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Changes in anatomical structure of apple fruitlet pedicels preceding June drop

HANNA HABDAS[1], LESZEK S. JANKIEWICZ[1], BOŻENA BORKOWSKA[2]

[1]Research Institute Vegetable Crops, 22 lipca 1/3, 96-100 Skierniewice; [2]Research Institute of Pomology, Pomologiczna 18, 96-100 Skierniewice, Poland

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Abstract

The anatomical structure of pedicels of apple fruitlets was investigated. The fruitlets of cv. 'McIntosh' and 'Bancroft' were collected on June 8th, 16th an 24th. The middle date coincided with the beginning of June drop. The pedicel structure of larger fruitlets which tended to be retained on the tree was compared with that of smaller fruitlets which tended to be shed of. In the pedicels of larger fruitlets, development of the xylem, especially secondary one, was more intensive. This difference increased in time. Lignification of cortex sclereids, phloem fibers, xylem parenchyma cells and pith cells was also more advanced. The differences in the amount of phloem tissue between both kinds of fruitlets were not large but usually significant. The mentioned differences especially in pedicel xylem development are considered to be partly responsible for the fact that smaller fruitlets loose gradually their ability to compete for nutrients. This finally leads to their starvation and shedding.

INTRODUCTION

Shedding of a part of too abundantly set fruitlets or flower buds takes place in several horticultural plants and is of economic significance (Kozlowski, 1973; Weinbaum et al., 1977; Subhadrabandhu et al., 1978; Plich, 1979). June drop of apple fruitlets with which this paper is dealing is well described in the literature, although its physilogical mechanism is only superficially understood, in spite of good progress of the investigations performed recently (Wertheim, 1971; Schneider, 1977; 1978a, b). More knowledge on the development of vascular tissues in apple pedicels seems, however, necessary for elucidation of the functioning of this mechanism. Studies on the pedicel anatomy of apple fruitlet are scarce and they deal mostly with the abscission zone (McDaniels, 1936; McCown, 1943).

The aim of the present study was to examine the anatomical changes which take place in pedicels of fruitlets differing markedly in size, in the time preceding June drop. As known, the larger fruitlets tend to be retained on the apple tree, whereas the smaller ones tend to be shed in late June or early July.

MATERIAL AND METHODS

Apple fruitlets of cv. 'McIntosh' and 'Bancroft' were collected on the following dates: June 8th, i. e. before June drop, June 16th – at the beginning of June drop, June 24th – during advanced June drop. The fruitlets were collected from 5 trees of each cultivar. Only the larger and smaller fruitlets were collected from a given spur whereas the middle ones were left unpicked. From each of the populations: of larger fruitlets and of smaller ones, 10 fruitlets were examined on each date. From them 4 average, randomly chosen fruitlets were taken for detailed analyses and measurements.

The pedicels were immersed in a CrAF mixture, embedded in paraffin and afterwards 12 μm thick cross-sections were cut from their proximal part, i. e. 1-2 mm below the future abscission zone, from their middle part and also from their distal part, i. e. 2-3 mm above the exocarp. The preparations were stained with aqueous 1% safranin and then with 0.2% ethanolic fast green. Moreover, part of the sections of fresh material were cleared with Javels water (NaOCl) and stained with 1% alum carmine containing 0.05% methyl green (Johansen, 1940). After staining the cross-sections were examined under the light microscope. Some longitudinal sections were also made to observe some details of the pedicel structure. The results were elaborated statistically by analysis of variance using Duncan's multiple range test for significance at $P = 0.05$. In some cases transformations of experimental data were applied according to the formula $z = \sqrt{x + 0.05}$ where x means experimental data.

RESULTS

Larger and smaller fruitlets from which the pedicel cross-sections were taken differed more and more in their volume as time elapsed (Fig. 1). Pedicels collected on subsequent dates showed marked developmental differences in their anatomical structure.

Pedicel structure of larger 'McIntosh' fruitlets

June 8th. The xylem layer was rather narrow in this stage of development and contained no secondary elements (Figs 5 and 6). At this date the differences in anatomical structure between the larger and smaller fruitlets were very small.

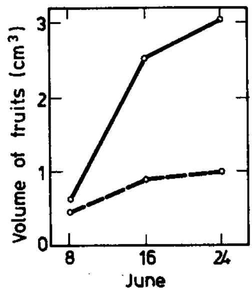

Fig. 1. Volume (cm^3) of larger (solid line) and smaller (broken line) fruitlets on three dates. Each point represents an average of 10 fruitlets. After measuring their volume the fruitlets were used for anatomical analysis of their pedicels

June 16th. Three parts of the pedical: proximal, middle and distal differed in their structure (Fig. 2 see also Fig. 7: photos 1-4; Table 1).

In the proximal part (Fig. 2) there were few layers of colenchyma under the epidermis. More centrally from them there were several layers or thin-walled cortex parenchyma cells containing, like colenchyma cells, chloroplasts. The inner cortex parenchyma cells bordering the phloem fibers were very large and, often had thick lignified walls. According to E s a u (1965) they can be regarded as sclereids. Inward from the cortex sclereids there was a system of large bundles of phloem fibers. The phloem fibers situated nearer the cortex were wider and had thick lignified walls, whereas those nearer the phloem were narrower and had thinner, less lignified walls. Phloem was rather thick and cambium was composed of 3-4 layers of cells. The xylem contained only proto- and metaxylem elements. There was a large pith region composed mostly of living thin-walled cells. Only near the xylem bundles there were some layers of pith cells with thick lignified walls. In the middle part of the pedicel (Fig. 2) the layer of the outer thin-walled cortex parenchyma cells was thinner than in the proximal part. The cortex sclereids were less lignified.

The phloem fibers zone was narrower and contained only cells with thick lignified walls. The development of the xylem was much more advanced and a large zone of secondary xylem was already visible. In the pith there were many lignified cells.

In the distal part (Fig. 2) the zone of cortex parenchyma was broad, but contained less lignified sclereids than the other parts of the pedicel. On the other hand, lignification of the cell walls of phloem fibers was much more advanced than in the proximal part. The amount of phloem tissue was similar to that in the middle part. The amount of secondary elements in the xylem was also similar to that in the middle part but was larger than in the proximal part. The pith cells were notlignified.

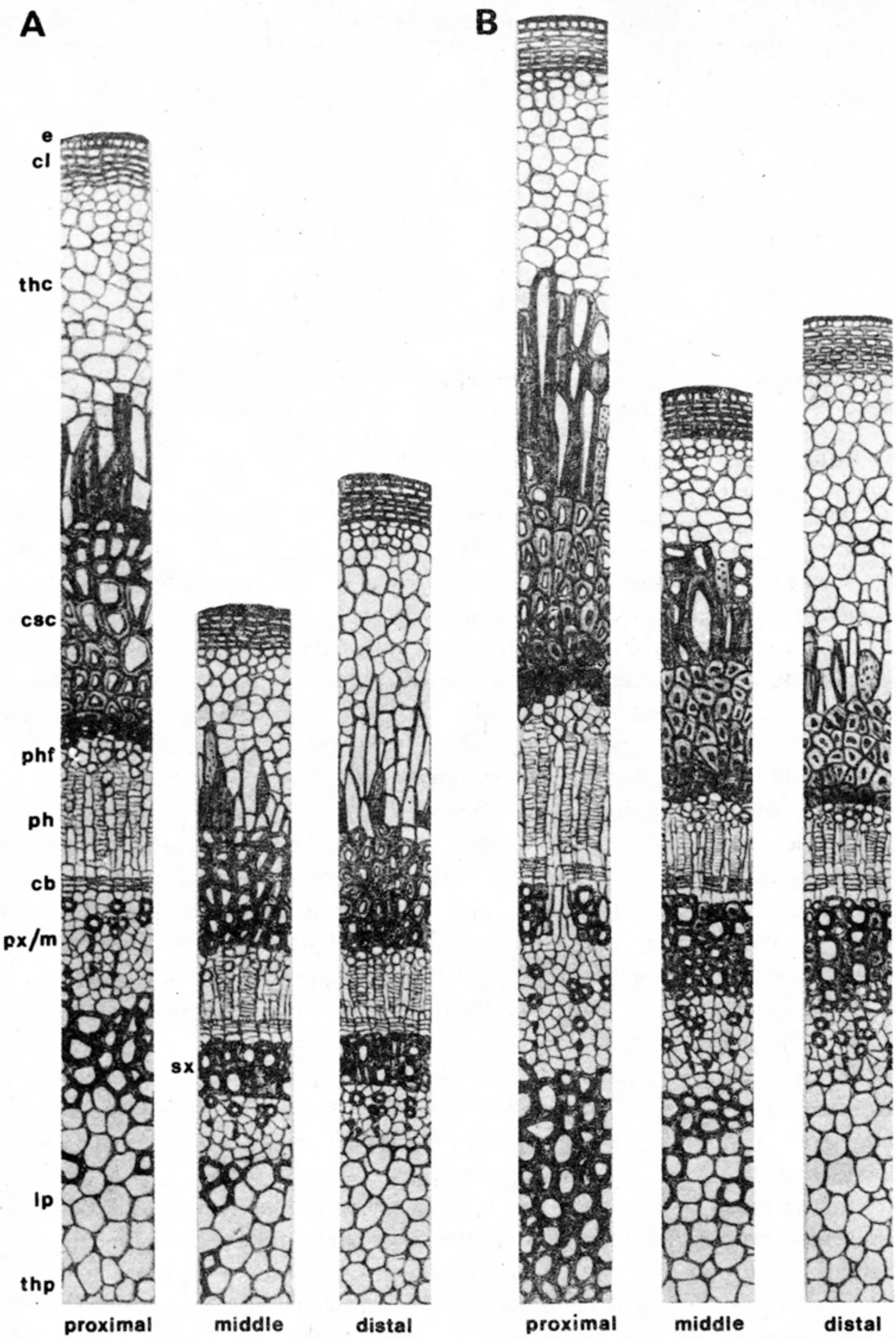

Fig. 2. Diagrams of cross-sections through proximal, middle and distal parts of pedicels of larger 'McIntosh' fruitlets harvested on June 16th (A) and 24th (B)

e – epidermis, cl – collenchyma, thc – thin-walled cortex parenchyma, cs – cortex sclereids, phf – phloem fibers, ph – phloem, cb – cambium, px/m – protoxylem and metaxylem, sx – secondary xylem, lp – lignified pith cells, thp – thin-walled pith cells. Magnification × 75

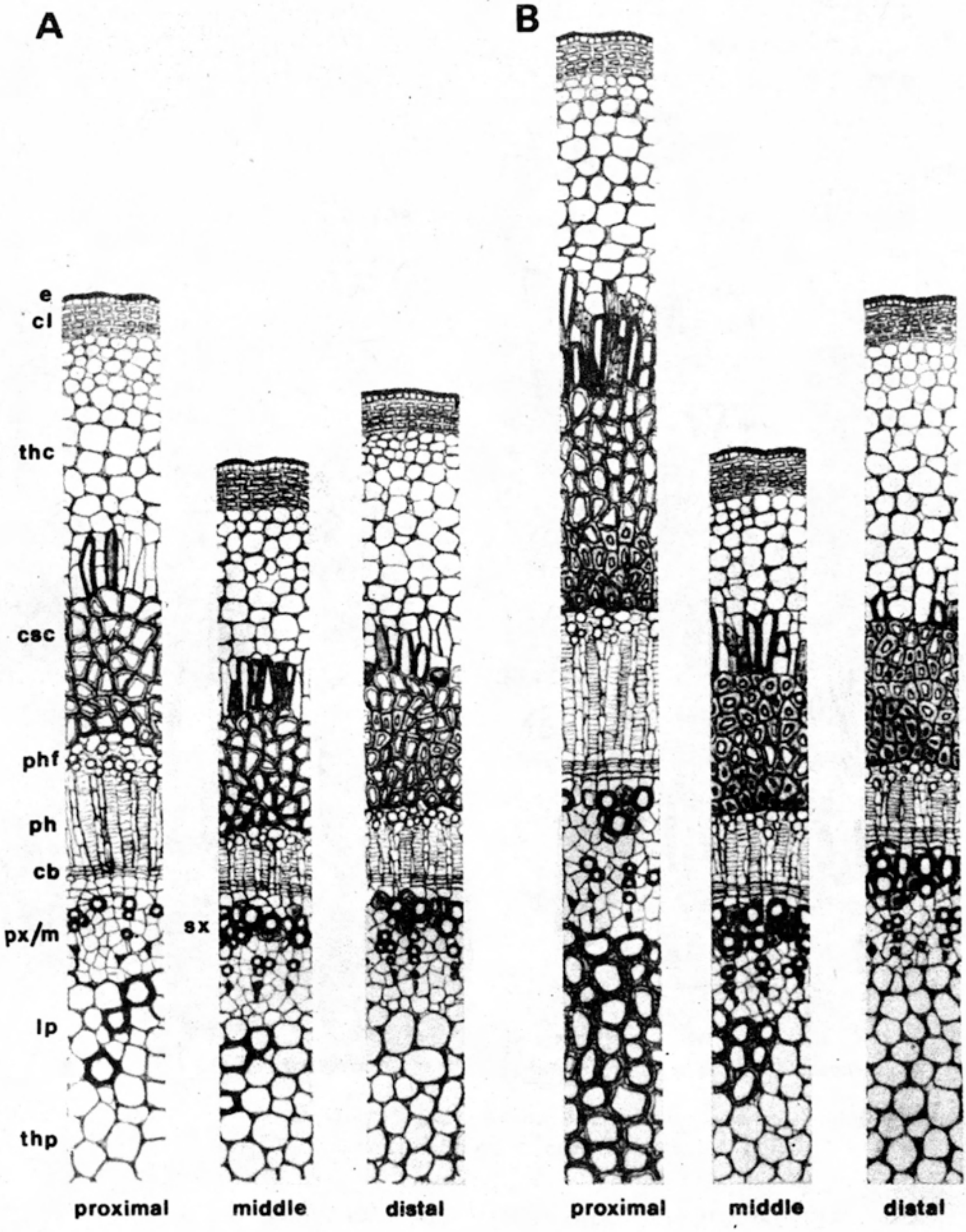

Fig. 3. Diagrams of cross-sections through pedicels of smaller 'McIntosh' fruitlets. For other details see Fig. 2

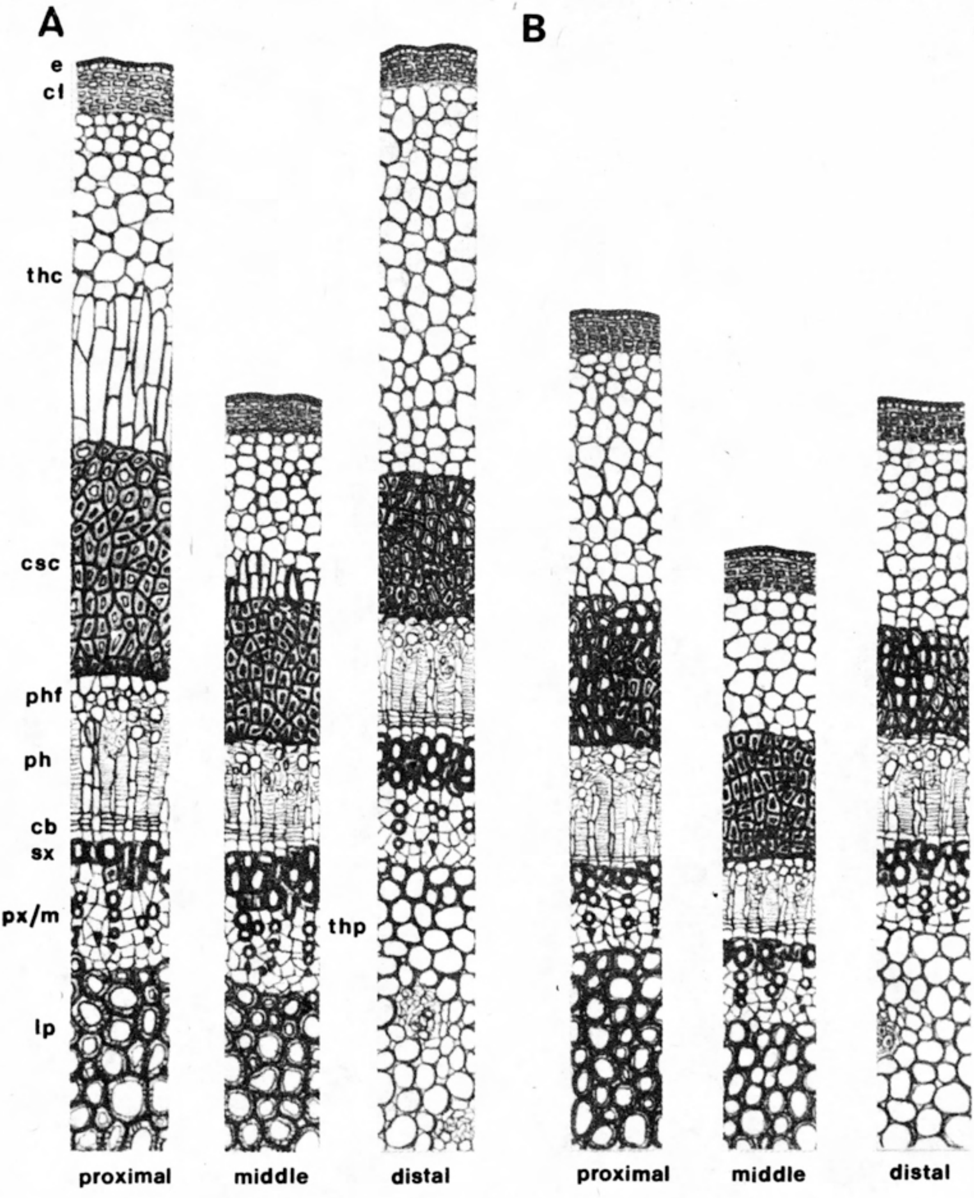

Fig. 4. Diagrams of cross-sections through pedicels of larger (A) and smaller (B) fruitlets of 'Bancroft' cv. harvested on June 16th. For other details see Fig. 2

June 24th. During the 8-day period since June 16th the development of pedicel structure became much more advanced (Fig. 2, Fig. 7: photos 5-8, Table 1). The ring of cortex parenchyma was broader. Lignification of cortex sclereids and of phloem fibers was more advanced, however, the differences between the particular parts of the pedicel persisted. The thickness of the phloem increased only slightly as compared with that on the previous date. There was of course much more xylem in all parts of the pedicel but it seems interesting that also on this date middle and distal parts of the pedicel contained much more xylem than the proximal part. Lignification of the pith in the proximal part of the pedicel was complete and in the middle part it was more advanced than on June 16th. In the distal part of the pedicel the cells were still nonlignified.

Pedicel structure of larger 'Bancroft' fruitlets

The arrangement of tissue in the pedicels of 'Bancroft' fruitlets was generally similar to that in 'McIntosh', but the differences between particular parts of the pedicel were less distinct (Fig. 4, and Table 1).

On June 8th the first secondary elements in middle and distal parts of the 'Bancroft' pedicels were noted whereas hardly any such elements were found in

Table 1

Degree of lignification of particular tissues in 'McIntosh' and 'Bancroft' pedicels. Differences between larger ans smaller fruitlets

Size of fruitlets	Date of harvest	The pedical part	'McIntosh'			'Bancroft'		
			cortex sclereids	floem fibers	pith	cortex sclereids	floem fibers	pith
Larger fruitlets	June 8th	proximal	+(+)	++	++	–	+	–
		middle	(+)	+++	–	–	+++	–
		distal	–	++	–	–	+(+)	–
	June 16th	proximal	++	+++	++	–	++++	++++
		middle	++	+++	+(+)	+	++++	++++
		distal	+	+++	–	–	++++	–
	June 24th	proximal	++++	+++(+)	+++(+)	++++	++++	++++
		middle	+++(+)	++++	+(+)	+++	++++	++++
		distal	+	++++	–	–	++++	–
Smaller fruitlets	June 8th	proximal	–	++	–	–	(+)	–
		middle	–	++(+)	–	–	(+)	–
		distal	–	++	–	–	(+)	–
	June 16th	proximal	(+)	++	(+)	–	+++(+)	++++
		middle	++	++(+)	(+)	–	++++	++++
		distal	+	++(+)	–	–	+++	–
	June 24th	proximal	+++	++(+)	+++(+)	+	++++	++++
		middle	++(+)	+++(+)	+	–	++++	++++
		distal	+	+++(+)	–	–	++++	–

Data in parentheses indicate that plant material was not uniform and on some cross-sections the elements were more lignified than on the others, for instance –(+) mean that the result is between – and +, i.e. between no lignification and very weak lignification.

Table 2

Differences in anatomical structure between larger (L) and smaller (S) fruitlet pedicels on 3 dates

Date		Semidiameter of pedicel (mm)	Thickness of cortex (mm)	Area of the phloem in one bundle (mm^2)	Thickness of phloem (mm)	Semidiameter of pith (mm)	Area of the xylem (mm^2)	Number of vessels	Number of xylem fibers	Number of lignified xylem tracheids and parenchyma cells
08.06	L	0.943^b	0.294^b	0.06^b	0.1295^b	0.2646^b	0.012^b	3.12^b	1.33^b	3.00^b
	S	0.823^a	0.263^a	0.03^a	0.1158^a	0.2346^a	0.008^a	0.08^a	0.04^a	0.08^a
16.06	L	1.300^b	0.475^b	0.10^b	0.1541^b	0.3133^b	0.025^b	10.96^b	3.62^b	21.66^b
	S	1.010^a	0.317^a	0.07^a	0.1356^a	0.2562^a	0.014^a	5.41^a	1.62^a	6.96^a
24.06	L	1.445^b	0.524^b	0.11^b	0.1788^b	0.3571^b	0.05^b	22.54^b	15.51^b	31.50^b
	S	1.150^a	0.393^a	0.09^a	0.1517^a	0.2892^a	0.03^a	10.71^a	4.16^a	16.87^a

Numbers marked with various letters differ significantly.

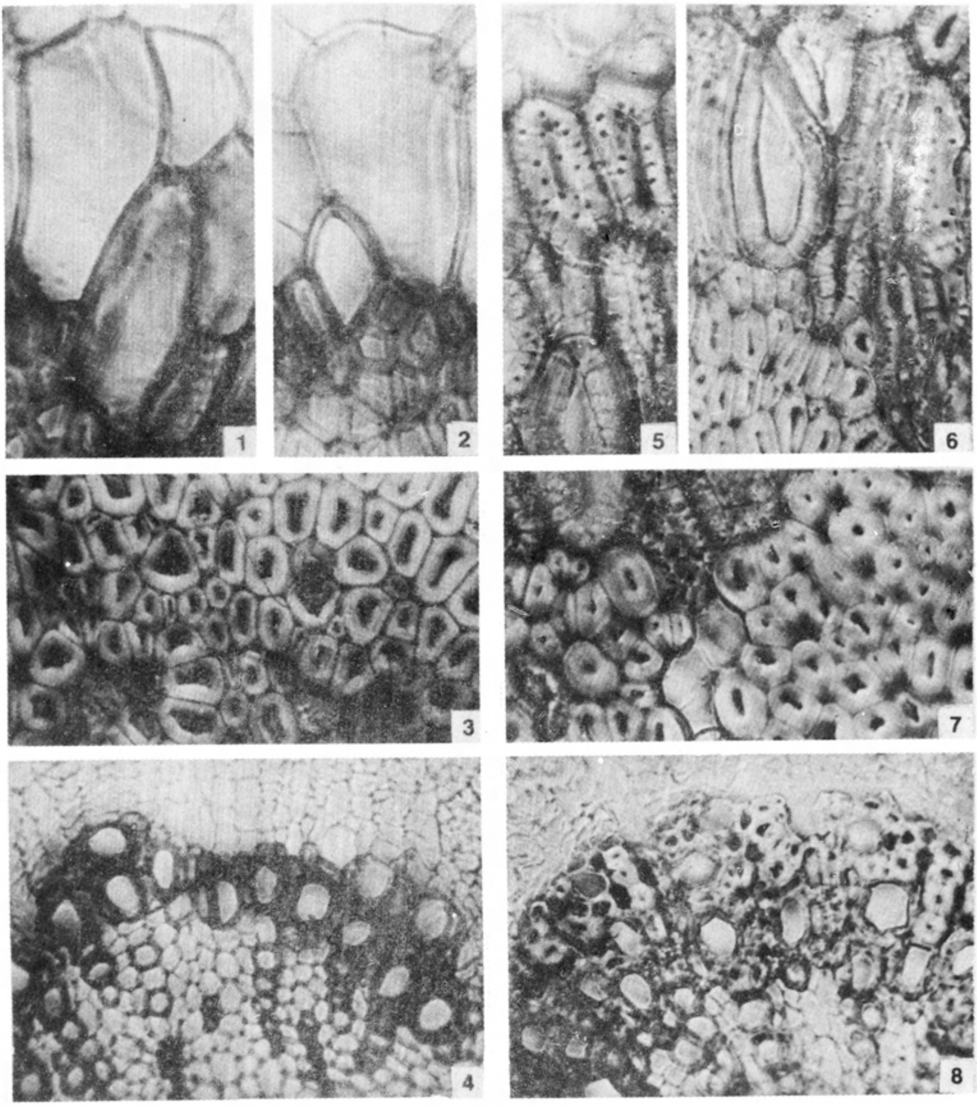

Fig. 7. Fragments of cross-sections through middle part of pedicels of 'McIntosh' larger fruitlets: progress of lignification of cortex sclereids (compare 1, 2 with 5, 6), phloem fibers (compare photos 3 with 7) and the development of secondary xylem (compare photos 4 with 8) between the dates June 16th (1,2,3,4) and 24th (5,6,7,8). Sections of fresh material clarified with Javel's water and stained with 1% alum carmine with 0.05% methyl green. Magnification × 166

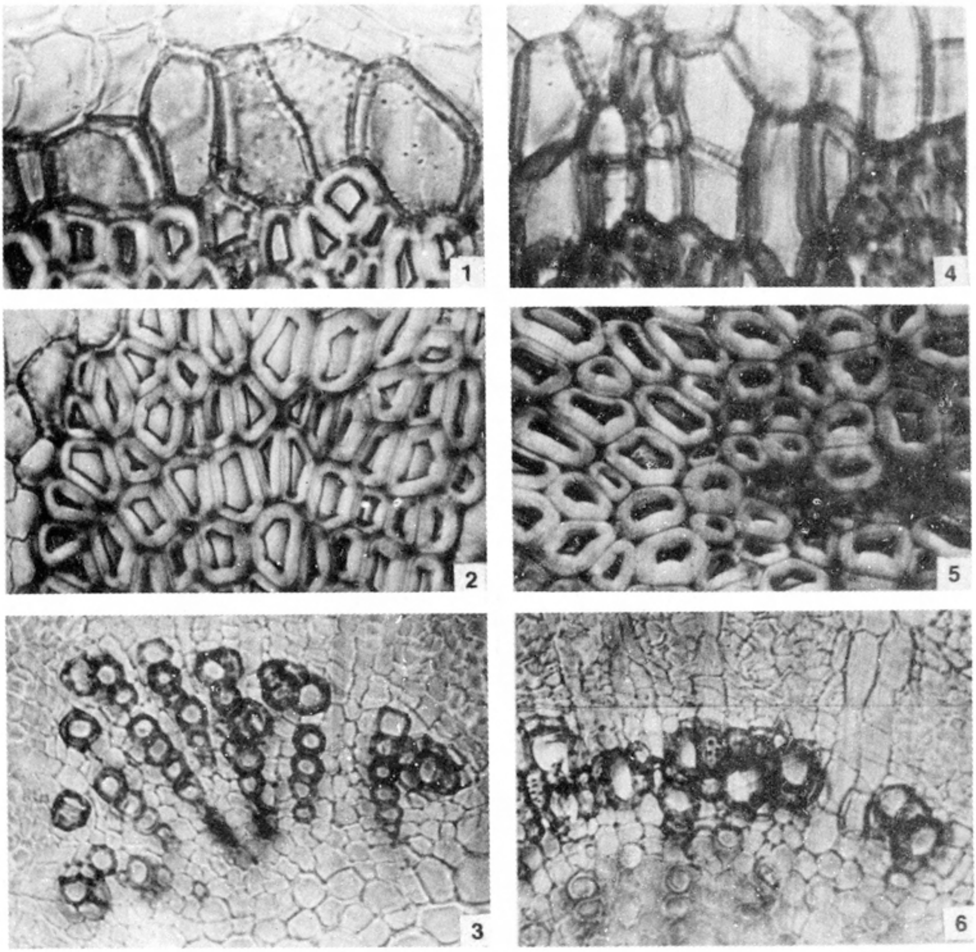

Fig. 8. Fragments of cross-sections through middle part of pedicels of 'McIntosh' smaller fruitlets: progress of lignification of cortex sclerids (compare 1 with 4), phloem fibers (compare 2 with 5) and the development of secondary xylem (compare 3 with 6) between the dates June 16th (1, 2, 3) and 24th (4, 5, 6). Sections of fresh material clarified with Javel's water and stained with 1% alum carmine with 0.05% methyl green. Magnification × 166

cortex thickness were small or null on June 8th but increased later. Cortex sclereids of larger fruitlets pedicels were larger, more numerous and more advanced in lignification than those of smaller fruitlets pedicels. In all parts of pedicels of smaller 'Bancroft' fruitlets cortex sclereids were even lacking up to June 24th. The area of phloem fibers was in most cases wider in larger fruitlets. The differences in phloem thickness were usually very small although significant. The differences in the pedicel xylem area between the two kinds of fruitlets seem to be very important: they were small or there were none on June 8th but increased in time. The same may be said of the number of vessels and of xylem fibers in the secondary xylem. An especially wide difference between the two kinds of fruitlets was found in the number of lignified xylem tracheids and xylem parenchyma cells. This difference increased markedly in time. The semidiameter of the pith was larger in pedicels of larger fruitlets. Besides, the pedicels of larger fruitlets showed more advanced lignification of cortex sclereids, phloem fibers and pith cells (Table 1).

DISCUSSION

The anatomy of the apple fruitlet pedicel has been described by several authors (McDaniels, 1936, McCown, 1938, 1943; Simons, 1963). They were not much concerned, however, with the differences in pedicel anatomy along its length. They described in detail only the differences in the abscission zone structure as compared with the rest of the pedicel. Our results show that, at the time of June drop, the proximal part of the pedicel shows, as compared with middle and distal parts, marked delay in secondary xylem development and at the same time vigorous and advanced development of the cortex sclereids, phloem fibers and advanced lignification of pith cells. The physiological meaning of these differences is not clear. It would be advisable to check in future experiments if the scarcer number of secondary xylem elements in the proximal part of the pedicel is an obstacle in solute transport through this part.

The differences in pedicel anatomy among larger and smaller apple fruitlets have not, according to our knowledge, been so far reported in the literature. Although Simons and Chu (1975) reported differences in the abscission zone region of presistent and ready to drop plum fruits. It seems interesting that the pedicels of larger and smaller apple fruitlets differ markedly in the amount of xylem (Fig. 6) (irrespective of the zone of the pedicel), but little in the amount of phloem (Fig. 5). It seems also important that the above mentioned difference in the amount of xylem increased gradually during the 16-day period preceding June drop. This phenomenon may play a role in the mechanism of June drop. Thus some of the fruitlets which are at the beginning only a little weaker than the others become gradually more suppressed owing to the increasingly delayed development of their vascular system. In consequence they probably lose gradually the ability to compete with larger fruitlets for nutrients and hormones supplied from the roots. This mechanism leads to shedding of only the weaker fruitlets with protection of the more vigorous ones. This mechanism seems to be similar to that responsible for differentiation of young apple tree buds into short and long shoots (Jankiewicz, 1972). During the critical period around mid June the competitive struggle between fruitlets for assimilates and nutrients becomes probably quite strong (Schneider, 1977, 1978a, b). At the same time the hormone balance of the tree (Champagnat, 1965) and of the fruitlet changes (Luckwill, 1953), this facilitating the final suppression of the smaller fruitlets and induction in them of premature senescence which leads to an increased production of abscission-accelerating substances (Dörffling et al., 1978) and to shedding (Jankiewicz, 1982).

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Zmiany w strukturze anatomicznej szypułek jabłek poprzedzające opad czerwcowy

Streszczenie

Badano budowę anatomiczną szypułek zawiązków jabłek odmiany 'McIntosh' i 'Bancroft'. Materiał zbierano w okresie poprzedzającym opad czerwcowy (8 VI) oraz w trakcie jego trwania (16, 24 VI). Badania struktury szypułek w części proksymalnej, środkowej oraz dystalnej wykazały zróżnicowanie stopnia rozwoju tkanek wzdłuż osi szypułki. Porównywano budowę szypułek zawiązków większych, które przeważnie nie są zrzucane w czasie opadu czerwcowego, z budową szypułek zawiązków mniejszych, które zwykle opadają. W szypułkach zawiązków większych stwierdzono silniejszy i wcześniejszy rozwój drewna wtórnego, jak również bardziej zaawansowaną lignifikację sklereidów w korze, włókien floemowych, komórek parenchymatycznych w ksylemie oraz komórek rdzenia, natomiast różnice w ilości floemu były niewielkie choć przeważnie istotne. Sugeruje się, że wspomniane, zwiększające się różnice w rozwoju drewna wtórnego między zawiązkami dużymi i małymi są jednym z czynników prowadzących do utraty przez zawiązki mniejsze zdolności do konkurowania z pozostałymi zawiązkami o substancje pokarmowe. Prowadzi to do przedwczesnego starzenia się i zrzucania mniejszych zawiązków.