PARENCHYMA CELL GROWTH IN POTATO TUBERS
I. DIFFERENT TUBER REGIONS

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ABSTRACT

Enlargement rates of starch-storage parenchyma cells during growth of Kennebec and Russet Burbank potato cultivars were determined for cortical, perimedullary, and pith tissuues of bud ends, midsections, and stem ends of tubers. Average volumetric size of parenchyma cells increased 7 to 18x during growth of Russet Burbank tubers, with the greatest increases occurring in cortical and perimedullary cells of bud ends and midsections, and the least in stem ends and pith tissues. In Kennebec tubers parenchyma cells in both stem end and midsection increased only 5 to 8 x, whereas increases in bud ends ranged from 8 to 20 times.

Cell enlargement to tuber enlargement ratios appproached unity early in growth of Russet Burbank tubers. As tubers increased beyond the 45 g size, cell enlargement and tuber enlargement rates were essentially equal. Calculations of cells per unit tissue volume agreed with ratio determinations. The timing of such unity appeared to be delayed in Kennebec tubers, and was not quite as pronounced as in Russet Burbank tubers. This may have been due to differences in growth rates of individual tubers in response to cultural conditions. In general, cells of harvest-mature Kennebec tubers were about 60% as large as similar cells of Russet Burbank tubers.

INTRODUCTION

Potato tubers grow as a result of cell division and subsequent cell enlargement, principally in the internal and external phloem areas (1). Perimedullary starch-storage parenchyma is produced in the internal phloem areas, and additional parenchyma is formed in the cortical area external to the xylem "ring" (1, 9). These tissues differ in cell size and composition at harvest. Cell sizes also differ between stem ends and bud ends of tubers, and among cultivars (10, 11). Cell sizes at harvest maturity also can be influenced by soil moisture and nitrogen nutrition during tuber growth (12). Cell sizes also relate to the culinary quality of different cultivars (5). However, little is known about the rates at which cells of the different tissues enlarge, or about the duration of active cell divisions.

Although Plaisted (6) concluled that cell division and cell enlargement continued concurrently throughout tuber growth, he did not account for possible variations in tuber shape, growth rates, and ratios of cell enlargement to tuber enlargement. Such information is necessary to evaluate the relative roles of cell division and cell enlargement in tuber growth, and to learn whether cell enlargement becomes equal to tuber enlargement.

A study of cell enlargement in different tissues during growth of Kennebec and Russet Burbank potatoes is presented here.

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Materials and Methods

Tubers were collected from Kennebec and Russet Burbank plants grown at Davis, California. The first collection was 83 days after planting, at which time the Kennebec tubers ranged from 1.5 to 310 g and the Russet Burbank tubers from 1.0 to 120 g. The second collection was 115 days after planting, 3 days after the vines had been removed. The Russet Burbank plants had received 135 kg N/ha and the Kennebec plants 67 kg N/ha, both as $(NH_4)_2SO_4$. In addition to the two levels of N, 118 kg P/ha of superphosphate were applied. Soil moisture tension was maintained about 0.5 atm by furrow irrigation and monitored with tensiometers.

All tubers 1 g and over were held overnight in a refrigerator, then sectioned fresh on a sliding microtome into thicknesses ranging from 80 to 240 microns according to apparent cell size. Tubers of 40 g or more were carefully selected for uniformity of shape, and sections were cut from blocks of tissue removed from bud ends, midsections, and stem ends as previously described (12). The smaller tubers were sectioned lengthwise, and only the near median sections were used for cell measurements. All freshly cut sections were preserved in 8% aqueous formalin until measurements were made.

Measurements of pith, perimedullary, and cortical cells were made with a microscope, with a calibrated eye-piece micrometer scale (12). Cells representing divisions in younger tubers could be readily detected in fresh sections by the new, very thin cross walls which provided new wall facets about equal to the diameters of parent cells.

One to three tubers of each size selected were measured. Cell diameters were converted to cell volumes as spheres to provide a realistic comparison between cell size and tuber size. Assuming that successively larger sizes of immature tubers and their parenchyma cells represent growth intervals, ratios of tuber enlargement and of cell enlargement each were calculated as older (or larger)/younger (or smaller). The ratios of cell enlargement ratio then were calculated, using perimedullary cell sizes from midsections of the tubers as indices. Number of perimedullary cells per unit votume of perimedullary tissue also was calculated, using the cube of the depth of the perimedullary tissue at midsection for each tuber size.

Results and Discussion

As shown in earlier studies (9), much of the growth comprising tuber initiation from the stolon tip is due to cell enlargement of the fundamental parenchyma cells in the pith area of the tip. Some cell division occurs in this tissue, but divisions are more frequent in the procambial derivatives of inner and outer phloem strands in the perimedullary and cortical regions of the very young tuber. Divisions in these areas accommodate for the cell enlargement of the pith, where some cell divisions parallel to the stolon axis add new files of the so-called rib meristem, or young pith. When the young tuber is 2 to 4 mm in diameter, the funadmental parenchyma cells range from about 40 μ diameter in the cortical area to over 80 μ in the pith-perimedullary area. Divisions have just well begun in the smaller cells surrounding the inner and outer phloem strands. Many of these

TABLE 1.—*Weight of tubers, thickness of perimedullary tissue in millimeters, and number of cells and size of cells at midsections of tubers harvested 83 and 115 days after planting.*

Cultivar	Days from planting	Size (g)	Avg cell diam (μ)	Thickness of perimedullary tissue	
				mm	Linear number cells
Russet Burbank	83	1.2	91	2.8	31
	83	15.0	136	9.9	73
	83	45.0	140	13.0	93
	83	90.0	154	15.5	101
	83	120.0	156	16.8	107
	115	70.0	165	12.0	73
	115	235.0	192	20.5	107
	115	300.0	213	22.0	103
Kennebec	83	1.5	92	2.8	30
	83	5.0	88	5.0	57
	83	32.0	110	10.5	95
	83	84.0	136	15.0	110
	83	146.0	145	16.4	113
	83	310.0	155	22.0	142
	115	340.0	176	23.5	133
	115	385.0	180	24.1	134

smaller cells contain only very minute starch granules. It is therefore likely that the mitotic figures in Bradbury's (2) observations on division of starch-containing cells were either of young pith or of cortical parenchyma cells in a 4 mm diameter tuber, rather than of the smaller procambial-like cells associated with phloem strands.

For the above reasons, it has seemed practical to consider cell enlargement vs. tuber enlargement only after both the inner and outer starch-storage parenchyma derived from procambial-like activity has been well established. In the present material these tissues were well differentiated in young tubers slightly over 1 g in weight.

Increased thickness of perimedullary tissue in Russet Burbank tubers over 45 g is directly related to cell enlargement (Table 1). Very nearly the same situation exists in Kennebec tubers over 32 g. Exceptions are the 70 g Russet Burbank as harvested 115 days after planting and the 310 g Kennebec tuber as harvested 83 days after planting. It seems reasonable that the small Russet Burbank tuber was a slow grower in which cell division had greatly diminished during early growth. Conversely, it seems reasonable that the 310 g Kennebec tuber was a rapid grower in which more divisions in the perimedullary tissue occurred during early growth.

Increases in average cell volume with tuber weight are shown in Fig. 1 and 2 for Kennebec and Russet Burbank, respectively. The smaller size of young perimedullary and cortical cells in the midsection of the 5 g Kennebec tuber (Fig. 1), as compared with the 1.5 g tuber, could reflect a higher frequency of divisions. One might expect such differences

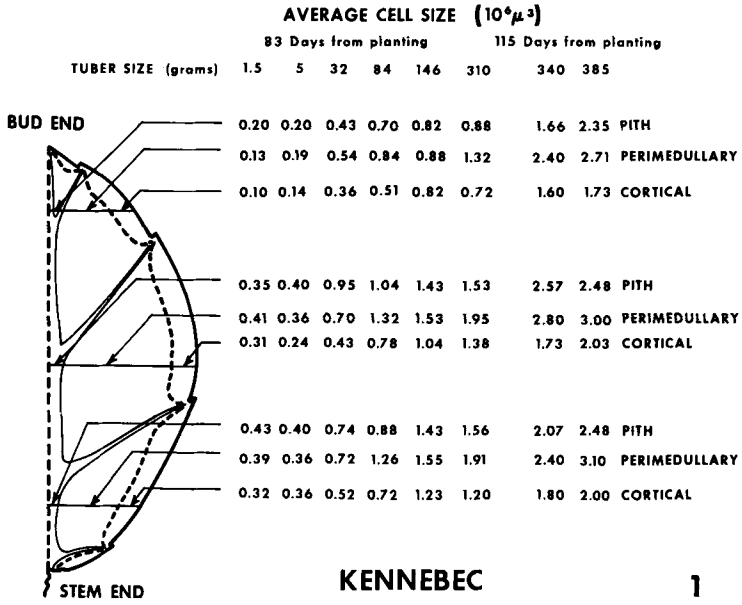

FIG. 1.—Cell size increase during growth of Kennebec tubers.

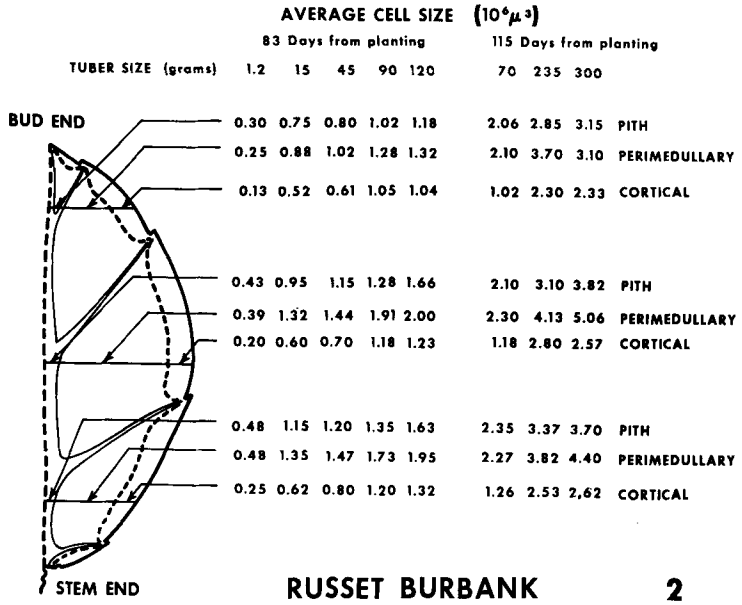

FIG. 2.—Cell size increase during growth of Russet Burbank tubers.

during these very early stages of tuber growth to be associated with stolon location on the parent plant.

Cell size during growth and at harvest maturity also revealed differences between cultivars. In general, cell size of the mature Kennebec tubers was about 60% that in mature Russet Burbank tubers (Figs. 1, 2). Similar distinctions between medium sized mature White Rose and Russet Burbank tubers have been previously reported (7). Again, exceptions in the present material were the slow growing 70 g Russet Burbank tuber and the rapidly growing 310 g Kennebec tuber.

No attempt was made to treat cell measurements statistically because of the deliberate selection of starch-storage parenchyma cells between phloem strands, as previously described in studies on nitrogen nutrition and cell size (12). This deliberate selection eliminated from study small parenchyma cells closely associated with the phloem. Thus, all measurements reflect dimensions of those cells which comprise the bulk of the starch-storage parenchyma of the tubers, and which represent, by their enlargement, the bulk of tuber growth. In general, within each set of cells measured, the diameters of larger cells averaged about ⅓ greater than diameters of the smaller cells. This would account for over a 2x range in volumetric size of individual cells. Volumetric size distribution followed a normal, broad curve slightly skewed to the smaller size. Such distribution was characteristic for cells of both immature and harvest-mature tubers.

The young expanding tuber grows like the axis of an expanding bud of a leafy shoot. New tissues are continuously formed apically as those earlier formed undergo cell enlargement. Thus, tissues formed in the bud end of a very young tuber soon become midsection tissues, and midsection tissues become relatively closer to stem end tissues as the tuber elongates. In addition, the potato tuber undergoes pronounced circumferential expansion which is most pronounced at midsection. Cell divisions would be expected to be most frequent in bud ends of young tubers, and more frequent at midsections than in stem ends.

As cell enlargement rapidly becomes the dominant mode of tuber growth, cell enlargement ratio and tuber enlargement ratio become nearly equal early in tuber growth. Thus, these ratios may be used as indices for cortical and perimedullary tissues of the Kennebec and Russet Burbank, respectively (Tables 2 and 3). In each, the ratios of cell enlargement to tuber enlargement include a consideration of the derivation of midsection tissues from bud end tissues, and stem end tissues from midsection tissues for all young tubers. However, the limited sampling does not account for variations in tuber shape at maturity.

Total tuber growth by weight, for both cultivars, ranged from 225- to 260-fold. However, cell size ranged from 5 to 20-x in Kennebec and from 7 to 18-x in the Russet Burbank. This indicates that many new cells were formed early in tuber growth. However, the data also show that cell enlargement became increasingly dominant in tubers beyond the 30- to 45- g size. About the same ratios of enlargement were noted for cortical and perimedullary cells in each region of the tubers, except that greater variation was found in Kennebec than in Russet Burbank. These observations closely agree with prior interpretations (7, 8) that, as starch granules in tubers about 2 cm (¾ in) in diameter begin to reach sizes

TABLE 2.—*Enlargement ratios of tubers and of cortical and perimedullary cells of Kennebec tubers.*

Tuber sizes (g)	83 days after planting					115 days after planting	
	1.5 to 5	5 to 32	32 to 84	84 to 146	146 to 310	146 to 340	146 to 385
Tuber enlargement ratio	3.33	6.4	2.62	1.74	2.13	2.4	2.63
			Cortical cell enlargement ratio / Tuber enlargement ratio				
Cell enlargement ratios compared							
Bud end older / Bud end younger	0.42	0.40	0.54	0.94	0.42	0.81	0.80
Midsection older / Bud end younger	0.72	0.49	0.83	1.17	0.79		
Midsection older / Midsection younger	(0.24)	0.28	0.69	0.76	0.60	0.70	0.74
Stem end older / Midsection younger	0.35	0.34	0.64	0.91	0.54		
Stem end older / Stem end younger	0.34	0.23	0.53	0.98	(0.47)	0.61	0.62
			Perimedullary cell enlargement ratio / Tuber enlargement ratio				
Bud end older / Bud end younger	0.44	0.45	0.59	0.60	0.65	1.13	1.17
Midsection older / Bud end younger	0.83	0.58	0.93	1.05	1.04		
Midsection older / Midsection younger	(0.27)	0.30	0.72	0.67	0.69	0.76	0.75
Stem end older / Midsection younger	(0.26)	0.31	0.70	0.68	0.59		
Stem end older / Stem end younger	(0.27)	0.31	0.67	0.71	0.58	0.65	0.76

peculiar to different tissues of mature tubers, the cell division rate greatly diminishes and further enlargement of the tuber is mainly by cell enlargement.

The 310 g Kennebec tubers, abnormally large at 83 days after planting, may possibly represent an abnormal growth rate related to development of hollow heart. Small pith cavities were found in the lower midsection and stem ends of both 310 g Kennebec tubers examined. Levitt (4) found hollow heart to be histologically associated with pith cell necrosis, as found also in our later studies (8). However, Levitt also suggested that more rapid growth of perimedullary than of pith tissues could initiate hollow heart.

Differences between cultivars in cell size of cortical and perimedullary cells, in different tuber zones, and differences in the extents of these tissues from bud ends to stem ends of tubers preclude any sensible calculation of cells per whole tuber. However, because the total solids contents of perimedullary tissues are more representative of the whole tuber (11), cells

TABLE 3.—*Enlargement ratios of tubers and of cortical and perimedullary cells of Russet Burbank tubers.*

Tuber sizes (g)	83 days after planting 1.2 to 15	15 to 45	45 to 90	90 to 120	115 days after planting 45 to 70	120 to 235	120 to 300
Tuber enlargement ratio	12.5	3.0	2.0	1.33	1.55	1.96	2.5
			Cortical cell growth ratio				
Cell enlargement ratios compared			Tuber growth ratio				
Bud end older							
Bud end younger	0.40	0.39	0.86	0.75	1.08	1.12	0.90
Midsection older							
Bud end younger	0.38	0.45	0.97	0.88			
Midsection older							
Midsection younger	0.24	0.39	0.84	0.74	1.08	1.16	0.84
Stem end older							
Midsection younger	0.25	0.44	0.85	0.84			
Stem end older							
Stem end younger	0.20	0.43	0.75	0.83	1.01	0.98	0.80
			Perimedullary cell enlargement ratio				
			Tuber enlargement ratio				
Bud end older							
Bud end younger	0.28	0.39	0.63	0.77	1.33	1.40	0.94
Midsection older							
Bud end younger	0.42	0.55	0.94	1.17			
Midsection older							
Midsection younger	0.26	0.36	0.66	0.79	0.96	1.05	0.97
Stem end older							
Midsection younger	0.36	0.37	0.60	0.77			
Stem end older							
Stem end younger	0.22	0.36	0.59	0.84	0.93	1.00	0.90

per unit volume of perimedullary tissue can be readily calculated for midsections of tubers, and also for total perimedullary tissue, using average perimedullary cell volume at midsection. It previously has been shown that total perimedullary tissues comprise about 52% of total mature tuber fresh weight in the Kennebec, and about 50% in the Russet Burbank (11). Thus, cells per total perimedullary tissue can be calculated on the assumption that a similar distribution holds for all but the younger tubers. It is also convenient to calculate cells per unit volume of perimedullary tissue based upon the cube of the thickness of perimedullary tissue at a given stage of tuber growth (Table 4).

The data in Table 4 agree with the linear-based calculations in Table 1, and with the ratios of cell enlargement to tuber enlargement in Tables 2 and 3, as based upon perimedullary tissue. Numbers of cortical cells follow a similar pattern but have not been included because of variations in thickness of cortical tissue in individual tubers. Thus, as tubers enlarge beyond 30-45 g, numbers of cells become relatively constant. This could only happen when cell division has become negligible.

TABLE 4.—*Numbers of perimedullary cells during tuber growth.*

Cultivar	Days after planting	Tuber size (g)	Number of cells: Per cube of perimedullary tissue midsection depth (10^5)	Number of cells: Per total of perimedullary tissue[2] (10^9)
Kennebec	83	1.5	5.3	1.9
	83	5.0	6.9	7.2
	83	32.0	16.5	23.8
	83	84.0	23.3	31.8
	83	146.0	28.8	48.7
	83	310.0	54.5	88.0
	115	340.0	46.3	63.8
	115	385.0	44.9	66.7
Russet Burbank	83	1.2	5.6	1.3
	83	15.0	7.3	5.7
	83	45.0	15.3	15.6
	83	90.0	19.5	25.1
	83	120.0	23.3	30.0
	115	70.0	7.5	15.2
	115	235.0	20.8	30.9
	115	300.0	21.0	29.6

[1]Based on average perimedullary cell volume at midsection.

[2]Total perimedullary tissue considered as 52% of total tuber weight (or vol.) for Kennebec and 50% for Russet Burbank.

These conclusions differ from those of Plaisted (6), whose detailed studies included many compositional factors expressed on a per cell basis. Plaisted, however, did not consider ratios of cell enlargement to tuber enlargement, or linear depths of perimedullary tissues at different stages of tuber size. He recognized tissue shrinkage as an artifact in use of thin sections from embedded tissue. Other artifacts may occur by compression and distortion which tend to increase in microtomy with increase in cell size in tissues sectioned (3, 13). In addition, the true diameter of a large, nearly spherical polyhedral cell cannot be accurately measured from 15μ thick sections, many of which reveal less than the greatest diameter. Despite these artifacts, it is remarkable that Plaisted's data, although not separated into earlier and later harvests, strongly indicate the inclusion of slower and faster growing tubers, as found here for Russet Burbank and Kennebec, respectively. Also, some of the combinations, of larger and smaller tubers in Plaisted's data, yield ratios of cell enlargement to tuber enlargement that approach unity.

Although cell division rate diminishes early in tuber growth, sampling of very small tubers was limited. Tubers weighing about 1 g, or having a diameter of 1 cm, already have undergone an appreciable amount of cell enlargement by comparison with stolon tips swollen to 2 or 3 mm in diameter. Growing location also could influence tuber shape and cell numbers.

Further studies are required to learn more precisely the comparative importance of cell division and cell enlargement in tuber growth.

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