ in dicotiledonous seedling roots.

The diameter of lateral roots was smaller than that of primary roots and varied from 154 to 515 μm. The larger the diameter of maternal root, the thicker the lateral roots that emerged from it (Fig. 1).

Dependence of Growth Rate of Roots on Their Diameter

The roots grew faster the thicker they were. This link was especially pronounced in seedling roots and weaker expressed in adventitious roots (Fig. 2). During the root stationary growth, its rate (V) was inversely proportional to the mitotic cycle duration (T) and directly proportional to the number of meristematic cells in one row (N_m) and to the length of cells that completed their growth (l_e) (Ivanov, 1974; Ivanov and Dubrovsky, 1997).

$$V = \frac{\ln 2 N_m l_e}{T}.$$

The distinct positive correlation between the root diameter and the number of meristematic cells in a row was observed especially in seedling roots; it was much weaker in adventitious roots (Fig. 3). Thinner lateral roots also comprised shorter meristems with fewer meristematic cells in a row in comparison with thicker roots.

In thicker roots, the meristem was longer, and its length reached almost two root diameters (Fig. 4, Table 1a). This ratio was clearly less than 1.0 only in the second order lateral roots of maize and pea seedlings (Table 1b). The cells that completed their growth were longer the thicker the root was. Correlation coefficients between the root diameter and the number of meristematic cells in a row and between the root diameter and the meristem length were larger than between the root diameter and the length of cells that completed their growth (Table 2).

There was no correlation between the root diameter and the cell-cycle duration (Table 2). Consequently, the obvious dependence of the root growth rate on its diameter is explained through the number of meristematic cells in a row. In addition, the cells completing their growth are longer in thicker roots. Similar conclusions were made by Gazques and Beemster (2017) after comparison of different publications.

The thinner the root, the larger is its specific area. This is one of the reasons for root thinning in root systems with higher branching orders, since this gains an advantage in adsorbing area. However, the rise in the specific area with the root thinning was not found

Table 1a. (D) Root diameter, (L_m) meristem length, and L_m/D ratio in primary roots of monocotyledonous and dicotyledonous seedlings and in adventitious roots of monocots (*)

Family and species	D, μm	L_m, μm	L_m/D	Family and species	D, μm	L_m, μm	L_m/D
Monocotiledons							
Amaryllidaceae				Melanthiaceae			
Allium aflatunense B. Fedtsch.*	494	1173	2.4	*Paris incomplecta* L.*	560	576	1.0
Allium altissimum Regel.*	689	1472	2.1	*Paris quadrifolia* L.*	560	592	1.1
Allium caeruleum Pall.*	452	804	1.8	Poaceae			
Allium carinatum L.	280	560	2.0	*Aegilops squarrosa* auct. (tauschii Coss.)	375	728	1.9
Allium cepa L.	340	740	2.2	*Aegilops umbellulata* Zhuk.	399	778	1.9
Allium cepa L.*	1042	1885	1.8	*Agrostis stolonifera* L.	97	120	1.2
Allium cristophii Trautv.*	578	1038	1.8	*Avena pilosa* L.	272	334	1.2
Allium porrum L.	310	615	2.0	*Avena sativa* L.	530	1240	2.3
Allium sativum L.	400	825	2.1	*Avena strigosa* Schreb	298	580	1.9
Allium schoenoprasum L.*	790	1480	1.9	*Dactylus glomerata* L.	125	200	1.6
Allium tuberosum Rottler ex Spreng.	380	740	1.9	*Eragrostis tef* (Zuccagni) Troffer	168	250	1.5
Allium unifolium Kellogg.*	500	976	2.0	*Festuca glauca* Vill.	213	302	1.4
Allium ursinum L.*	742	1269	1.7	*Festuca rubra* L. subsp. rubra	192	308	1.6
Allium victoriális L.*	523	977	1.9	*Hordeum bulbosum* L.	410	725	1.8
Galanthus nivalis L.*	456	683	1.5	*Hordeum vullgare* L.	350	750	2.1
Narcissus pseudonarcissus L.*	957	1688	1.8	*Lolium perenne* L.	247	470	1.9
Nectaroscordum siculum (*Ucria*) Lindl*	484	1240	2.6	*Oryza sativa* L.	377	729	1.9
Asparagaceae				*Panicum miliaceum* L.	400	900	2.3
Hyacinthus orientalis L.*	877	1602	1.8	*Pennisetum americanum* (L.) Leeke	438	847	1.9
Iris reticulata M. Bieb.*	622	914	1.5	*Phalaris canariensis* L.	265	591	2.2
Ornithogalum umbelatum L.*	689	973	1.4	*Phleum pratense* L.	151	205	1.4
Puschkinia scilloides Adams*	278	474	1.7	*Secale cereale* L.	450	970	2.2
Scilla siberica Andrews*	440	843	1.9	*Sorghum bicolor* (L.) Moench	470	920	2.0
Juncaceae				*Triticale* Wittm. & A. Camus	492	980	2.0
Luzula elegans L.	120	135	1.1	*Triticum aestivum* L.	490	950	1.9
Liliaceae				*Triticum diccocum* Schrank	483	976	2.0
Fritillaria imperialis L.*	1104	1288	1.2	*Triticum dicoccoides* Schweinf.	520	1050	2.0
Fritillaria persica L.*	1420	1762	1.2	*Triticum durum* Desf.	480	980	2.0
Lilium longiflorum L.*	1058	1489	1.4	*Triticum monococcum* L.	471	923	2.0
Lilium martagon L.*	938	1198	1.3	*Triticum spelta* L.	537	1044	1.9
Tulipa tarda Stapf.*	370	638	1.7	*Triticum timopheevii* Zhuk.	430	862	2.0
				Zea mays L.	970	1680	1.7
Dicotiledons							
Apiaceae				*Cucumis sativus* L.	400	750	1.9
Coriandrum sativum L.	315	665	2.1	*Cucurbita pepo* L.	570	1200	2.1
Daucus carota L.	250	485	1.9	Fabaceae			
Asteraceae				*Glycine max* (L.) Merr.	472	920	1.9
Agoseris retrorsa (Benth.) Greene	285	544	1.9	*Lathyrus articulatus* L.	762	1493	2.0

Table 1a. (Contd.)

Family and species	D, μm	L_m, μm	L_m/D	Family and species	D, μm	L_m, μm	L_m/D
Agoserris heterophylla L.	241	456	1.9	*Lathyrus latifolius* L.	570	1015	1.8
Anacyclis radiatus L.	205	408	2.0	*Lathyrus odoratus* L.	550	1090	2.0
Anthemis austriaca L.	158	283	1.8	*Lathyrus tingitanus* L.	443	873	2.0
Anthemis cota L.	160	243	1.5	*Lupinus polyphylus* Lindl.	570	1100	1.9
Anthemis tinctoria (L.) J. Gay ex Guss.	170	320	1.9	*Pisum sativum* L.	725	1370	1.9
Artemisia absinthium L.	136	216	1.6	*Vicia faba* L.	1117	2250	2.0
Artemisia annua L.	120	160	1.3	*Vicia grandiflora* Scop.	411	775	1.9
Carthamus tinctorius L.	520	1160	2.2	*Vicia hirsuta* (L.) Gray	248	464	1.9
Cosmos bipinnatus Cav.	205	361	1.8	*Vicia sativa* L.	577	1192	2.1
Crepis capillaris L.	153	261	1.7	Linaceae			
Crepis tectorum L.	249	486	2.0	*Linum ussitatissimum* L.	350	970	2.8
Helianthus annuus L.	455	940	2.1	Onagraceae			
Lactuca sativa L.	200	370	1.9	*Epilobium hirsutum* L.	135	220	1.6
Pyrrohopappus caroliniana L.	262	488	1.9	Papaveraceae			
Balsaminaceae				*Papaver nudicaule* L.	150	205	1.4
Impatiens balsamina L.	300	580	1.9	*Papaver orientale* L.	200	310	1.6
Brassicaceae				*Papaver somniferum* L.	220	315	1.4
Brasica napus L.	254	462	1.8	Polygonaceae			
Brassica juncea (L.) Czern.	340	700	2.1	*Fagopyrum esculentum* Moench.	440	774	1.8
Brassica nigra L.	370	900	2.4	*Rumex thyrsiflorus* Fingerh.	243	450	1.9
Brassica rapa L.	224	451	2.0	Ranunculaceae			
Camelina sativa (L.) Crantz	195	410	2.1	*Nigela damascena* L.	295	500	1.7
Capsella bursa pastoris (L.) Medik.	130	215	1.7	Solanaceae			
Lepidium ruderale L.	109	210	1.9	*Capsicum annuum* L.	374	745	2.0
Noccaea caerulescens (J. Presl & C. Presl) F.K. Mey	152	268	1.8	*Capsicum baccatum* L.	384	832	2.2
Rhaphanus sativus L.	430	875	2.0	*Capsicum chinense* Jacq.	219	451	2.1
Sinapis alba L.	470	1000	2.1	*Capsicum frutescens* L.	308	578	1.9
Caryophyllaceae				*Capsicum pubescens* Ruiz & Pav.	262	560	2.1
Melandrium album (Mill.) Garcke	203	399	2.0	*Lycopersicon esculentum* L. ssp. Cultum	276	567	2.1
Chenopodiaceae				*Nicotiana alata* Link & Otto	120	227	1.9
Beta vulgaris L.	370	733	2.0	*Nicotiana plumbaginifolia* Viv.	117	137	1.2
Cucurbitaceae				*Nicotiana tabacum* L.	117	190	1.6
Citrullus vulgaris Schrad.	378	795	2.1	Tropaeolaceae			
Cucumis melo L.	460	1080	2.3	*Tropaeolum majus* L.	630	1270	2.0

to reduce the cell-cycle duration and, consequently, did not increase the relative growth rate of meristematic cells. Similar results were obtained for elongating cells. The relative elongation rate did not correlate with the root diameter (Table 2). Therefore, the faster growth of the thicker roots is accounted for by a high content of meristematic and elongating cells rather than higher relative rates of cell division and elongation.

DISCUSSION

The present investigation is the first in which root diameters of 122 plant species were measured,

and their correlations with several parameters of root growth at cellular level were established as well as with seed weight and the DNA content normalized to the haploid chromosome number of each plant species.

Upon comparison of different species, the clear allometric ratios between root diameters and meristem sizes (Fig. 4) are conspicuous. With an increase in root diameter, the number of meristematic cells in a row increases along with the meristem length, which approximates to the doubled diameter of the root (Table 2). Although the literature scarcely reports comparative data on root diameter and length of its meristem measured on any one object, some publications support this conclusion. For example, Goodvin and Avers (1956) compared their results obtained on *Phleum pratense* L. with those on *Zea mays* L. (Erickson and Sax, 1956). In *P. pratense*, the root diameter was 0.18 mm and meristem length was 0.4 mm; in *Z. mays*, the values were 1.11 and 2.0 mm. Analyses of the published photographs of thin roots or root longitudinal slices of quite diverse plants also show that their meristem is as long as, approximately, two root diameters. These examples include *Triticum aestivum* L. (Grif et al., 2002), *Oryza sativa* L. (Shafiq et al., 2017), *Teucrium chamaedrys* L., *Veronica spicata* L., *Carum carvi* L. (Kutschera et al., 1992), *Glyceria maxima* (Hartm.) Holmb. (Kutschera et al., 1982), and *Zea mays* L. (Kutschera-Mitter, 1972).

The question arises as to what determines this rather strict ratio between the root diameter and the length of the apical meristem. It is so far uncertain why thin roots with long meristems or, on the contrary, thick roots with short meristems are not yet found. In this regard, hypotheses exist concerning roles of various phytohormones and some genes in determining sizes of apical meristems in roots (Dello Ioio et al., 2007; Galincha et al., 2007; Ubeda-Tomas et al., 2009; Hacham et al., 2011; Su et al., 2011). However, these speculations do not answer the above-stated question, because they do not explain how the necessary phytohormone distribution is maintained.

Apparently, one possible approach to the interpretation of the revealed dependence is the hypothesis that the meristem itself determines its size. The idea is that the intensity of influx of necessary substances to the meristem depends on its size and functional state. The meristem receives the necessary nutrients from the above-situated tissues. Under shading, the flux of assimilates to the root decreases leading to decrease in size of the root apical meristem (Shmanaeva and Leman, 1970; Muller et al., 1998). These relationships may explain the link found between the seed weight and the root growth rate ($r = 0.72$ at $n = 35$ in monocots and $r = 0.41$ at $n = 63$ in dicots). The flow rate to the meristem apparently depends on the root diameter, because at least the apical part of the meristem does not yet contain a functioning phloem.

Table 1b. (D) Root diameter, (L_m) meristem length, and L_m/D ratio in lateral roots of the first and second (*) order in monocotyledonous and dicotyledonous seedlings

Species	D, μm	L_m, μm	L_m/D
Fagopyrum esculentum Moench.	222	401	1.8
Beta vulgaris L.	157	305	1.9
Pisum sativum L.	515	941	1.8
Pisum sativum L.*	370	360	1.0
Lycopersicon esculentum L. ssp. Cultum	154	283	1.8
Citrullus vulgaris Schrad.	245	487	2.0
Citrullus vulgaris Schrad.	189	418	2.2
Brassica rapa L.	163	301	1.8
Brassica rapa L.	155	297	1.9
Cosmos bipinnatus Cav.	165	210	1.2
Capsicum annuum L.	207	354	1.7
Triticum durum Desf.	250	365	1.4
Carthamus tinctorius L.	320	643	2.0
Zea mays L.	363	893	2.4
Zea mays L.*	270	320	1.1

Bigger embryos possess thicker roots. We have no quantitative data on how embryonic roots differ in size from each other in seeds of different species. However, the visual assessment of the examined specimens shows that the bigger seeds contain bigger embryonic roots. Importantly, the studied objects do not include species with underdeveloped embryos and periods of seed germination (the period usually lasted 3–30 days). Therefore, one may expect that species with bigger seeds have bigger embryonic roots, wherein both

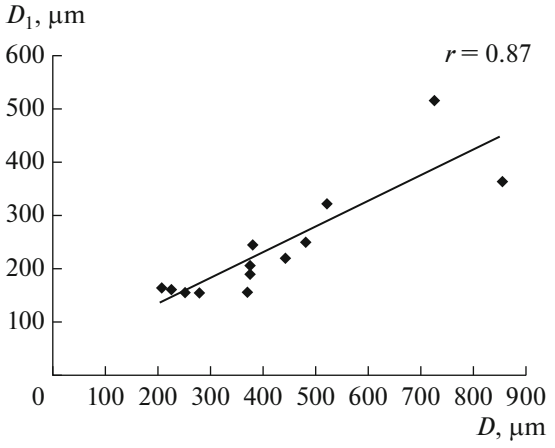

Fig. 1. Dependence of (D_1) diameter of lateral root on (D) diameter of primary root in 11 plant species.

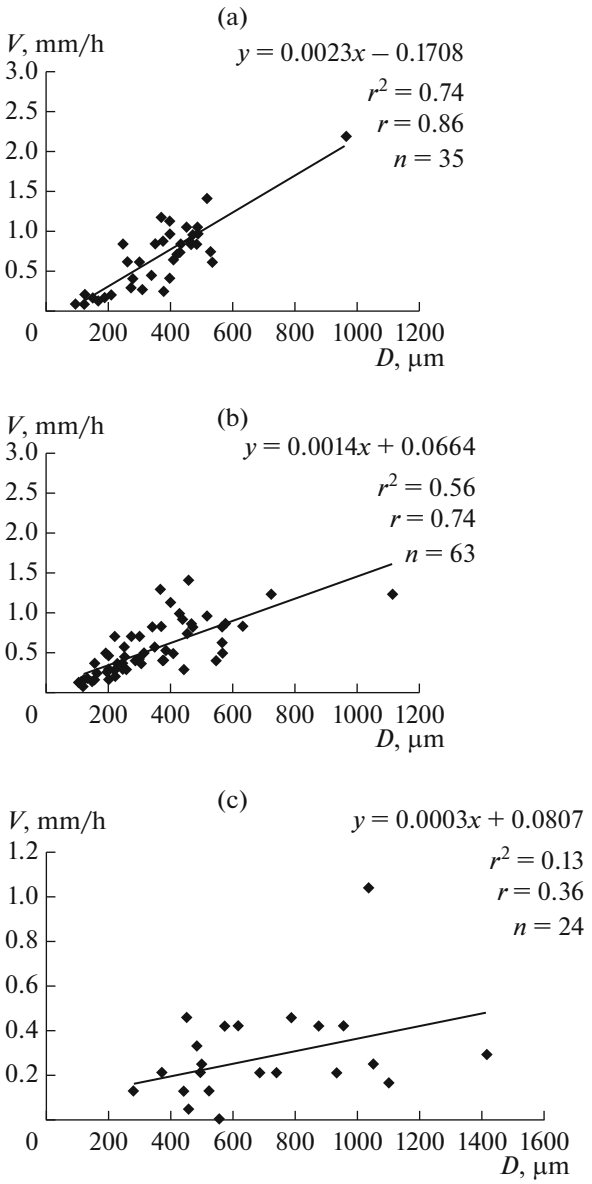

Fig. 2. Dependence of (V) growth rate of primary root on (D) its diameter in seedlings of (a) monocots, (b) dicots, and (c) in adventitious roots of monocots.

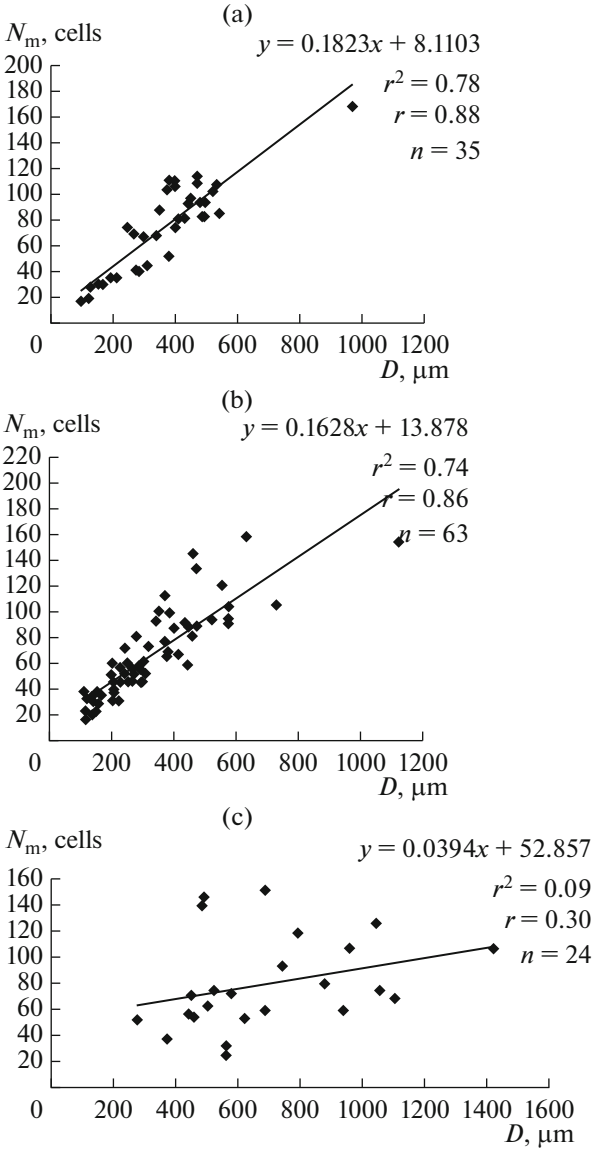

Fig. 3. Dependence of (N_m) meristematic cell number in one row on (D) root diameter in seedlings of (a) monocots, (b) dicots, and (c) in adventitious roots of monocots.

diameter and meristem length are greater in comparison with the embryonic roots in smaller seeds. Over the monitoring period in our experiments, the differences between roots growing from seeds of different sizes were maintained. Actually, the roots of the bigger seeds grew faster and had bigger meristems and bigger cells that had finished their growth; hence, such roots had received a larger quantity of necessary substances from bigger seeds.

Development of lateral roots displayed a similar phenomenon. The thinner was the maternal root, the thinner the lateral roots appeared from it (Fig. 1). Visual observations clearly confirm this relationship. The size of a primordium of a lateral root formed before its exit from a thinner maternal root was smaller than in the case of a thicker maternal root. A smaller primordium produced a thinner root.

Therefore, we can assume that not only the diameter but also size of the embryonic root or primordium of the lateral root is important. The bigger the size of the organ, the more intensively it consumes the delivered substances; the consumption decreases their concentrations, which increases their inflow. In addition, meristems synthesize cytokinins (Kudo et al., 2010), which take attracting action (Werner et al., 2008). Presumably, the bigger primordium is capable of synthe-

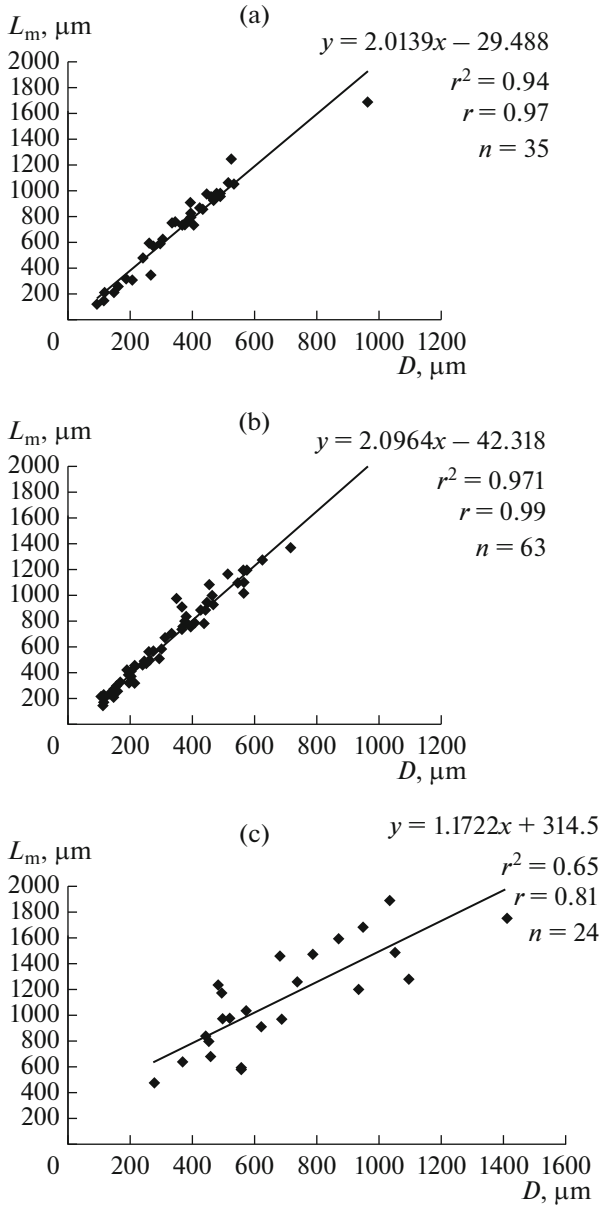

Fig. 4. Dependence of (L_m) meristem length on (D) root diameter in seedlings of (a) monocots, (b) dicots, and (c) in adventitious roots of monocots.

sizing more amounts of cytokinins. Although subtle details of these processes are far from being clearly understood, the simple observations presented in this work make their existence quite feasible.

We have demonstrated that thicker roots grow faster than thinner ones. It can be expected that the cells growing more rapidly are dividing more frequently. However, our calculations did not find correlations between the root diameter and mitotic cycle duration (Table 2). Therefore, the high growth rate was determined by the multiplication of dividing cells rather than the frequency of their division. We emphasize that, in a thicker root, the higher import of nutrients from the upper parts favors elongation of the cells completing their growth.

Table 2. (r) Correlation coefficients at $p = 0.05$ between (D) root diameter and (C_{val}) DNA content normalized to haploid chromosome number, (P) seed weight, and different parameters of root growth, as follows: (L_m) meristem length, (N_m) number of meristematic cells, (l_m) length of meristematic cells, (l_e) length of cells that completed their growth, (V) growth rate, (T) mitotic cycle duration, and (K_e) relative rate of elongation in primary roots of monocots and dicots and adventitious roots of monocots (*)

Parameter	Monocotiledons		Dicotiledons
	$n = 35$	$n = 24$ (*)	$n = 63$
C_{val}, pg	0.23	0.18	0.29
P, g	0.78	–	0.70
L_m, μm	0.97	0.81	0.99
N_m, cells	0.88	0.30	0.86
l_m, μm	0.39	0.41	0.67
l_e, μm	0.61	0.44	0.55
V, mm/h	0.86	0.36	0.74
T, h	0.03	–0.05	0.34
K_e, h^{-1}	0.19	0.05	–0.13

The current growth rate of the root is determined by the growth of elongating cells, since they grow much faster than meristematic cells. However, the maintenance of growth rate requires a shift to elongation of new cells from the meristem. In fact, the faster growth of the roots of a bigger diameter is a result of more numerous elongating cells rather than the higher relative rate of their growth (Table 2). In this case, like that of the mitotic cycle, the richer influx of necessary substances does not accelerate the growth itself but increases the number of elongating cells. These two interesting examples demonstrate that the enhanced growth rate may be accomplished due to quite different cellular mechanisms.

ACKNOWLEDGMENTS

This work is dedicated to the memory of Prof. L. Kutschera. We are very grateful to I.V. Seregin for the critical discussion of the results. This study was supported in part by the Russian Foundation for Basic Research, project no. 15-04-02502a.

REFERENCES

Dello Ioio, R., Linhares, F.S., Scacchi, E., et al., Cytokinins determine *Arabidopsis* root-meristem size by controlling cell differentiation, *Curr. Biol.*, 2007, vol. 17, pp. 678–682.

Erickson, R.O. and Sax, K.B., Elemental growth rate of the primary root of *Zea mays, Proc. Am. Philos. Soc*., 1956, vol. 100, pp. 499–514.

Galinha, C., Hofhuis, H., Luijten, M., et al., PLETHORA proteins as dose-dependent master regulators of *Arabidopsis* root development, *Nature*, 2007, vol. 449, pp. 1053–1057.

Gazques, A. and Beemster, G.T.S., What determines organ size differences between species? A meta-analysis of the cellular basis, *New Phytol*., 2017. doi 10.1111/nph.14573

Goodvin, R.H. and Avers, C.J., Studies on roots. III. An analysis of root growth in *Phleum pretense* using photomicrographic records, *Am. J. Bot*., 1956, vol. 43, pp. 479–487.

Grif, V.G., Ivanov, V.B., and Machs, E.M., Cell cycle and its parameters in flowering plants, *Cytologia*, 2002, vol. 44, pp. 936–980.

Hacham, Y., Holland, N., Butterfield, C., et al., Brassinosteroid perception in the epidermis controls root meristem size, *Stem Cells Dev.*, 2011, vol. 138, pp. 839–848.

Ivanov, V.B., *Kletochnye osnovy rosta rastenii* (Cellular Basis of Plant Growth), Moscow: Nauka, 1977.

Ivanov, V.B. and Dubrovsky, J.G., Estimation of the cell-cycle duration in the root apical meristem: a model of linkage between cell-cycle duration, rate of cell production, and rate of root growth, *Int. J. Plant Sci.*, 1997, vol. 158, pp. 757–763.

Ivanov, V.B., *Kletochnye mekhanizmy rosta rastenii* (Cellular Mechanisms of Plant Growth), Moscow: Nauka, 2011.

Ivanov, V.B. and Dubrovsky, J.G., Longitudinal zonation pattern in plant roots: conflicts and solutions, *Trends Plant Sci.*, 2013, vol. 18, pp. 237–243.

Kudo, T., Kiba, T., and Sakakibara, H., Metabolism and long-distance translocation of cytokinins, *J. Integ. Plant Biol*., 2010, vol. 52, no. 1, pp. 53–60.

Kutschera, L., Lichtenegger, E., and Sobotik, M., *Wurzelatlas mitteleuropaischer Grunlandpflanzen*, Bd. 1: *Monocotyledoneae*, Stuttgart, Jena, New York: Gustav Fisher, 1982.

Kutschera, L., Sobotik, M., and Lichtenegger, E., *Wurzelatlas mitteleuropaischer Grunlandpflanzen*, Bd. 2: *Pteridophyta und Dicotyledoneae (Magnoliopsida)*, Teil 1: *Morphologie, Anatomie, Okologie, Verbereitung, Soziologie, Wirtschaft*, Stuttgart, Jena, New York: Gustav Fisher, 1992.

Kutschera-Mitter, L., Erklarungen des geotropen Wachstums aus Standort und Bau der Pflanzen, in *Land- und forstwirtschaftliche Forschung in Osterreic*, 1972, vol. 5, pp. 40–89.

Malamy, J.E. and Benfey, P.N., Organization and cell differentiation in lateral roots of *Arabidopsis thaliana, Development*, 1997, vol. 124, pp. 33–44.

Muller, B., Stosser, M., and Tardieu, F., Spatial distributions of tissue expansion and cell division rates are related to irradiance and to sugar content in the growing zone of maize roots, *Plant Cell Environ*., 1998, vol. 21, pp. 149–158.

Shafiq, S., Chen, C., Yang, J., et al., DNA topoisomerase 1 prevents R-loop accumulation to modulate auxin-regulated root development in rice, *Mol. Plant*, 2017. doi 10.1016/j.molp.2017.04.001

Shmanaeva, T.N. and Leman, V.M., Effect of temporary darkness on the morphogenesis of tomatoes and the nucleic acid content in the apical meristem, *Izv. TSKhA*, 1970, vol. 2, pp. 25–32.

Su, Y.-H., Liu, Y.-B., and Zhang, X.-S., Auxin-cytokinin interaction regulates meristem development, *Mol. Plant*, 2011, vol. 4, pp. 616–625.

Ubeda-Tomas, S., Federici, F., Casimiro, I., et al., Gibberellin signaling in the endodermis control *Arabidopsis* root meristem size, *Curr. Biol.*, 2009, vol. 19, pp. 1194–1199.

Verbelen, J.P., De Cnodder, T., Le, J., et al., The root apex of *Arabidopsis thaliana* consists of four distinct zones of growth activities: meristematic zone, transition zone, fast elongation zone and growth terminating zone, *Plant Signal. Behav.*, 2006, vol. 1, pp. 296–304.

Werner, T., Holst, K., Pors, Y., et al., Cytokinin deficiency causes distinct changes of sink and source parameters in tobacco shoots and roots, *J. Exp. Bot*., 2008, vol. 59, pp. 2659–2672.

Zhukovskaya, N.V., Bystrova, E.I., and Ivanov, V.B., Length of meristematic and fully elongated root cells related to haploid DNA content, *Russ. J. Dev. Biol*., 2016, vol. 47, pp. 326–334.

Translated by A. Aver'yanov