FRUIT DEVELOPMENT AND SOME TREE FACTORS AFFECTING IT

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SUMMARY

The rate and duration of apple fruit growth, cell division, and cell expansion, were considered in relation to within-tree factors affecting them. Fruit size at harvest was found to be related to the position of fruit on the spur, seed number, spur size, number of fruits set on the spur, and the date of flowering. The position of fruit on the spur, and spur size, were related to blossom size, but not to the subsequent rate of fruit growth. The rate of growth appeared to be increased by higher seed numbers for the first few weeks after blossom, but there was some evidence that fruit with higher seed numbers had a lower rate of growth in the later stages. The effect of some of these factors on fruit set was also considered.

INTRODUCTION

Though there has been some previous work on the effect of various factors on fruit size at harvest, little is known about their effect on fruit development. The aim of the present work was to relate some within-tree factors to the rate and duration of apple fruit growth, cell division, and cell expansion. Incidentally to this, some data were obtained on the general pattern of fruit development, and on some varietal differences.

Previous Literature on Fruit Development

At full bloom, fruitlet growth is reported to be slow, or to cease for a few days (MacArthur and Wetmore, 1941; Smith, 1950 in apples; Nitsch *et al.*, 1960 in grapes). The duration of this preliminary period of slow growth varies from season to season (Denne, 1960); this may be related to the interval between pollination and fertilisation, though fertilisation is reported to occur before the end of this period in the grape (Nitsch *et al.*, 1960). The time from pollination to fertilisation appears to be very variable; in the apple it has been shown to take from 48 hours (Modlibowska, 1945) to 12 days (Wanscher, 1939).

After fertilisation there is a phase of rapid growth, which is exponential at first in cucurbits (Sinnott, 1945), and apples (Denne, 1960). Subsequently, the rate of growth may decline until harvest, giving a simple sigmoid type of growth curve, or there may be a period of little or no expansion between the rapid enlargement after fertilisation and the final swelling. The simple

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sigmoid type of growth curve is characteristic of the apple (Tetley, 1931, among many others), tomatoes and cucurbits (Gustafson, 1926), citrus (Elze, 1947; Bain, 1958), and the date (Haas and Bliss, 1935; Aldrich and Crawford, 1940). The double type of growth curve has been shown to occur in stone fruits (Tukey, 1933; Tukey and Young, 1939), black currant (Wright, 1956), and raspberry (Hill, 1958; Boynton and Wilde, 1959). Both parthenocarpic and seeded figs were found to have the double sigmoid growth curve (Crane, Bradley, and Luckwill, 1959), but Nitsch *et al.* (1960), showed that while the "Concord" grape has a double growth curve, the variety "Concord Seedless" has a simple one. The seeded banana has also been reported to have a simple growth curve, while parthenocarpic varieties show various types of curve, being concave or convex, but not sigmoid (Simmonds, 1953).

The duration of cell division reported in the flesh of a number of fruits is summarised in Table 1. In general, there appears to be a division phase after pollination, lasting for a few days or weeks. There is some disagreement about the duration of division in some fruits; no doubt the duration depends on variety and on environmental conditions to some extent. In the apple, there is an exponential increase in cell number throughout the period of rapid increase in fruit weight, followed by division at a diminishing rate until at least 6 to 7 weeks after pollination. Cell division was stimulated to continue at a relatively rapid rate almost until harvest by thinning the variety Miller's Seedling (Denne, 1960).

Cell enlargement has been shown to begin soon after pollination, and expansion continues through the cell division period (Smith, 1950; Denne, 1960 in apples; Sinnott, 1939 in cucurbits; Sterling, 1953 in the plum; Long, 1943 in the date). In apples, the cells expand very rapidly until about 7 weeks after pollination, then at a diminishing rate until harvest (Denne, 1960).

Within a tree, differences in apple fruit size were found to be due to differences in cell number rather than cell size (Bain and Robertson, 1951), though there were indications that the smallest apples had smaller cells. Schroeder (1953) pointed out that the later growth of the avocado is due to cell division rather than cell expansion. Consequently, the size of mature avocado fruits was shown to be related to cell number, fruits of different sizes having similar cell sizes.

MATERIALS AND METHODS

All the fruit was grown in orchards of the Fruit Research Division. The Cox's were collected from trees at Owairaka, Auckland; the Cox A samples (collected in 1960–61) came from four 25-year-old trees on Northern Spy rootstock, Cox B (1961–62) from five 8-year-old trees on rootstock MIX. The Dougherty fruit came from trees at Oratia, Auckland; Dougherty A samples were taken from five similar trees on rootstock 779 in the 1960–61 season; the B samples from a single tree on MXVI in the following year. The Sturmers were from the manurial trial plot at Appleby, Nelson. The trees were 44 years old in the first year (season A), on Northern Spy rootstock.

TABLE 1—Reported Duration of Cell Division in the Flesh of Fruit

Fruit	Duration After Blossom	Reference
Apple	3–4 weeks	Bain and Robertson, 1951 Tetley, 1931 Tukey and Young, 1942
	Until end of June	MacArthur and Wetmore, 1941 Smith, 1950
	(Cox) at least 6–7 weeks (Miller's) at least 12 weeks	Denne, 1960
Pear	Early var. 25–30 days Late var. 45 days	Toyama and Hayashi, 1957
	6–8 weeks in bulk flesh 12 weeks at periphery	Sterling, 1954
Peach	1 month	Reeve, 1959
Plum	4 weeks	Sterling, 1953
Sour cherry	10 days	Tukey and Young, 1939
Tomato	*L. esculentum* ceases before flowering *L. pimpinellifolium* continues throughout development	Houghtaling, 1935
	Continues after flowering	Smith, 1935
Lemon	Until fruit 20 mm diam.	Ford, 1942
Date	16 weeks (basal meristematic zone)	Long, 1943
Avocado	Until harvest	Schroeder, 1953

The position of the blossom on the spur was numbered in spiral sequence from the base of the spur towards the tip. The lowest three blossoms (1, 2, and 3) are usually in the axils of foliage leaves. There is usually a vegetative shoot (the "bourse" shoot) in the axil of the next leaf in the spiral below that subtending blossom 1, this shoot continues the growth of the spur in the following season.

The spurs were tagged when blossoms in positions 2 and 3 were at the "balloon" stage, that is, just before their stamens and styles were exposed. All spurs used were on wood two or more years old, none was on first year wood, and secondary blossom (that is, blossom borne on the bourse shoot) was excluded. The blossoms were not hand pollinated.

The Cox spurs were tagged in the early, middle, and late part of the blossom season which extended over 14 days in the first season, and 8 days in the second. Dougherty spurs were tagged on two dates, early and late in the blossom season which lasted about 9 days in both years. The Sturmers were not tagged in the first season, samples being taken at random, excluding any fruit obviously over- or under-sized. In the second season, Sturmers were tagged at about the time of full bloom.

Samples were taken from tagged spurs at intervals through the season, leaving a large sample to be collected at harvest. As the samples were small relative to the total crop on the trees, there was unlikely to be an appreciable thinning effect.

The following data were noted for each sample:

1. Maximum fruit diameter.
2. Fresh weight of fruit.
3. Position of fruit on the spur.
4. Seed number in fruit.
5. Spur diameter.
6. Number of leaves on the spur.
7. Number of fruits on the spur.
8. Length of the bourse shoot.
9. Position of spur on the branch (lateral or terminal).

The fresh weight of the fruit was determined after removal of stalk, sepals, petals, stamens, and styles. Spur diameter was measured just below the current year's foliage leaves. At harvest, the number of apparently good, full seeds was recorded separately from the number of aborted, flattened but full length seeds, but as the separated data appeared to have no relation to the factors under consideration, only the combined total seed number is shown here.

The diameter of individual fruitlets was measured on the tree at weekly intervals. With Dougherty B, the diameter of each fruitlet on 75 spurs was measured from blossom onwards. The Cox blossoms were more crowded in the cluster than the Dougherty, having shorter stalks, so measurements could not be begun until 7 days after blossom. In Cox B, the individual fruitlet diameter was measured on 20 to 30 spurs for each date of tagging on each tree. For each tagged spur, spur diameter was measured at, or soon after, blossom, and again at harvest. Hence the rate of fruit growth could be compared with spur diameter at blossom, or at harvest, or with seed number at harvest, etc.

The method of counting cell number across the flesh of the fruit has been described previously (Denne, 1960). Mean cell diameter in the flesh was calculated from the width of the flesh divided by the mean number of cells across it. The index of estimated total cell number in the flesh was obtained by calculating the volume of the flesh from the known fruit and core diameters, and dividing this by the calculated cell volume. Since the total fruit volume, core volume, and cell volume are all calculated on the assumption that fruit, core, and cell are spherical, and as the calculation makes no allowance for variations in the amount of intercellular space, it is obvious that this estimated cell number can only be a very rough approximation.

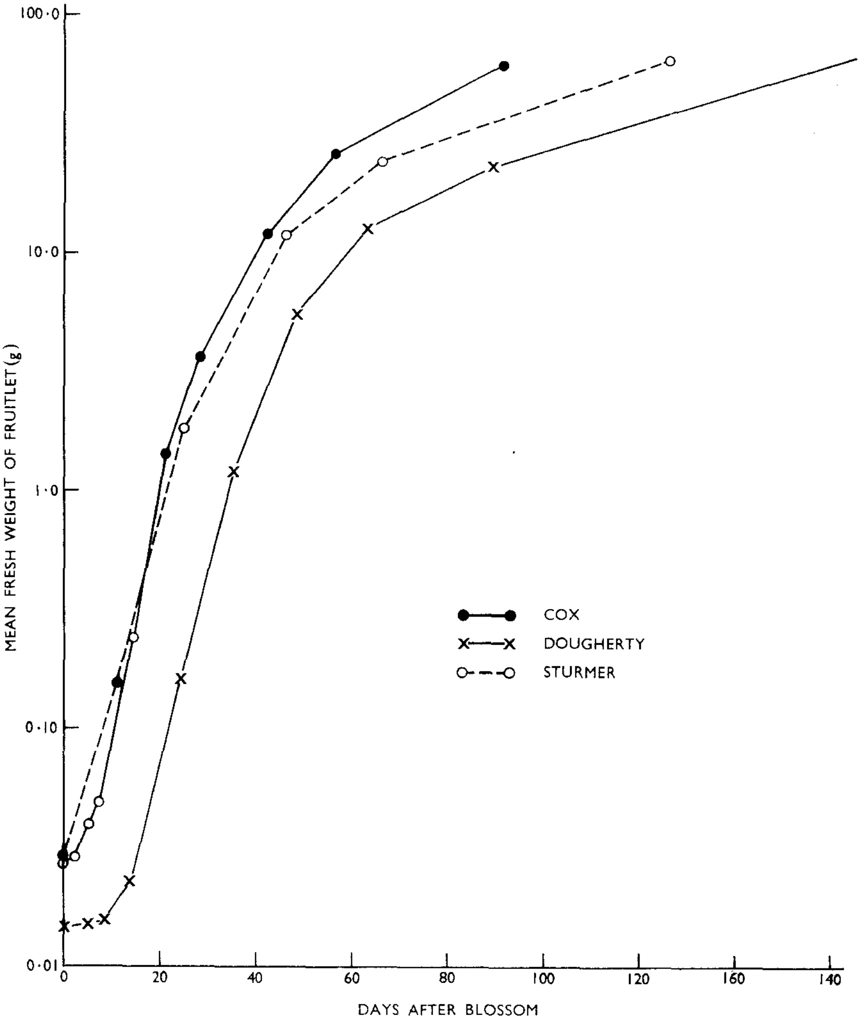

FIG. 1—Fresh weight of developing fruitlets.

RESULTS

Fruit Growth Curves in Cox, Dougherty, and Sturmer Apples

The general shape of these growth curves was similar to that already described for Cox and Miller's Seedling (Denne, 1960). Figs 1, 2, and 3 show the mean fruit weight, cell number and cell size, of samples collected during development of Cox, Dougherty, and Sturmer fruitlets.

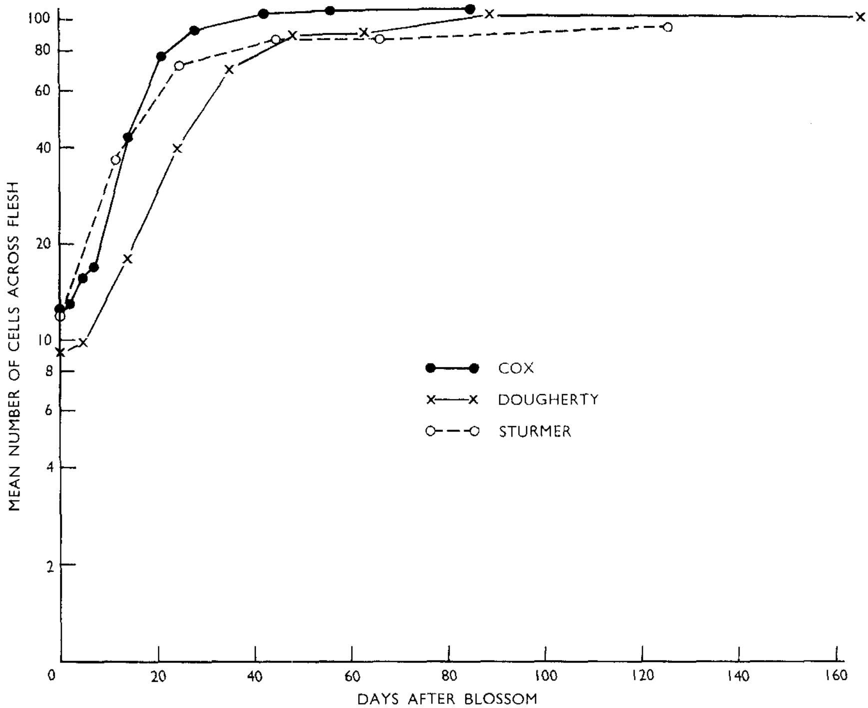

FIG. 2—Number of cells across flesh of developing fruitlets.

The Dougherty blossoms were considerably smaller than the Cox or Sturmer blossoms, and contained fewer, and smaller cells. In Cox and Sturmer fruitlets the initial period of slow growth lasted only about 2 to 3 days after full bloom, but in the Dougherty's it took about 11 days in the first season, and about 8 days in the second.

The final cell number was similar in all three varieties, the Dougherty's having a slower rate, but a longer duration of cell division than Cox or Sturmer's. Cell expansion was also more rapid in Cox's and Sturmer's during the first few weeks, but from about 4 weeks after blossom it appeared to continue at about the same rate in all three varieties.

Within-tree Factors Affecting Fruit Development

TIME OF FLOWERING IN THE BLOSSOM SEASON

Spurs flowering late in the blossom season tended to be smaller than those flowering earlier, with fewer blossoms per spur, and a shorter bourse shoot with fewer expanded leaves at the time of flowering (Table 2).

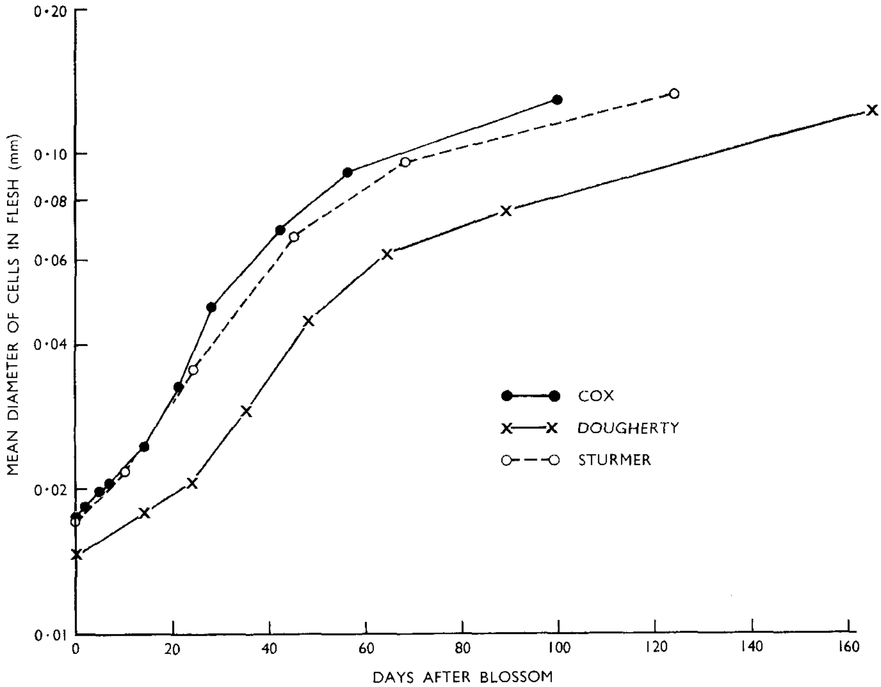

FIG. 3—Cell diameter number in flesh of developing fruitlets.

TABLE 2—Diameter, Number of Blossoms, and Leaf Number at Blossom of Spurs Flowering at Different Times in the Blossom Season

—		Spur Diam. (mm)			Blossom No./Spur		Expanded Leaves/Spur	
		Early	Mid	Late	Early	Late	Early	Late
Dougherty	A	4·24	—	4·05	5·96	5·64	1·2	0·8
	B	4·28	—	4·01	5·98	5·88	—	—
Cox	A	5·07	4·82	4·60	—	—	—	—
	B	4·86	4·65	4·32	—	—	—	—

Blossom Size

The late blossom is markedly smaller and lighter than the early blossom (Table 3). This seems to be mainly accounted for by difference in spur size; differences in blossom size diminish, and possibly disappear, when spurs of a similar size range are compared (Table 4).

TABLE 3—Size and Weight of Blossoms Opening at Different Times in the Blossom Season

		Blossom Diam. (mm)			Blossom Wt. (g)		
		Early	Mid	Late	Early	Mid	Late
Dougherty	A	2·58	—	2·52	·0153	—	·0140
	B	2·77	—	2·65	—	—	—
Cox	A	3·33	3·35	3·26	·0281	·0270	·0242
	B	3·47	3·37	3·31	·0309	·0274	·0266

TABLE 4—Size of Blossom Opening at Different Times in the Blossom Season in Relation to Spur Size

(Figures in brackets show numbers of blossoms in each category)

Spur Diam. Range (mm)	Mean Blossom Diameter (mm)				
	Cox B			Dougherty B	
	Early	Mid	Late	Early	Late
3·5–3·9	3·20(11)	3·18(36)	3·07(28)	2·62(92)	2·64(63)
4·0–4·9	3·45(119)	3·32(392)	3·37(194)	2·80(157)	2·70(61)
5·0 +	3·54(113)	3·55(159)	3·53(20)	2·90(48)	2·86(5)

Growth Rate and Size at Harvest

Fruitlets from the late Dougherty blossom had a slightly faster rate of growth than those from early blossom for the first few weeks, though they were still slightly smaller when picked at the same time interval after blossom (Table 5). There was no apparent difference in growth rate of fruitlets from early and late Cox blossoms, so differences in blossom size were maintained throughout the fruitlet growth until harvest (Table 5). As with the blossom, these differences in fruit size tend to disappear when a limited range of spur size is considered (Table 5).

TABLE 5—Size of Fruits at Harvest from Early and Late Blossom in Relation to Spur Size

(Figures in brackets show numbers of fruit in each category)

Spur Diam. Range (mm)	Mean Fruit Diameter at Harvest (mm)			
	Cox B		Dougherty B	
	Early	Late	Early	Late
All	48·4(91)	46·9(92)	42·4(116)	41·7(37)
Up to 5·4	46·2(20)	46·0(66)	42·4(32)	40·4(20)
5·5–6·9	47·8(49)	49·0(22)	41·9(31)	41·7(12)
7·0 +	50·4(22)	52·5(4)	42·7(53)	45·2(5)

Percentage Set

The percentage set is expressed as the number of fruit harvested per 100 blossoms. As shown in Table 6, early blossoms set much better than late in Cox A and Dougherty B, but in Cox B the mid-season blossom set better than either early or late.

TABLE 6—Percentage Set of Blossoms Opening at Different Times in the Blossom Season

(Figures in brackets show the number of fruits harvested)

—		Early	Mid	Late
Cox	A	11·9% (467)	4·8% (662)	3·3% (279)
	B	12·1% (91)	19·0% (161)	11·7% (92)
Dougherty	B	38·7% (116)	—	24·7% (37)

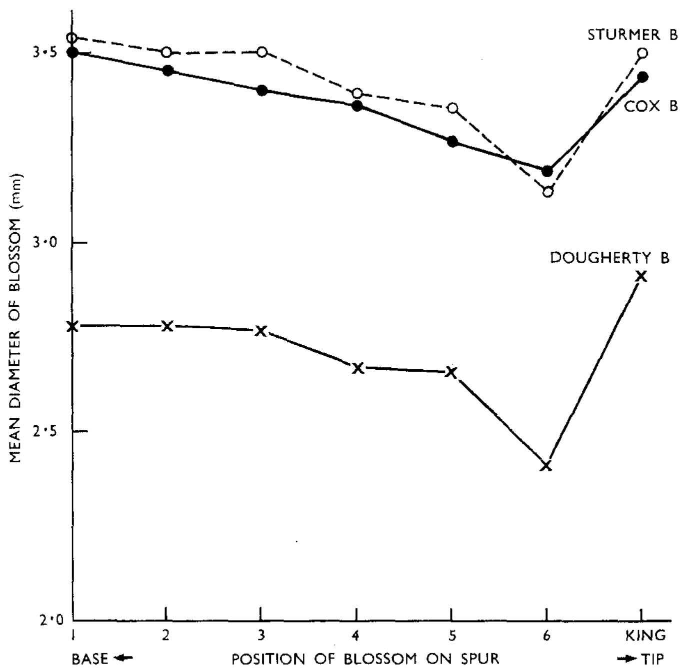

FIG. 4—Variation in blossom diameter (measured across receptacle) with the position of blossom on the spur.

Statistical analysis: Brackets enclose measurements not significantly different at the stated level.

Sturmer B	1	King	2	3	4	5	6	at 1% level.
Cox B	1	2	King	3	4	5	6	,, ,, ,,
Dougherty B	King	1	2	3	4	5	6	,, ,, ,,

THE POSITION OF FRUIT ON THE SPUR

Blossoms in positions 1, 2, and 3 tend to open more or less simultaneously, about a day later than the Kings, followed by 4 and 5, with position 6 opening last.

Blossom Size

Figure 4 shows the variation in blossom diameter with position on spur in season B, similar relationships were noted in the season A. In all three varieties, blossoms towards the tip of the spur (4, 5, 6) were significantly

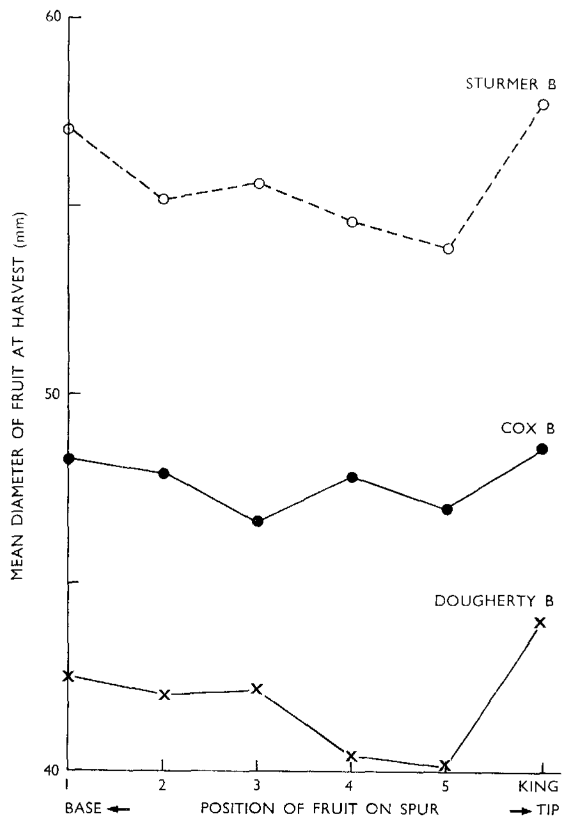

FIG. 5—Variation in fruit diameter at harvest with position of fruit on the spur. *Statistical analysis:*

Sturmer B	King	1	3	2	4	5	at 5% level.
Cox B	No significant differences						,, ,, ,,
Dougherty B	King	1	3	2	4	5	,, ,, ,,

smaller than the Kings, or those at the base (1, 2, 3). King blossoms were significantly larger than all the others in Dougherty, but not significantly larger than 1, 2, or 3 in Cox and Sturmer.

Fruit Size at Harvest

The relation between blossom diameter and position on the spur was maintained through until harvest in Sturmer, Dougherty, and Cox A, the fruits in positions 4 and 5 being significantly smaller at harvest than the Kings or positions 1, 2, or 3 (Fig. 5). The differences did not reach the 5% level of significance in Cox B, although except for fruit in position 4 the same trends were shown.

There was no consistent relationship between seed number and position on spur. In Cox B, positions King and 3 had significantly fewer seeds (at the 5% level) than 1 and 5, but apart from this, there were no significant differences in other years or other varieties.

There was some evidence of a change in diameter/length ratio with position of fruit on the spur; the fruits became relatively longer towards the tip of the spur (Fig. 6).

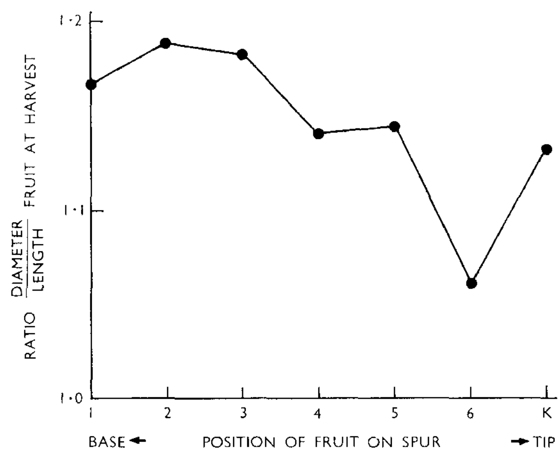

FIG. 6—Variation in fruit shape at harvest with position of fruit on spur in Sturmer B.
Statistical analysis:

2 3 1 5 4 King 6 at 1% level.

Percentage Set

Fig. 7 shows the percentage set in Cox B and Dougherty B, expressed as the number of fruit harvested per 100 blossoms in each position on the spur. Table 7 shows the proportional set, that is, the number of fruit harvested from each position as a percentage of the total crop.

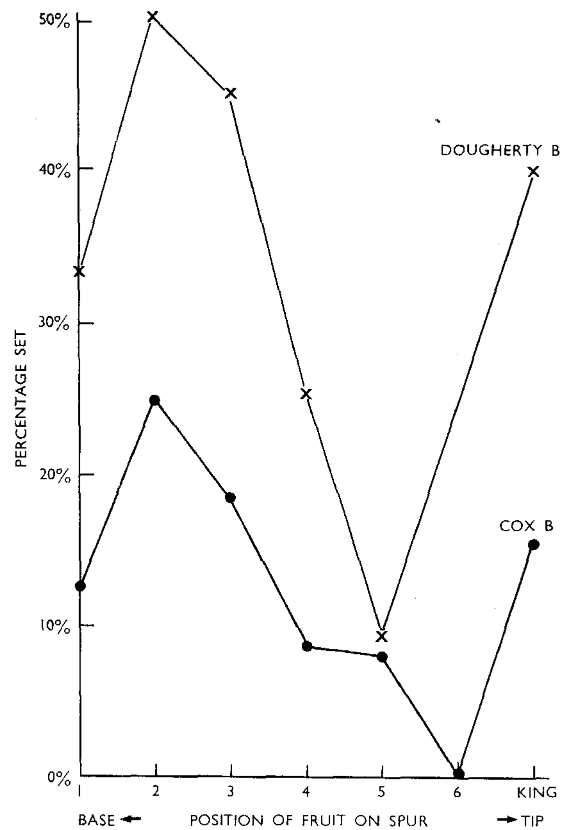

FIG. 7—Variation in % set (number of fruits harvested per 100 blossoms) with position of fruit on spur.

TABLE 7—Number of Fruit Harvested from Different Positions on the Spur as a Percentage of the Total Crop

—		Position of Fruit on the Spur							Total Sample
		Base 1	2	3	4	5	6	Tip King	
Cox	A	23	26	17	14	7	–	14	1,387
	B	13	28	21	10	9	–	18	346
Dougherty	A	23	17	8	12	7	–	33	259
	B	16	25	22	12	5	–	20	153
Sturmer	A	10	22	19	11	14	2	22	348
	B	9	15	17	12	8	5	35	184

In general, position 1 did not set as well as position 2 (except in Dougherty A). King fruits had the best set in Dougherty A and Sturmer B, but did not set better than 2 in other samples.

THE SEED NUMBER

Fruit Size at Harvest

The mean fruit weight at harvest increased with seed number (Fig. 8). There was a better correlation when aborted seeds (that is, flattened, but full length seeds) were included than when they were omitted. There was some evidence that fruit diameter was increased proportionally more than length as the seed number increased, as is shown by the ratio diameter/length in Table 8.

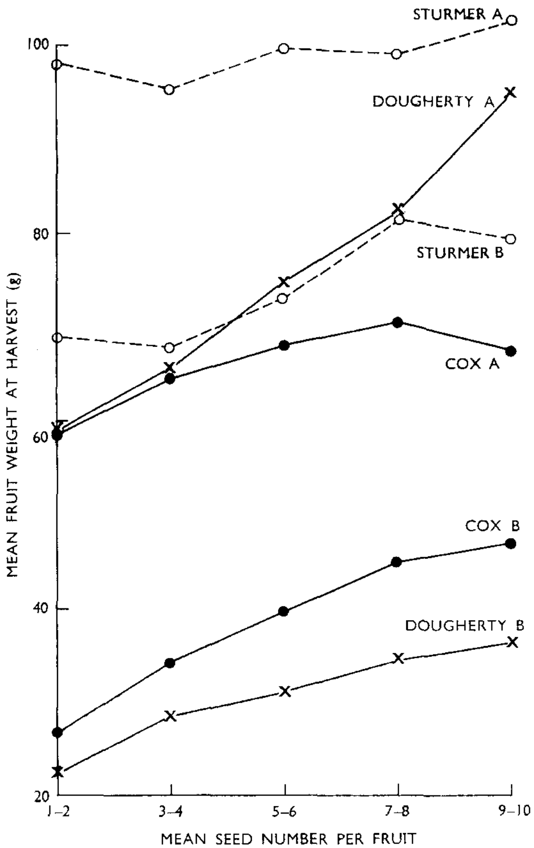

FIG. 8—Variation in fruit weight at harvest with seed number in the fruit.

TABLE 8—Variation in Fruit Shape with Seed Number, and the Effect of Seed Number on the Relative Proportions of Flesh and Core

(The figures in brackets show the number of fruits in each category)

—		1–2 Seeds	3–4	5–6	7–8	9–10 Seeds
Ratio diam./length { Sturmer	B	—	1·138(58)	1·155(69)	1·175(33)	1·145(8)
Ratio diam./length { Dougherty	B	—	1·115(36)	1·143(20)	1·144(16)	1·170(4)
core diam. (mm)	,,	21·9(10)	25·1(16)	25·5(16)	26·0(12)	28·3(7)
Flesh width (mm)	,,	17·7(10)	15·7(16)	18·1(16)	17·7(12)	17·6(7)
Ratio flesh wt/core wt	,,	6·25(10)	6·28(16)	6·18(16)	6·58(12)	6·30(7)

As would be expected, the core diameter is considerably increased by increasing seed number (Table 8). Though the width of the flesh remains approximately constant as seed number increases, the total volume and weight of the flesh is increased in proportion to that of the core, as is shown by the ratio flesh wt./core wt. in Table 8.

Rate of Growth

Fig. 9 shows the relation between seed number and diameter of developing fruitlets of Cox B (early blossom). There was no significant association between seed number and fruitlet diameter at 12 days after blossom, but by 16 days fruitlets with 9–10 seeds were significantly larger than the others at the 5% level. Fruitlets from mid and later blossom had a difference in

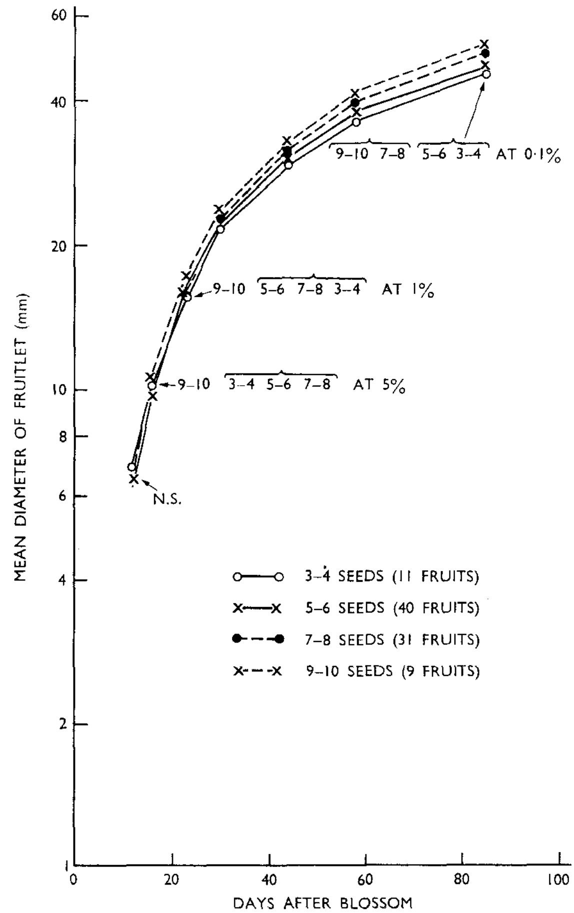

FIG. 9—Variation in diameter of developing fruitlets with seed number in the fruit in Cox B (early blossom).

mean diameter related to seed number by 7 days after blossom, but this was not significant at the 5% level. Fruitlets with more seeds continued to have a higher rate of growth until about 40 days after blossom, after this there appeared to be little or no further effect of seed number on % growth rate (Fig. 9).

TABLE 9—Percentage Increase in Fruitlet Diameter per Day in Relation to Seed Number

—	Dougherty B		Cox A
	7–22 Days	43–112 Days	36–90 Days
1– 2 seeds	9·29	1·27	2·05
3– 4 „	10·95	1·19	—
5– 6 „	12·02	1·12	—
7–10 „	12·57	1·07	1·91

Statistical analysis: Brackets enclose categories not significantly different at the level stated.

Dougherty 7–22 days 1–2 3–4 [5–6 7–10] at 1%

Dougherty 43–112 days [1–2 3–4] [5–6 7–10] at 5%

Cox 36–90 days [1–2 7–10] N.S. at 5%

In Dougherty B (Fig. 10), there was a highly significant effect of seed number on fruitlet diameter by 7 days after blossom (this being the first measurement taken after blossom). The fruitlets continued to grow at a faster rate with higher seed numbers until about 3 weeks after blossom (Table 9). But, from about 6 weeks after blossom, fruits with fewer seeds grew significantly faster than those with more seeds.

In Cox A there was also some evidence that fruitlets with fewer seeds had a faster rate of growth after about 5 weeks after blossom (Table 9), though this did not reach the 5% level of significance.

Cell Size and Cell Number

There was no consistent relation between cell size and seed number except in Dougherty B (Table 10). The estimated total cell number increased with seed number in each variety, and though it should be stressed that this is a very rough estimate, it probably does indicate a real increase in the total cell number.

SPUR DIAMETER

The mean diameter of the blossom increased significantly with spur diameter in all three varieties, in both seasons (Fig. 11).

The fruit size at harvest increased with spur size, whether the spur measurements were taken at harvest (Fig. 12) or at, or soon after, blossom (Figs 13, 14).

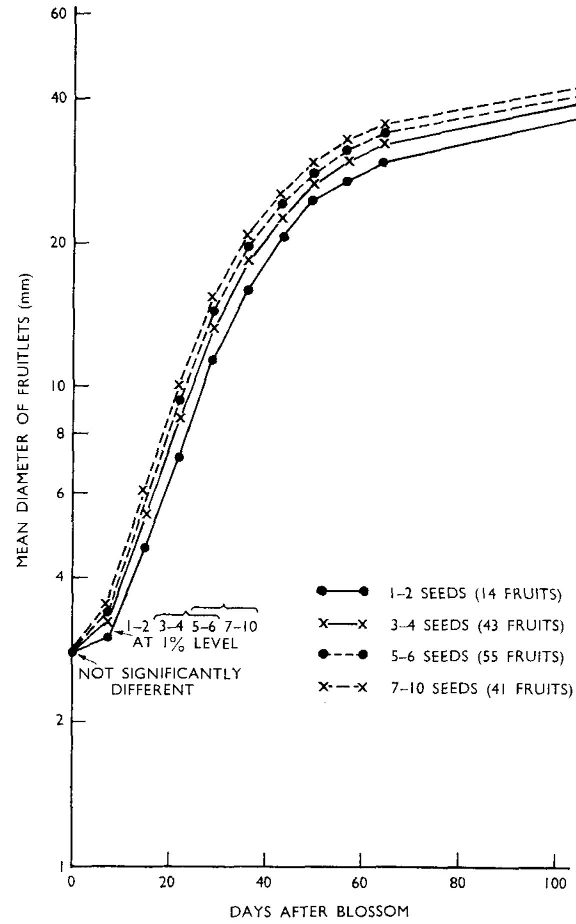

FIG. 10—Variation in diameter of developing fruitlets with seed number in the fruit in Dougherty B.

The size of the spur appeared to have no effect on growth rate of the fruitlet after blossom; in both Cox and Dougherty, the relationships found between blossom size and spur size were maintained unchanged with fruitlet growth until harvest (Figs 13, 14).

Cell size increased significantly with spur size in Cox A, but there appeared to be no such relationship in the other examples (Table 11). Cell number appeared to be related to spur size, either when measured as cell number across the flesh, or as estimated total cell number in the flesh (Table 11).

TABLE 10—Cell Size and Cell Number in the Flesh of Fruits in Relation to Their Seed Number

—	Seed Number	Cell Diam. (mm)	Cell Number Across Flesh	Index of Estd Total Cell Number	Sample Size
Dougherty B	1–2	·0845	92·50	69·0	10
	5–6	·0883 *	86·15	82·5	15
	7–8	·0919	84·4	84·0	15
Sturmer B	1–2	·1332	94·36	58·0	7
	3–4	·1330 N.S.	93·64	62·2	20
	5–6	·1313	—	—	38
	7–10	·1345	92·68	62·5	11
Cox A	1–2	·1278	92·71	57·4	29
	3–4	·1259 N.S.	96·69	67·0	32
	5–6	·1259	95·78	68·6	27
	7–10	·1284	97·22	81·5	13
Cox B	1–4	·1133	91·16	54·0	12
	5–6	·1129 N.S.	91·83	60·4	47
	7–10	·1122	91·16	68·3	69

*Statistical analysis—all significantly different at 5% level.

TABLE 11—Cell Size and Cell Number in the Flesh of Fruits in Relation to Spur Diameter

—	Spur Diam. Range (mm)	Cell Diam. (mm)	Cell Number Across Flesh	Index of Estd Total Cell Number	Sample Size
Cox A	4·1–5·5	·1264	97·7	68·5	57
	5·6–6·5	·1297 *	106·2	76·7	71
	6·6–8·0	·1301	112·4	86·4	44
Cox B	up to 5·4	·1132	88·1	55·5	18
	5·5–6·9	·1141 N.S.	91·2	62·3	42
	7·0 +	·1106	96·0	66·9	25
Dougherty B	up to 5·4	·0905	83·6	77·0	14
	5·5–6·9	·0885 N.S.	89·0	86·3	12
	7·0 +	·0880	88·2	85·0	16

*Statistical analysis 4·1–5·5 5·6–6·5 6·6–8·0 at 1% level.

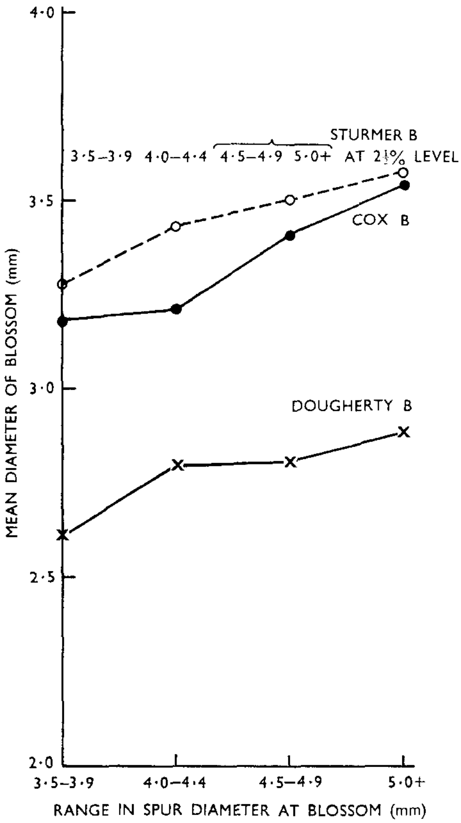

FIG. 11—Variation in blossom diameter (measured across receptacle) with spur size.

Percentage Set

The percentage set was expressed as number of fruit harvested per 100 blossoms in each spur size category. The set was markedly influenced by spur size, many of the smaller spurs failing to set any fruit (Fig. 15).

POSITION OF SPUR ON THE BRANCH

The position of the spur on the branch appeared to have no effect on growth rate of Dougherty B fruit. Fruit of the terminal spurs remained significantly larger than those on lateral spurs from blossom through until harvest (Table 12).

On the other hand, in Cox B fruit, there was no significant difference between fruitlet diameter from terminal and lateral spurs at 7 days after blossom (Table 12, Fig. 16), but a highly significant difference was shown at harvest. Fruit from terminal spurs grew at a more rapid rate than those on lateral spurs for about 27 days after blossom; there appeared to be no significant effect on growth rate after this time.

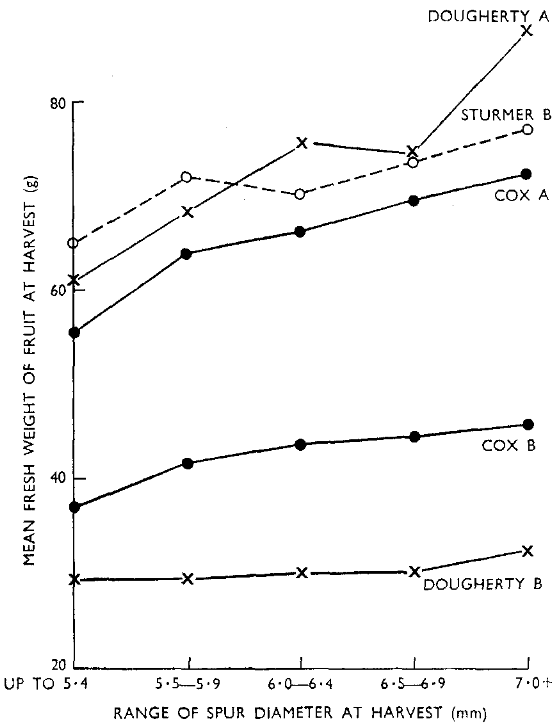

FIG. 12—Variation in fruit weight at harvest with spur size.

TABLE 12—Size of Developing Fruitlets from Terminal and Lateral Spurs

Diameter of Fruitlet in mm.

——	Cox B				Dougherty B		
	Days After Blossom 7	27	85	Sample Size	Days After Blossom 0	112	Sample Size
Lateral spurs	4·35	17·88	46·01	74	2·790	42·08	94
Terminal spurs	4·41	19·62	50·50	18	2·875	43·54	24
% difference	1·2	9·7	9·75		3·05	3·5	
Significance	N.S.		·1%		5%	5%	

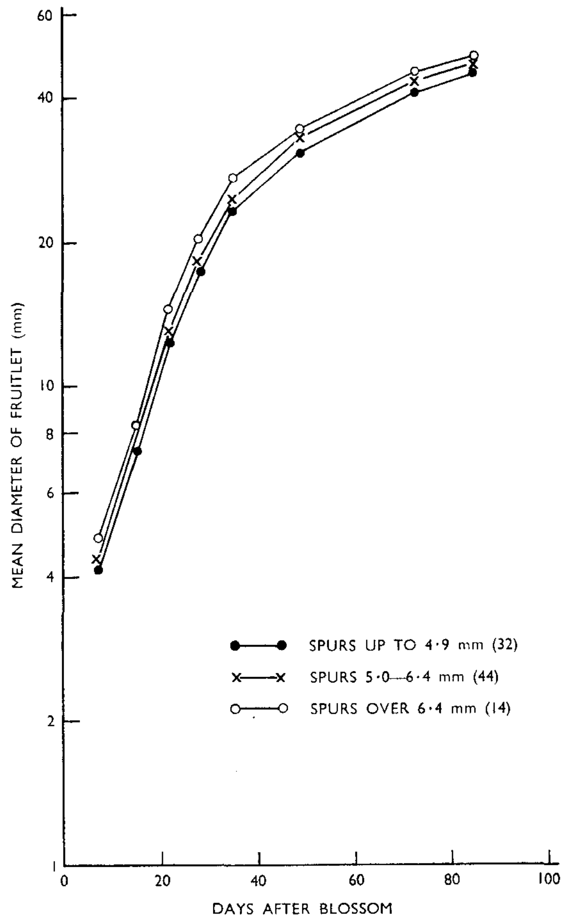

FIG. 13—Variation in diameter of developing fruitlets with spur size at blossom (Cox B).

THE NUMBER OF FRUITS ON THE SPUR

In the Dougherty B fruit, spurs with a higher fruit set 14 days after blossom tended to produce small fruit at harvest (Table 13). The fruit size could not be correlated with the number of fruit which remained on the spur until harvest.

DISCUSSION

It happened that fruit of the three varieties used in these investigations all reached a similar size at harvest, with similar cell sizes and cell numbers. But when sampled at the same time interval after blossom, they showed

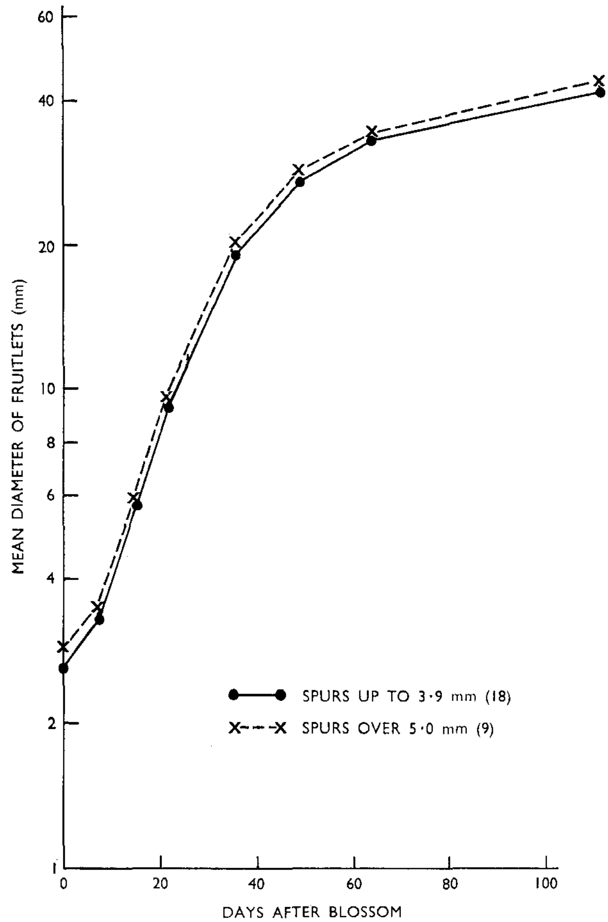

FIG. 14—Variation in diameter of developing fruitlets with spur size at blossom (Dougherty B).

marked differences, due to the initial differences in cell number and size, and the different rates of cell division and cell expansion. The Dougherty's, for instance, were considerably smaller than the other two varieties at blossom, but the fruit finally reached about the same size at harvest due to their longer duration of growth. Similarly, Smith (1950) showed that the fruit size characteristic of an apple variety does not appear to be determined at blossom (though the characteristic varietal shape may already be indicated by this time, as shown by Smith (1950) in apples, and Houghtaling (1935) in tomatoes). The data of Fig. 1 suggest that there may be a varietal

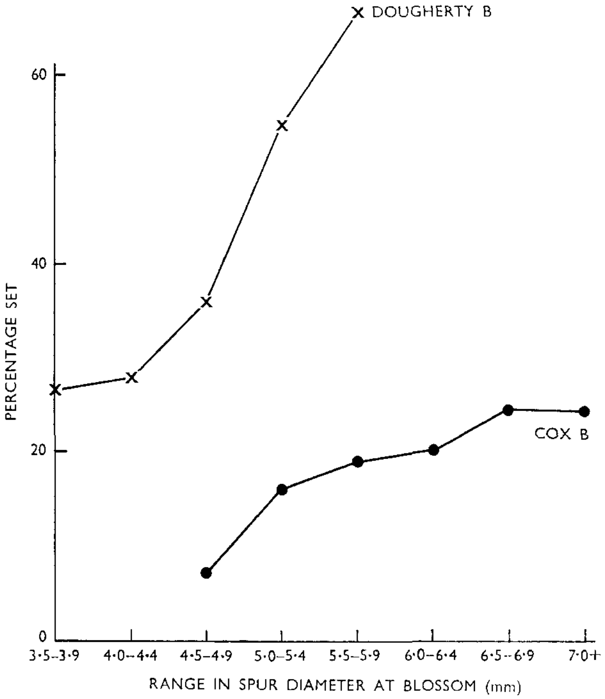

FIG. 15—Variation in % set (number of fruits harvested per 100 blossoms) with spur size at blossom.

difference in the length of the period of slow growth after blossom, which was longer in the Dougherty's than in the other two varieties, though this difference might equally well be attributed to the rootstock, soil, or climatic conditions.

TABLE 13—Fruit Diameter in Relation to the Number of Fruit on the Spur. Dougherty B.

Fruit number per spur (at 14 days after blossom)	3	4	5	6	7
Mean fruit diameter at harvest (mm)	43·3	43·1	42·6	40·7	40·3
Statistical analysis	3 4 5	6 7	at 5%		

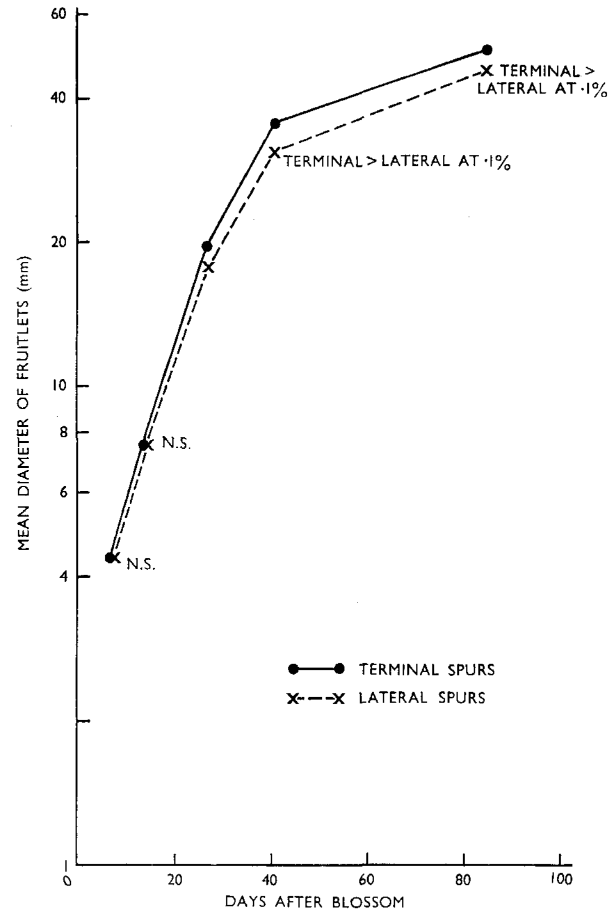

FIG. 16—Variation in diameter of developing fruitlets with position of spur on branch (Cox B).

THE DATE OF BLOSSOM

The date of blossom is related to some extent to position of the spur on the tree. Blossom on first-year wood tends to open later than that on older wood, and secondary blossom tends to be later still. However, all the blossoms used in these investigations were on spurs from wood two or more years old, and in these, there did not appear to be any relation between the date of blossom and age of wood, or position on the tree.

Differences in flower size from early and late blossoming spurs appear to be partly, if not entirely, attributable to differences in spur size, with larger spurs tending to flower earlier than smaller ones. The fruit set of early and late blossoms may also be related to spur size, though the set of late blossoms is probably influenced by the fruitlets already developing; if the early blossom had failed to set well, presumably the late ones would have done so better.

POSITION OF FRUIT ON THE SPUR

Fruit size and shape has been shown to be determined to some extent by the position of fruit in the cluster. Fig. 4 shows that the distribution of blossom size on apple spurs is similar to that described by Gayner (1941) for pears, where flower size increases from the first flower below the King towards the base of the cluster, the King being about the same size as the largest below. A similar trend was noted here with fruit size at harvest (Fig. 5), though Schander (1956b) indicates the reverse, the weight of fruit below the King decreasing towards the base of the cluster. Fruit size has also been reported to be related to position in the cluster in black currants (Teaotia and Luckwill, 1955), but Young (1952) could not find such a relationship in Vaccinium.

Though there appeared to be no consistent relationship between fruit length and position on the spur in the fruit investigated here, there were indications that the ratio diameter/length decreased towards the tip of the spur, that is, the fruits became relatively longer (Fig. 6). Elsewhere, the terminal King apple is stated to be longer than the others, with a more or less pronounced "beak" (Hinton and Swarbrick, 1930). Fruit length is reported to decrease, whilst stalk length increases, from the King to the lowest on the spur (Hinton, Jones, and Lewis, 1932; Visser, 1955). Schander (1956a) noted that in pears the King blossom is longer and narrower than the lower flowers on the spur, already suggesting the "Schinkenknochenform" of the mature King fruit.

The relation between fruit set and position in the cluster may be attributed to blossom size, or to the order of flowering. Visser (1955) noted that the lowest flower in the cluster sometimes did not set as well as those immediately above it; this is confirmed by the data given in Fig. 7 and Table 7.

SEED NUMBER

Fruit size has been related to seed number in a wide range of fruits, and in general, that is confirmed here. Many authors have qualified this relationship, noting that the correlation is better with the smaller fruits on the tree (Murneek and Schowengerdt, 1935; Einset, 1939; Cameron *et al.*, 1960), or in the lower range of seed number (Schander, 1956a); thus large fruit may be found with low seed numbers, and small fruit with high ones. Luckwill (1959) suggests that the correlation may be disturbed by parthenocarpic tendencies in some fruits, and conversely (quoting Schander) that high seed numbers may depress fruit growth through competition effects. An inverse relationship between seed number and fruit size has been reported in pears by Rodrigues and Menezes (1951).

The results presented here suggest that the rate of fruit growth is increased by the presence of viable seeds for the first few weeks after blossom, but after this fruits with fewer seeds may grow more rapidly than those with many, thus tending to eliminate the earlier differences in fruit size. In this connection, Abbott (1959) observed that removal of seeds had no apparent effect on apple growth after about 7 weeks from petal fall. On the other hand, Nitsch (1950) showed that the growth of strawberry fruits was affected by seed removal a few days before maturity.

There was a higher correlation between fruit size and seed number when aborted (but full length) seeds were included; this had been previously noted in the apple by Einset (1939), though Olmo (1946) found that the berry weight of grapes was related to the number of hard seeds only.

The effect of seed number is interrelated with other factors affecting fruit size. It has been reported that there are fewer seeds in King fruits than in those in other positions on the spur (Heinicke, 1917; Visser, 1955; Schander, 1956a; Rake, 1960), though the present data did not confirm this. Visser (1955) found that King flowers tended to have more ovules than others, but produced fruit with fewer and lighter seeds. Heinicke (1917) reported that fruits with fewer seeds tend to be found on larger spurs, implying that weaker spurs can only set fruit with a relatively high seed number. Since fruit with few seeds tend to be small, and fruit from large spurs tend to be large, this may lead to some confusion unless these two factors are considered separately. Similarly, the average seed number per fruit tends to be lower where the fruit set is light (Schander, 1956a). Again, seed number and crop size tend to have opposite effects on fruit size.

Fruit shape has been related to both number and distribution of seeds. The ratio of diameter to length has been shown to increase with increasing seed number in the pear (Rodrigues and Menezes, 1951; Schander, 1956a) and the apple (Schander, 1956b); the results given in Table 18 support this. Lop-sidedness has been attributed to uneven distribution of seeds in the apple (Schander, 1955), cucumber (Seaton, 1937), tomato (Luckwill, 1939, and strawberry (Nitsch, 1950).

There appears to be a marked effect of seed number on total cell number in the fruit (Table 9), as might be expected from the effect on growth rate during the period of rapid cell division. The effect on cell size is less distinct, possibly a higher seed number may stimulate cell enlargement during the first few weeks, but inhibit it later, with a net affect of increasing or decreasing cell size according to which tendency is dominant.

SPUR SIZE

Spur diameter has been shown to be related to blossom size (Fig. 11), and hence to fruit size at harvest. Sinnott (1955) demonstrated a correlation between the relative growth of the fruit and fruit stalk of *Cucurbita pepo*; since his experimental reduction of the stalk diameter had no apparent effect on fruit size, it did not seem likely that fruit size was directly dependent on the cross-sectional area of the stalk. Though the data are not presented here, the leaf number per spur, and the length of the bourse shoot, were also closely related to fruit size at harvest. Heinicke (1917) comments that fruit size is determined partly by the "vigour" of the spur. Visser's observation (1955) that fruit weight is correlated with number of flowers in the cluster, that is, larger fruits are produced by spurs that had a higher flower number, might also be related to the "vigour" of the spur.

Position of Spur on the Tree

The data recorded here show that fruit of a terminal spur (that is, the spur immediately below a pruning cut, on second-year or older wood) tended to be larger than that of a lateral spur. As would be expected from their position, terminal spurs were usually larger than laterals, with a considerably longer bourse shoot. The larger size of the terminal fruit might be attributable to this difference in spur size, or to a difference in the microclimate. Fruit at the top of the tree are often larger than those below (Davidson and George, 1959; Schander, 1956b), though the reverse may be found with oranges (Wallace, Cameron, and Wieland, 1955). Shaw (1914) noted that apples on the upper South quarter of the tree (that is, on the sunny side) were larger and flatter than those on the opposite part.

Number of Fruits on the Spur

There is some evidence that fruit size at harvest is related to the number of fruit set 14 days after blossom (Table 18). Since larger spurs tend to have a higher fruit set, it may be difficult to distinguish the effect of "vigour" of spur from the opposite effect of competition between fruits at an early age. In general, however, it appears that when spurs of the same "vigour" are compared, fruit size is related to the number of fruit set, bearing in mind the effects of position on the spur, and seed number.

Conclusions

The size of apple fruits at harvest is influenced by position of the fruit on the spur, seed number, spur size, number of fruits set on the spur, position of the spur on the branch, and the date of flowering within the blossom season.

The position of fruit on the spur, and spur size, are both related to the blossom size; these factors do not appear to have any subsequent effect on fruit growth rate.

For the first few weeks after blossom, fruit growth rate is increased by higher seed numbers, but there is some evidence that in later stages of development fruit with higher seed numbers have a slower rate of growth.

Apart from the obvious dependence on efficiency of pollination, fruit set also appears to be determined by position of fruit on the spur, by spur size, and by date of flowering within the blossom season.

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