THE DROP OF FLOWERS AND FRUITS IN APPLE, WITH SPECIAL REFERENCE TO THE JUNE DROP OF COX'S ORANGE PIPPIN AND ITS CONTROL WITH GROWTH REGULATORS

BLOEM- EN VRUCHTVAL BIJ APPEL, MET NADRUK OP DE JUNIRUI VAN COX'S ORANGE PIPPIN EN DE BESTRIJDING DAARVAN MET GROEIREGULATOREN

. J. WERTHEIM

THE DROP OF FLOWERS AND FRUITS IN APPLE, WITH SPECIAL REFERENCE TO THE JUNE DROP OF COX'S ORANGE PIPPIN AND ITS CONTROL WITH GROWTH REGULATORS

Bloem- en vruchtval bij appel, met nadruk op de junirui van Cox's Orange Pippin en de bestrijding daarvan met groeiregulatoren

Dit proefschrift met stellingen van

SAMUEL JOHANNES WERTHEIM,

Landbouwkundig ingenieur, geboren te 's Gravenhage, 26 maart 1936, is goedgekeurd door de promotor, Dr. Ir. S. J. Wellensiek, hoogleraar in de Tuinbouwplantenteelt.

De Rector Magnificus van de Landbouwhogeschool
J. M. Polak

Wageningen, 5 oktober 1971

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(with a summary in Dutch)

PROEFSCHRIFT
TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN
OP GEZAG VAN DE RECTOR MAGNIFICUS, MR. J. M. POLAK,
HOOGLERAAR IN DE RECHTS- EN STAATSWETENSCHAPPEN
VAN DE WESTERSE GEBIEDEN
TE VERDEDIGEN TEGEN DE BEDENKINGEN VAN EEN
COMMISSIE UIT DE SENAAT
VAN DE LANDBOUWHOGESCHOOL TE WAGENINGEN
OP VRIJDAG 10 DECEMBER 1971 TE 16 UUR

DOOR

SAMUEL JOHANNES WERTHEIM

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STELLINGEN

I

De rol die de wind speelt bij de overdracht van stuifmeel bij appel en peer is groter dan algemeen wordt aangenomen.

WERTHEIM, S. J. Meded. Dir. Tuinb. 31, 1968: 438-446.

II

Er is in de wereld plaats voor nog een tuinbouwkundig tijdschrift, speciaal voor publicaties op het gebied van het teeltonderzoek van tuinbouwgewassen.

III

Het verdient aanbeveling om het chemisch ontsmetten van voor fruitteelt bestemde gronden met chloorpicrine te vervangen door het planten van de bomen in plantgaten, die met verse grond gevuld worden.

WESTERLAKEN, J, De Fruitteelt 61, 1971: 100-102.

IV

De vrees, dat vruchtbomen, vrij van de bekende virussen, wegens een sterkere vegetatieve groei minder vruchtbaar zouden zijn dan virus-bevattende bomen, lijkt ongegrond.

PEERBOOMS, H. De Fruitteelt 61, 1971: 94-96.

V

Met een gereorganiseerd afzetsysteem kan de Nederlandse fruitteelt een goede concurrentiepositie opbouwen.

VI

De hoge kosten van plant- en steunmateriaal maken de aanlegkosten van intensieve appelboomgaarden zò hoog, dat het aanbeveling verdient het veredelingsonderzoek te richten op het vervangen van de dure combinatie entras-onderstam en op het onnodig maken van elke ondersteuning van de bomen.

VII

De huidige criteria, die bepalen of een groeiregulator ontheffing krijgt voor praktisch gebruik in land- en tuinbouw, dienen waar mogelijk te worden uitgebreid met de eis dat de betreffende verbinding van nature in de plant moet voorkomen.

VIII

De huidige verdeling van het tuinbouwkundig onderzoek in Nederland over twee verschillende directies binnen het Ministerie van Landbouw en Visserij is ondoelmatig.

S. J. WERTHEIM
Wageningen, 10 december 1971

CONTENTS

1. INTRODUCTION

The development of the ovary of the apple flower into a fruit is dependent on the import of nutrients. HANSEN (1970) showed that photosynthesis of the apple fruit is insufficient to cover its own carbohydrate requirements. Apparently the apple fruit acts as a metabolic sink (HANSEN, 1967 a), which in all probability is related to a high hormonal level in the fruit (DAVIES and WAREING, 1965; KRIEDEMANN, 1968a; WEAVER et al., 1969; LUCKWILL et al., 1969; CRANE, 1969; BOLLARD, 1970).

Pollen germination, pollen tube growth, fertilization, and subsequent seed development, are thought to be accompanied by high levels of growth-promoting substances (GUSTAFSON, 1939a, 1942; LUCKWILL, 1957a; LEOPOLD, 1962, 1964; CRANE 1964, 1969; LUCKWILL et al., 1969; NITSCH, 1970), and may therefore be regarded as decisive for normal fruit development (CRANE, 1964, 1969). When these processes do not occur or take place defectively, the production of growth-promoting hormones may be too low for normal fruit development. As a result, ovaries and fruits cease to grow and then abscise. At the reduced level, too, the growth substances are no longer capable of inhibiting the breakdown of the cell walls in the abscission zone, a process which is activated by ethylene (BARLOW, 1953), the gaseous hormone invariably present in the plant tissues. An inadequate vascular connection of the fruit to the circulatory system of the plant may also play a role, the formation of good vascular elements being controlled by endogenous hormones (NITSCH, 1970).

In the apple, abscission is not restricted to one distinct period during development, but can occur at widely differing times, i.e. shortly after flowering ('first drop'), in June and July ('June drop'), and shortly before picking ('preharvest drop').

During the first drop, mainly non-pollinated and non-fertilized ovaries are shed, together with fruitlets in which embryonic growth was arrested at an early stage (VON VEH, 1933; BABALEANU, 1938; VYVYAN, 1946, 1949; MURNEEK, 1954). The cause of this drop is probably due to an excessive low level of growth-promoting substances in the ovary. In the abscence of pollination the level of these hormones may be low at anthesis, as found in the grape flower (ITO et al., 1969). STÖSSER (1970a) has shown that fertilization greatly enhanced the import of ^{32}P in young cherry fruits. Parthenocarpic fruits form an exception in this respect, since the unpollinated or unfertilized ovary itself contains sufficient hormones to insure further development (GUSTAFSON, 1939b; BARLOW, 1953; LEOPOLD, 1964; HAYASHI et el., 1969; WAREING and PHILLIPS, 1970). In addition, when competition from other sinks is eliminated (ABBOTT, 1960, 1965), the ovary does not have to be a strong sink to remain on the tree. Finally, increasing abscisic acid levels might also be involved in abscission shortly after flowering, as was found in cotton fruits (ADDICOTT and LYON, 1969).

During the June drop, varying numbers of fruitlets of various sizes fall from the tree. It has been suggested that June drop is restricted to fruitlets containing an insufficient number of normally developing seeds for a given position on the tree (HEINICKE, 1917), and consequently produce insufficient hormones to attract nutrients for further development (see also MOSTAFAWI et al., 1970). The variation in the hormone content of the seeds is also involved here; a peak in auxin production is followed by a period of diminished fruit drop. The low auxin level in the seeds, caused by the digestion of the endosperm by the rapidly growing embryo, is thought to be the principal cause of the June drop in apple (LUCKWILL, 1953a). When the embryo is full grown, the auxin production rises again and this coincides with the end of the June drop. So the fluctuations in hormone content throughout the season reflect the changes in the amount and condition of the endosperm tissue, and these are reflected in the amount of fruit drop.

Fruits that survive June drop may still fall from the tree during the preharvest drop (VYVYAN, 1946). The cause of this drop may again be due to an inadequate hormonal level in the fruit. The fully developed seeds no longer produce significant quantities of hormones (LUCKWILL, 1953a; GAASH and LAVEE, 1968) and there is also an increase in ethylene production by fruits when maturity is reached (LEOPOLD, 1964). Both these factors promote the premature separation of cells within the abscission zone at the pedicle base.

With respect to the practical aspects for apple growing, the first drop is a desirable phenomenon, because of the limited capactity of the tree to supply fruits of a marketable size. For the same reason, June drop may be desirable when initial fruit set is heavy; but when fruit set is light or moderate this drop should not be excessive. Finally, pre-harvest drop may be a serious problem, but can often be adequately controlled with auxin sprays (GARDNER et al., 1940; VYVYAN, 1946, 1949; LEOPOLD, 1958).

When initial fruit set is sufficient, the June drop remains an uncertain factor due to which the final yield may yet be too low. This applies, for example, to Cox's Orange Pippin. Because this cultivar is the second of importance in The Netherlands (ANON., 1970), it seemed worth-while to gather more information about its fruit set and June drop and to investigate the practical possibilities for reduction of the latter. This is the more important because a reduction in June drop would indirectly diminish the amount of 'bitter pit' and 'Cox's disease', i.e. via an increase in the amount of fruit per tree: when the crop is light, the majority of the fruits tend to be larger, and the occurrence of the bitter pit disorder is related to the size of the fruits, larger fruits being affected more than smaller ones (FAUST and SHEAR, 1968). The same holds for Cox's disease, which invariably is associated with low fruit numbers per tree (OUD, 1968).

The study on the control of June drop has concerned the application of growth regulators, because, as already mentioned before, these substances have proven to be successful in reducing pre-harvest drop as well as first drop. A reduction of first drop or an increase in fruit set, can be achieved in apple with a number of gibberellins (LUCKWILL, 1960; DAVISON, 1960; THOMAS, 1963; BUKOVAC, 1963, VARGA, 1964, 1966; BUKOVAC and NAKAGAWA, 1967; DENNIS

1967; WILLIAMS and LETHAM, 1969). These findings are consistent with the conception that drop is caused by a shortage of certain hormones within the fruit. June drop control has been investigated mainly for auxins (VYVYAN and BARLOW, 1947, 1948a, b; VYVYAN 1949; VYVYAN and TROWELL, 1951; HANSER, 1966). A few studies were made with gibberellic acid (SRIVASTAVA and AGARWAL, 1966, GROCHOWSKA, 1968). The results of these investigations have not led to practical recommendations, however, because the results obtained with auxins have been divergent. In addition, auxins may have an inhibitory effect on apple fruit development, and the drop reduction may be only temporary. (BARLOW, 1953, HANSER, 1966). Therefore, not only auxins but also other regulators were included in the present trials, especially those known to be present in the apple fruit during development, i.e. cytokinins (GOLDACRE and BOTTOMLEY, 1959; LETHAM and BOLLARD, 1961; LETHAM and WILLIAMS, 1969). gibberellins (NITSCH, 1958; DENNIS and NITSCH, 1966; HAYASHI et al., 1968; LUCKWILL et al., 1969), and dormins (MILLBORROW, 1967; PIENIANZEK and RUDNICKI, 1967). Because also auxins occur in developing apple fruits (LUCKWILL, 1948, 1949, 1953a, b; VON RAUSSENDORFF-BARGEN, 1962; LETHAM and WILLIAMS, 1969), these hormones were included in the trials as well.

In this publication the experimental material is discussed first with respect to first drop and June drop. First drop as influenced by the pollination intensity, June drop also by pollination intensity and further by seed content of the fruits, number of leaves per spur, and the presence of bourse shoots. The second part mainly deals with the effect of growth regulators on June drop. A general discussion follows, including also pre-harvest drop.

2. MATERIALS AND METHODS

Unless otherwise stated, all experiments were done on full-grown trees on rootstock M IX in the experimental orchard at Wilhelminadorp.

2.1. EXPERIMENTS ON THE EFFECT OF INTENSITY OF POLLINATION

Experiments 1968.1, 1969.1. Experiments on the effect of intensity of pollination on fruit set and June drop were carried out on Golden Delicious trees in 1968 (experiment 1968.1) and on Cox's Orange Pippin trees in 1969 (experiment 1969.1). A large number of two-year-old branch-parts distributed over the available trees, were selected for uniformity. Five (Golden Delicious) or 4 (Cox's Orange Pippin) flower buds on each branch-part were labelled. In the balloon stage the flower clusters were thinned to 2 lateral flowers per cluster, (29 April 1968, 9 May 1969). In this stage one of the 2 flowers was hand-pollinated using James Grieve pollen for Golden Delicious and Golden Delicious pollen for Cox's Orange Pippin. Pollination was performed by carefully rubbing open anthers against the stigmas. Regulating the intensity of pollination, the number of stigmas was reduced to 0, 1, 2, 3, or 4, or not reduced. Reduction was obtained by removing the appropriate number of free styles with a pair of nail scissors, either before pollination (Golden Delicious) or immediately thereafter (Cox's Orange Pippin). Golden Delicious flowers without free styles were not pollinated. The second flower was only used when the procedure had failed with the first; otherwise, this second flower was removed. A number of freely pollinated flowers with 5 styles served as controls; these were also thinned to 1 flower per cluster. In all 7 treatments, 50 flowers were treated in 1968, divided over 10 branch-parts per treatment. In 1968, per treatment 48 flowers were involved, divided over 12 branch-parts. In total 70 and 84 branch-parts were involved in these two years, spread over 45 and 13 trees, respectively.

Full bloom occurred on 3 May in 1968 and on 12 May in 1969. At regular intervals, the diameter of 20 (1968) or 12 (1969) fruits per treatment was measured with a vernier callipers. Abscised fruitlets fell into plastic baskets attached to the branches (Fig. 1).

The baskets were inspected weekly from one to several times. In the abscised fruits the diameter and the number of normal looking and aborted seeds were determined. After harvest (4 October in 1968, 12 September in 1969), the diameter (mm), height (mm), weight (g), and volume (cm^3) of the fruits were determined, and all fruits were judged for symmetry. Volume was determined by displacement of water. The numbers of good and deaf seeds were determined per fruit, as well as the numbers of locules with seeds. For Golden Delicious the number of locules with $\geqslant 3$ seeds were determined separately. On 29 July, in both years, the number of spur leaves and the number, length, and leaf number of possibly present bourse shoots ($>$ 5 cm) on each labelled spur were determined.

Fig. 1. Basket used to catch abscised ovaries and fruitlets from labelled spurs.

2.2. EXPERIMENTS ON THE EFFECT OF GROWTH REGULATORS

2.2.1. Application of growth regulators to individual fruitlets

Experiments 1968.2 and 3, 1969.2 and 3, and 1970.1. Experiments concerning the effect of growth regulators on June drop were done on Cox's Orange Pippin in 1968 to 1970. In 1970, trees on rootstock M II were used. In these experiments various growth regulators were applied to individual fruitlets. The fruits were obtained in the same way as described for experiments 1968.1 and 1969.1. In 1968, fruitlets arose from flowers with 5 styles per flower, in 1969 and 1970 from flowers with 2 styles per flower whose stigmas has been hand-pollinated. The style number of 2 per flower was chosen in 1969 and 1970, because hand-pollination of 5 per flower in 1968 only led to a negligible June drop. In the following years, therefore, 3 styles per flower were cutt off directly after pollination in the balloon stage. The pollen sources were Golden Delicious (1968), James Grieve (1969), and Benoni (1970). Hand-pollination was carried out from 1 to 6 May in 1968, 9 to 13 May in 1969, and 13 to 16 May in 1970, depending on when the right stage of the flower was reached, i.e. shortly before opening. Full bloom occurred on 3 May in 1968, 12 May in 1969, and 19 May in 1970.

The growth regulators were applied to the fruitlets with a brush, both the fruit and stalk being thoroughly wetted. In 1968, gibberellic acid (GA_3), α –

naphthylacetamide (NAAm), and benzyladenine (BA) were used. In 1969, GA_3, gibberellins $A_4 + A_7$ (GA_{4+7}), α- naphthylacetic acid (NAA), BA and abscisic acid (ABA). In 1970, only GA_{4+7} was used. More details about the regulators are mentioned under 2.2.3. (p.6). The various treatments are summarized in Table 1 (p. 8). The fruits were picked on 1, 12, and 3 September in the three successive years, respectively. The measurements and observations were essentially the same as mentioned for 1969.1. On 21 April 1971, the flower buds and leaf buds were counted on all the bourses of experiment 1970.1, to determine whether GA_{4+7} had affected flower-bud formation.

2.2.2. Application of growth regulators to individual fruitlets, spur leaves, or whole spurs

Experiment 1970.2. In experiment 1970.2, GA_{4+7} was applied to fruitlets with a brush, but in addition spur leaves and whole spurs were sprayed with a hand sprayer. For spur leaves the fruit on the spur was shielded against the spray with a glass tube. The various treatments are given in Table 1 (p. 9). The same data are given for this experiment as for experiment 1970.1. The same measurements and observations were made as in experiment 1969.1. On 21 April 1971, the flower buds and leaf buds were counted on all bourses, to determine whether the treatments had affected flower-bud formation.

2.2.3. Application of growth regulators to whole branches or trees

Experiments 1968.4,1969.4, and 1970.3. In addition to the detailed trials as described in the foregoing, whole branches or trees were sprayed on various times after flowering with growth regulators. The branches (1968, 1969) or trees (1970) were sprayed to point of dripping. The treatments of these three experiments are also given in Table 1 (p. 9). Experiment 1970.3 was carried out at Oudelande. Except in 1968, flower clusters were counted before treatment, either per branch (1969) or also per tree (1970). Fruits were counted at regular intervals throughout the season, for trees on 1 to 3 scaffold limbs per tree on which the flower clusters had been counted before. Full bloom occurred on 3 May in 1968, 12 May in 1969, and 17 May in 1970. In 1969 and 1970, fruits were counted and weighed at harvest (18 September 1969, 21–22 September 1970), in 1970 also per tree. In 1970, the height and diameter of 25 fruits per tree were measured with a vernier callipers after picking, and the numbers of good and deaf seeds were determined. On 20 and 21 October 1970, all fruits were judged for the occurrence of bitter pit. In 1971, flower clusters were counted on the same limbs as in 1970 in experiment 1970.3, to see whether the flower-bud formation had been affected by the treatments. The number of branches or trees per treatment is given in Table 1 (p. 9).

The growth regulators used, were:

ABA	abscisic acid (kindly put at my disposal by Dr. J. van Bragt, Department of Horticulture of the Agricultural University at Wageningen).
BA	benzyladenine, brand Verdan, 7.5 g a.i. per l, obtained from Shell Nederland Chemie N.V., 's Gravenhage.

GA_3	gibberellic acid, brand Berelex, 90% a.i., obtained from I.C.I. (Holland) N.V., Rotterdam.
GA_{4+7}	gibberellins $A_4 + A_7$, brand Berelex A_4/A_7, 90% a.i., obtained from I.C.I. (Holland) N.V., Rotterdam.
NAA	α-naphthylacetic acid, wettable powder 10% a.i., obtained from Luxan N.V. Chemical Industries, Arnhem.
NAAm	α-naphthylacetamide, brand Amid Thin, 8.33% a.i., obtained from Luxan N.V. Chemical Industries, Arnhem.

TABLE 1. Growth regulator treatments on Cox's Orange Pippin fruitlets, spur leaves, spurs, branches or trees in 1968 to 1970. For abbreviations of the growth regulators see chapter 2.2.3. (p. 6).

Year and experiment	Treatment	Time of application in days after full bloom	Date of application	Fruits from hand(H) or free (F) pollination	Number of styles per flower	Number of replications =branchparts (bp), branches(b) or trees (t)	Number of fruits per replication
On individual fruitlets							
1968.2	0 (water)	31	3 June	F	5	5 bp	5
	0 (water)	10 or 21 or 31	13, 24 May, 3 June	H	5	5 bp	5
	30 ppm GA_3	10 or 21 or 31	13, 24 May, 3 June	H	5	5 bp	5
	30 ppm NAAm	10 or 21 or 31	13, 24 May, 3 June	H	5	5 bp	5
	10 ppm BA	10 or 21 or 31	13, 24 May, 3 June	H	5	5 bp	5
	All 4 combinations	10 or 21 or 31	13, 24 May, 3 June	H	5	5 bp	5
1968.3	0 (water)	21	24 May	F	5	5 bp	5
	0 (water)	21	24 May	H	5	5 bp	5
	3, 10, 30, 100 ppm GA_3	21	24 May	H	5	5 bp	5
	3, 10, 30, 100 ppm NAAm	21	24 May	H	5	5 bp	5
	3, 10, 30, 100 ppm BA	21	24 May	H	5	5 bp	5
1969.2	0 (water)	10 or 21 or 30	22 May, 2, 11 June	F	5	12 bp	4
	0 (water)	10 or 21 or 30	22 May, 2, 11 June	H	2	12 bp	4
	30 ppm GA_3	10 or 21 or 30	22 May, 2, 11 June	H	2	12 bp	4
	30 ppm NAA	10 or 21 or 30	22 May, 2, 11 June	H	2	12 bp	4
	10 ppm BA	10 or 21 or 30	22 May, 2, 11 June	H	2	12 bp	4
	All 4 combinations	10 or 21 or 30	22 May, 2, 11 June	H	2	12 bp	4

1969.3	0 (water)	21	2 June	F	5	12 bp	4
	0 (water)	21	2 June	H	2	12 bp	4
	10, 30, 100, 300, 1000 ppm GA_3	21	2 June	H	2	12 bp	4
	10, 30, 100, 300, 1000 ppm GA_{4+7}	21	2 June	H	2	12 bp	4
	10, 30, 100, 300, 1000 ppm NAA	21	2 June	H	2	12 bp	4
	10, 30, 100, 300, 1000 ppm BA	21	2 June	H	2	12 bp	4
	10, 30, 100, 300 ppm ABA	21	2 June	H	2	12 bp	4
1970.1	0 (water)	21	8 June	F	5	12 bp	4
	0 (water)	21	8 June	H	2	12 bp	4
	10, 30, 100, 300, 1000 ppm GA_{4+7}	21	8 June	H	2	12 bp	4
On fruitlets, spur leaves or whole spurs							
1970.2	0	—	—	H	2	12 bp	4
	30 ppm GA_{4+7}	20 and/or 30	8, 18 June	H	2	12 bp	4
On branches							
1968.4	0 (water)	42	14 June	F	5	2 b	
	30 ppm GA_3	42	14 June	F	5	2 b	
	30 ppm NAAm	42	14 June	F	5	2 b	
	10 ppm BA	42	14 June	F	5	2 b	
	All 4 combinations	42	14 June	F	5	2 b	
1969.4	0 (water)	11 or 21 or 30 or 39	23 May, 2, 11, 20 June	F	5	10 b	
	30 ppm GA_3	11 or 21 or 30 or 39	23 May, 2, 11, 20 June	F	5	10 b	
	30 ppm NAA	11 or 21 or 30 or 39	23 May, 2, 11, 20 June	F	5	10 b	
	10 ppm BA	11 or 21 or 30 or 39	23 May, 2, 11, 20 June	F	5	10 b	
	All 4 combinations	11 or 21 or 30 or 39	23 May, 2, 11, 20 June	F	5	10 b	
On trees							
1970.3	0 (water)	20	6 June	F	5	8 t	
	30, 100, 300, 1000 ppm GA_{4+7}	20	6 June	F	5	7 to 8 t	
	30 ppm GA_{4+7}	20 and/or 30 and/or 40	6, 16, 26 June	F	5	7 to 9 t	

3. RESULTS

3.1. THE EFFECT OF INTENSITY OF POLLINATION, SEED NUMBER, NUMBER OF LEAVES PER SPUR, AND THE BOURSE SHOOT

3.1.1. Fruit drop

Experiment 1968.1. Fig. 2 shows the drop patterns of the Golden Delicious fruits. First drop occurred from 16 to 27 May, during which all ovaries 'without styles' dropped, as did many of the free-pollinated ones. In all other treatments first drop was light, indicating that these treatments promoted good fruit set. With a decreasing number of styles per flower, an increase in first drop occurred. Nevertheless, as Fig. 2 shows, only 1 style per flower may be sufficient to obtain a very good fruit set.

A very light June drop occurred from 28 June to 8 July, and since only a few fruits dropped, this experiment does not supply much information about the effect of pollination intensity on June drop. Still, this drop may have been slightly greater when only 1 or 2 styles per flower were present. Since almost all the free-pollinated flowers dropped during first drop, June drop could hardly occur in this treatment.

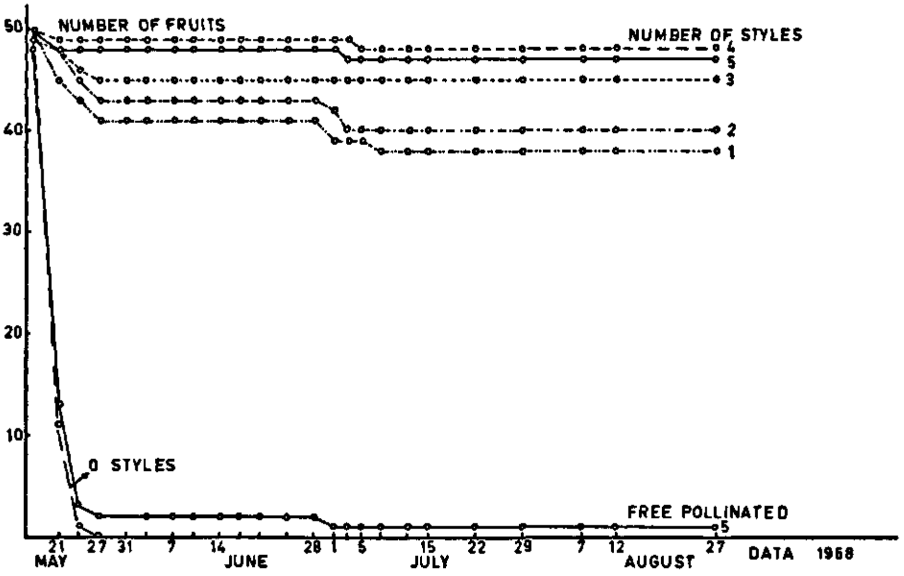


Fig. 2. Experiment 1968.1. Drop patterns of Golden Delicious ovaries and fruitlets deriving from hand-pollinated flowers with 0 to 5 styles per flower (50 flowers per treatment).

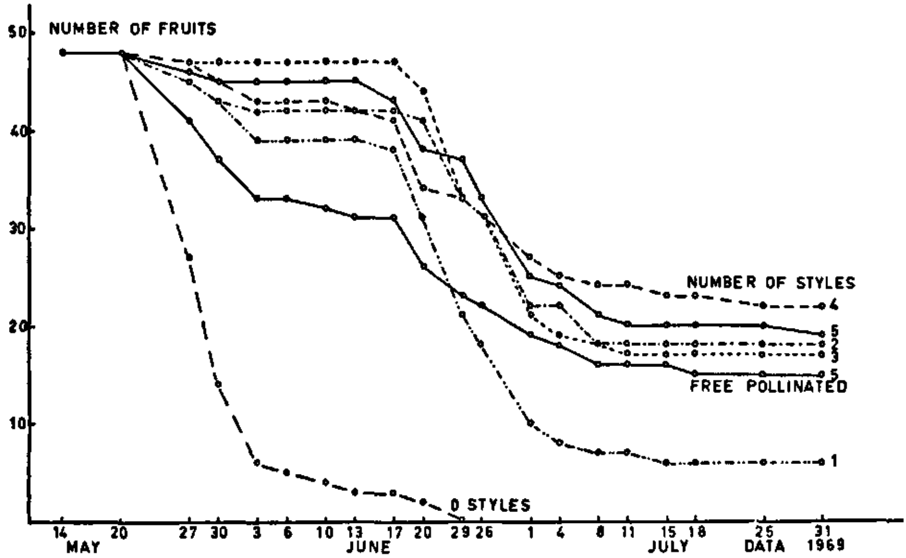


Fig. 3. Experiment 1969.1. Drop patterns of Cox's Orange Pippin ovaries and fruitlets deriving from hand-pollinated flowers with 0 to 5 styles per flower (48 flowers per treatment).

Experiment 1969.1. The drop pattern of Cox's Orange Pippin fruits in experiment 1969.1 is given in Fig. 3. When all styles were removed, almost all ovaries were shed during first drop, which lasted from 20 May to 3 June. Retention of $\geqslant 1$ style per flower greatly reduced first drop. The first drop of free-pollinated flowers was less than that of the flowers with 0 styles but greater than that of hand-pollinated flowers with $\geqslant 1$ style.

The very conspicuous June drop lasted from about 17 June to about 1 July, during which period all remaining fruitlets 'without styles' were shed. June drop was heaviest when 1 style per flower had been retained. In all other treatments June drop was about equal.

Observations on the fruitlets shed during June drop and on the spurs loosing their fruit, are mentioned in the upper part of Table 2. Because the number of dropped fruitlets per treatment was too low for reliable averages, fruitlets of all treatments were taken together. There were no clear differences between the fruitlets of the various treatments. The figures in Table 2 show that the abscised fruitlets of the first part of the June drop period were smaller and contained a lower number of normal seeds as compared to those of the second part of the June drop period. In the beginning and at the end of the June drop period, fruitlets were shed from spurs with fewer leaves than in the middle part of the June drop period.

Table 3 (upper part) shows the relation between first drop and June drop and the effect of the bourse shoot on fruit drop. First drop was stronger from spurs

TABLE 2. Experiments 1969.1,2 and 3. Size and seed content of Cox's Orange Pippin fruitlets dropped during June drop and the average number of leaves per spur of fruit-loosing spurs without a bourse shoot. Total of all treaments.

Experiment	June				July				
	17	20	24	26	1	4	8	11	15
1969.1	1 to 5 styles /flower hand-pollinated								
Number of judged fruitlets	4	28	29	13	40	8	8	2	1
Fruitlet diameter mm	13.7	15.2	17.9	19.3	21.8	26.9	26.9	26.7	29.4
Normal seeds/fruitlet	0.7	0.6	0.6	1.5	2.1	3.9	1.8	2.5	6.0
Aborting seeds/fruitlet	4.7	2.4	3.0	2.4	2.0	0.9	3.1	5.5	1.0
Leaves/spur	2.5	7.9	7.8	9.6	9.2	8.7	9.1	6.5	7.0
1969.2	2 styles/flower hand-pollinated								
Number of judged fruitlets	15	88	107	35	144	50	57	23	7
Fruitlet diameter mm	13.1	14.3	16.6	18.9	22.0	25.0	28.0	30.0	29,7
Normal seeds/fruitlet	1.9	0.8	1.2	1.9	2.8	3.8	4.2	5.1	5.1
Aborting seeds/fruitlet	1.1	2.5	2.1	1.5	1.4	1.2	1.3	0.4	1.3
Leaves/spur	6.9	5.7	7.7	8.4	8.5	8.5	9.2	10.4	10.6
1969.3	2 styles/flower hand-pollinated								
Number of judged fruitlets	8	25	200	22	171	65	38	15	12
Fruitlet diameter mm	12.3	14.0	17.1	19.7	21.1	25.5	27.8	29.1	32.3
Normal seeds/fruitlet	0.4	0.3	0.8	2.3	1.5	4.1	4.7	4.9	3.4
Aborting seeds/fruitlet	2.3	3.4	2.9	2.4	2.9	1.0	0.9	0.6	1.2
Leaves/spur	6.0	5.6	6.2	7.2	7.7	8.8	8.3	9.0	9.0

TABLE 3. Experiments 1969.1,2 and 3. Relation between first drop and June drop and between fruit drop and occurrence of bourse shoot(s) (> 5 cm) of Cox's Orange Pippin spurs. Total of all treatments.

Experiment	Starting number of spurs (=fruits).		Number and (%) of dropped ovaries or fruitlets.				Number and (%) of remaining fruits after June drop	
			First drop		June drop			
	− shoot	+ shoot	− shoot	+ shoot	− shoot	+ shoot	− shoot	+ shoot
1969.1	285	47	73 (25.6)	17 (36.2)	120 (56.6)	15 (50.0)	92 (43.4)	15 (50.0)
	332		90 (27.1)		135 (55.8)		107 (44.2)	
1969.2	1134	160	110 (9.7)	26 (16.3)	508 (49.6)	59 (44.0)	516 (50.4)	75 (56.0)
	1294		136 (10.5)		567 (49.0)		591 (51.0)	
1969.3	1123	125	120 (10.7)	19 (15.2)	521 (51.9)	52 (49.1)	482 (48.1)	54 (50.9)
	1248		139 (11.1)		573 (51.7)		536 (48.3)	

developing a shoot than from spurs without such a bourse shoot. June drop, however, was slightly stronger from spurs without a bourse shoot. We shall return to these subjects in the next section.

Experiments 1969.2 and **1969.3.** Although these experiments were done in order to elucidate the effect of the various growth regulators on June drop, some general observations on first drop and especially June drop are worth mentioning here. This does not include the experiments done in 1968 and 1970 on Cox's Orange Pippin, in which June drop was too light.

The drop patterns of the Cox's Orange Pippin fruitlets obtained from free-pollinated flowers and from flowers with 2 hand-pollinated stigmas, are to be found in Figs. 6 and 7 for the experiments 1969.2 and 3, respectively. Fruits from free-pollinated flowers showed a considerable first drop and June drop. The first drop was heavier than that of the hand-pollinated flowers with only 2 styles. The June drop was about equal in both treatments. First drop lasted from about 20 May until 3 June, June drop from about 20 June until 11 to 15 July.

The observations on the fruitlets shed during June drop are given in the middle and lower parts of Table 2 (p. 12). The fruitlets of all treatments were taken together in both experiments to obtain more reliable averages. This was permissible because there were no clear differences in the appearance of the dropped fruitlets of the various treatments. The values in Table 2 indicate that dropped fruitlets of the first part of the June drop period were smaller, contained fewer seeds, and originated from spurs with a lower leaf number as compared to those of the second part of the June drop period. The largest diameter of the dropped fruitlets was about 30 mm.

Table 3 (middle and lower rows) (p. 13) shows the relation between first drop and June drop and the effect of the bourse shoot on fruit drop. The amount of first drop had no effect on the degree of June drop. In experiment 1969.1, for example, during first drop 27.1% of the ovaries abscised, in the other two experiments only 10.5% and 11.1%. Still, June drop was roughly the same in all three experiments: 55.8%, 49.0% and 51.7%, respectively. In both trials the first drop was heavier from spurs developing a bourse shoot than from spurs without such a shoot. June drop, however, was slightly stronger from spurs without a bourse shoot, although in experiment 1969.3 the difference was very small. In experiment 1969.2 the bourse shoot had a mean ultimate length of 21.2 cm on spurs shedding their fruit during the first part of the June drop period, and 25.1 cm on spurs which shed in the last part of this period. For experiment 1969.3, these figures were 16.4 anf 17.4 cm, respectively. Hence, the length of the bourse shoot had no effect on the time at which the fruits were shed during June drop. Shoot lengths up to 35 cm had no effect on the amount of fruit dropped. Longer shoots showed a tendency to increase June drop. In experiments 1969.1,2, and 3 the numbers of leaves per spur of spurs losing their fruit in first drop or June drop were 8.6, 7.7, and 7.3, respectively. For spurs keeping their fruit until picking, these figures were 9.7, 9.5, and 8.8, respectively. Spur leaves develop soon after leafing out, and are all present during flowering. Hence, spurs shedding their fruit in one of the two drop periods had, on the average, fewer leaves per spur than did spurs on which the fruit remained.

In Table 4 (p. 16), the abscised and picked fruits are classified according to seed content. Although only 2 styles were present per flower, many fruits contained more seeds than the expected maximum number of 4 per fruit. It is striking that the great majority of the fruits did not contain more than 8 seeds per fruit. Apparently, all 10 ovules could not be reached by the pollen tubes under the prevailing conditions. Table 4 shows clearly the differences in seed content between abscised fruitlets (upper part) and picked fruits (lower part). It is also evident that there were abscised fruitlets with many seeds and picked fruits with very few seeds or even no seeds at all. Over 50% of the shed fruitlets had no more than 4 seeds per fruit, whereas the majority of the picked fruits had 4 to 8 seeds per fruit.

3.1.2. Fruit size, shape, and seed content

Experiment 1968.1. Fig. 4 shows the growth rate of fruits of Golden Delicious resulting from hand-pollination of 1 to 5 stigmas per flower. Fruits from free-pollinated flowers were not available in sufficient numbers, and no fruits could be measured during the greater part of the season for the treatment '0 styles', since they all abscised. In Fig. 4 a temporary difference can be seen in fruit growth, favouring fruits from flowers with 5 styles per flower. Fruits of all other treatments grew at the same rate throughout, except those of the 1 style per

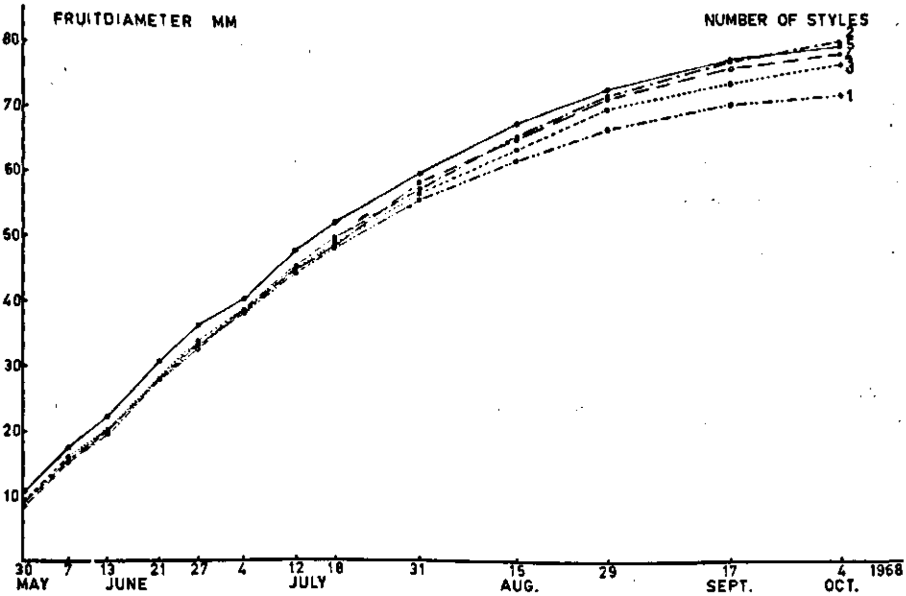


Fig. 4. Experiment 1968.1. Growth curves of Golden Delicious fruits obtained from hand-pollinated flowers with 1 to 5 styles per flower. (Means of 20 fruits per treatment).

TABLE 4. Experiments 1969.2 and 3. Numbers of abscised fruitlets during June drop and picked fruits of Cox's Orange Pippin classified for good and aborted seeds. Total of all treatments.

Aborted seeds in abscised fruitlets.

	1969.2											1969.3										
Good Seeds	0	1	2	3	4	5	6	7	8	9	10	0	1	2	3	4	5	6	7	8	9	10
0	20	13	23	30	33	26	22	13	3	–	–	6	15	33	65	72	31	45	7	6	–	–
1	28	8	4	4	1	4	–	–	–	–	–	4	8	6	3	6	2	–	2	–	–	
2	35	7	9	1	2	–	–	–	–			22	4	12	7	1	1	–	–	–		
3	29	11	9	3	5	2	–	–				27	12	7	3	1	1	–	–			
4	40	17	4	3	–	–	–					36	11	5	1	–	–	–				
5	42	6	2	–	–	1						24	6	4	–	–	–					
6	22	10	1	–	–							25	4	3	–	–						
7	19	3	–	–								13	5	–	–							
8	8	–	–									6	–	–								
9	3	–										–	–									
10	–											–										

1969.2: Number of fruits with maximum of
4 seeds 294 (55.8%)
8 seeds 522 (99.3%)

1969.3: Number of fruits with maximum of
4 seeds 325 (58.8%)
8 seeds 552 (100%)

Aborted seeds in picked fruits.

Good seeds	0	1	2	3	4	5	6	7	8	9	10	0	1	2	3	4	5	6	7	8	9	10
0	3	4	3	6	14	22	28	26	18	4	3	4	–	4	10	16	33	44	22	6	5	–
1	–	2	15	24	25	29	32	5	5	–		3	3	7	16	21	26	12	14	1	–	
2	6	5	15	13	31	24	11	4	2			1	3	8	24	28	20	4	1	1		
3	2	3	18	20	12	8	4	1				10	5	20	21	15	5	4	–			
4	4	6	21	19	6	–	–					7	10	2	10	4	1	–				
5	5	6	8	7	2	2						5	8	6	6	–	–					
6	5	5	4	2	–							1	3	4	2	1						
7	1	2	–									2	1	–	–							
8	3	–	–									1	–	–								
9	–	–										–	–									
10	–											–										

1969.2: Number of fruits with maximum of
4 seeds 106 (19.1%)
8 seeds 526 (94.8%)

1969.3: Number of fruits with maximum of
4 seeds 97 (19.8%)
8 seeds 475 (96.8%)

flower group, which stayed behind after the middle of July.

The upper part of Table 5 gives the results of the determinations made on picked fruits. As could be expected from the divergent drop patterns in Fig. 2 (p. 10), the number of picked fruits varied between the various treatments. The fewer the number of styles per flower, the more asymmetric fruits were picked. The data on fruit size indicate that flowers with only 1 style gave the smallest fruits. These fruits also contained the lowest number of seeds. Fruits of the groups with 2 and 5 styles per flower were larger than those of the two remaining treatments. The fewer styles retained, the lower the number of well-developed seeds per fruit and also the more elongated the fruits, as indicated by the height: diameter ratio. The fruits contained few aborted seeds. The number of seeds per fruit decreased with decreasing numbers of styles per flower except when 3 or 4 styles were present.

It was expected that each style would correspond with seed formation in one locule. However, the number of locules with seeds in fruits from flowers with 1 to 3 styles was higher than this expected value, and for 4- or 5-style flowers it was lower. It was also expected that not more than 2 seeds could be formed per locule, but a number of fruits proved to contain locules with 3 or occasionally even more seeds. With fewer styles per flower this occurred less frequently. Only a minority of the fruits had the expected seed number (= twice the number of styles) and the expected number of locules with seeds (= number of styles present).

Although not mentioned in Table 5, the number of leaves per spur did not vary between the treatments. Hence, the differences mentioned were not caused by variations in the numbers of leaves per spur.

Experiment 1969.1. Fruit growth of Cox's Orange Pippin fruits of the various treatments of experiment 1969.1 is shown in Fig. 5. There were no great differences in fruit growth between the various treatments. Because so many fruits abscised in this experiment, new fruits often had to be taken for the measurements. Therefore, the curves in Fig. 5 are less reliable. Fruits of the 1 and 2 styles per flower treatments were ultimately slightly smaller than those of the other treatments.

The lower part of Table 5 gives the results of the determinations on picked fruits. The number of asymmetric fruits varied widely between the treatments and lacked correlation with the treatments. The conclusion stated above, i.e. that fruits of the treatments with 1 or 2 styles were the smallest, is not fully confirmed by the values in Table 5, since fruits of the treatment with 5 styles had the same size as the 1- and 2-style fruits. The height: diameter ratio increased with a decreasing number of styles. However, the few fruits of the 1-style treatment did not follow this trend. Possibly, the number of fruits of this treatment was too low for reliable comparison. There were no clear differences in seed content. It is remarkable that the fruits contained so many deaf seeds. The number of locules with seeds was higher than expected, except for the fruits from the treatment with 5 styles. When only 1 style was left, an average of 3

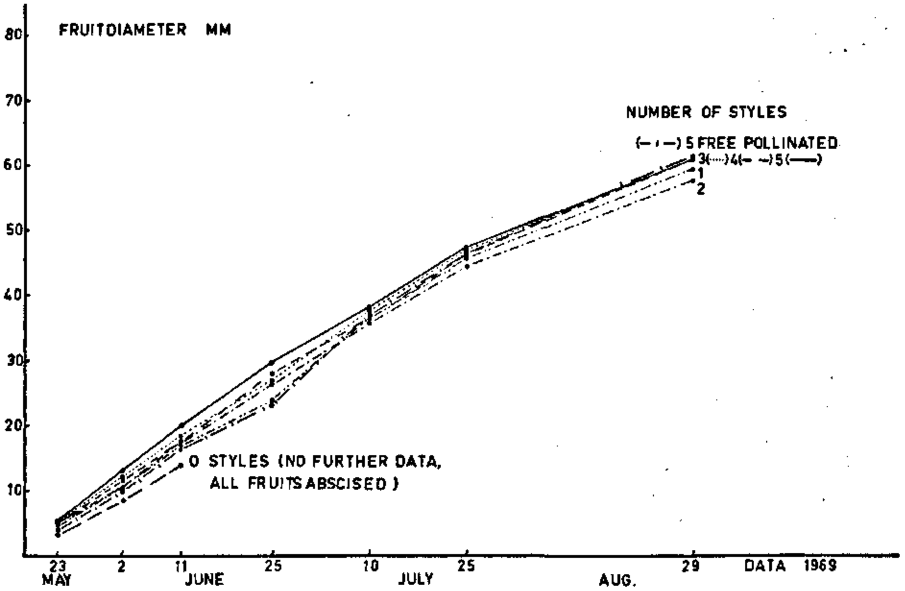


Fig. 5. Experiment 1969.1. Growth curves of Cox's Orange Pippin fruits obtained from hand-pollinated flowers with 1 to 5 styles per flower. (Means of 12 fruits per treatment).

locules with seeds still occurred. The number of leaves per spur varied a little between the treatments, but the differences in fruit characters between the treatments could not be ascribed to these differences. Finally, it was striking that free-pollinated flowers gave rise to the largest fruits, the highest number of good seeds, and also the highest percentage of asymmetric fruits.

Experiments 1969.2 and 1969.3. It was observed that fruit size on spurs with a long shoot was larger than that on spurs with a short shoot. For experiment 1969.2, the average fruit diameter on spurs with a 5 to 15 cm shoot was 67.6 mm, with a 16 to 25 cm shoot 69.5 cm, with a 26 to 35 cm shoot 70.5 mm, and with still longer shoots even 72.3 mm. For experiment 1969.3, this relation was not so clear, fruit diameter for the first three classes of spurs being 65.5, 67.2, and 66.5 mm, respectively. No spurs with shoots longer than 35 cm occurred in this experiment.

3.1.3. Conclusions

– Flowers in which all styles were cut off in the balloon stage dropped during first drop in almost all cases. This holds for Golden Delicious and for Cox's Orange Pippin. The few remaining fruits of the latter cultivar in this treatment all dropped during June drop.
– Pollination of only 1 stigma per flower strongly suppressed the first drop, i.e. induced good fruit set, again for both cultivars involved.
– First drop after retention of 1 to 5 hand-pollinated styles per flower was about

TABLE 5. Experiments 1968.1 and 1969.1. Results of determinations on picked fruits of Golden Delicious and Cox's Orange Pippin. Starting number 50 or 48 fruits per treatment respectively.

Experiment	Number of styles/flower hand (H) or free (F) pollinated	Number of picked fruits (% asymmetric fruits)	Average fruit				Height/ diameter	Seeds/fruit		Number of locules with seeds	Number of locules with ≥ 3 seeds/locule	Number of fruits with expected seed content
			weight (g)	volume (cm^3)	diameter (mm)	height (mm)		Normal	Deaf			
1968.1	Golden Delicious											
	5 H	46 (34.8)	196	247	77.3	72.3	0.94	7.3	0.1	4.1	9	5
	4 H	46 (45.6)	189	236	75.6	72.8	0.96	5.3	0.1	3.4	5	1
	3 H	44 (45.5)	181	225	74.5	72.7	0.98	5.4	0.1	3.3.	6	2
	2 H	40 (55.0)	200	247	76.9	76.1	0.99	4.0	0.1	2.8	1	2
	1 H	37 (54.0)	171	210	72.1	72.7	0.99	2.5	0.0	1.7	1	11
	0 H	0	–	–	–	–	–	–	–	–	–	–
	5 F	1	–	–	–	–	–	–	–	–	–	–
1969.1	Cox's Orange Pippin.											
	5 H	19 (26.3)	101	106	62.5	51.4	0.83	1.4	5.4	4.7		
	4 H	22 (40.9)	107	121	64.4	53.0	0.83	1.2	5.1	4.3		
	3 H	17 (47.0)	112	116	62.5	53.1	0.85	0.9	6.0	4.3		
	2 H	18 (33.3)	100	108	61.3	52.4	0.86	1.4	3.8	3.8		
	1 H	6 (16.7)	102	109	62.8	49.2	0.78	0.8	3.2	3.0		
	0 H	0	–	–	–	–	–	–	–	–		
	5 F	14 (64.3)	117	130	65.3	54.0	0.83	2.0	3.9	4.1		

equally light, with only a slight difference at the expense of 1 or 2 styles per flower.

- First drop after free-pollination of flowers with an unreduced number of styles was heavier than after retention of ⩾ 1 hand-pollinated styles per flower. For Golden Delicious, first drop after free-pollination even equalled that of the first drop of flowers without styles.
- The amount of June drop was very light for Golden Delicious, but condsiderable for Cox's Orange Pippin. Possibly, the June drop of the former cultivar was slightly greater with 1 or 2 styles per flower than when ⩾ 3 styles per flower were retained. For Cox's Orange Pippin, June drop was the heaviest in the 1 style per flower treatment and similar in all other treatments.
- June drop after free-pollination could not be judged for Golden Delicious, since almost all the fruits had already dropped before that time. In Cox's Orange Pippin, June drop after free-pollination equalled that of the June drop of hand-pollination treatments with ⩾ 2 styles per flower.
- Abscised fruitlets of Cox's Orange Pippin shed during the first part of the June drop period were smaller, contained fewer seeds and originated from spurs with fewer leaves than those of the second part of the June drop period.
- For Cox's Orange Pippin, first drop was stronger from spurs developing a shoot, but June drop was slightly lower on those spurs as compared to spurs without a bourse shoot.
- No relationship existed between the amount of first drop and June drop in Cox's Orange Pippin.
- The length of the bourse shoot had no effect on the time at which the fruitlets were shed during the June drop.
- The largest diameter of the abscised fruitlets shed during June drop was about 30 mm.
- On the average, abscised fruitlets contained fewer seeds than those remaining to the tree.
- Fruit size of the fruits still on the trees at picking time was smallest when 1 style per flower was retained in Golden Delicious. Fruit size did not vary clearly between the other treatments of either this cultivar or Cox's Orange Pippin.
- The fewer the styles retained in Golden Delicious, the lower the number of well-developed seeds per fruit, the taller the fruit, and also the more asymmetric the fruit shape. For Cox's Orange Pippin, no relationship could be established between number of styles and seed content or asymmetry of the fruits. Fruit length showed the same trend as in Golden Delicious, except for the few fruits derived from flowers with only 1 style.
- Few fruits of both cultivars behaved as expected with respect to seed content, i.e. the number of styles pollinated did not give certainty as to the number of seeds in the fruit. With 1 to 3 (Golden Delicious) or 4 (Cox's Orange Pippin) styles per flower, the seed number was higher than expected; with more styles it was lower.
- Golden Delicious fruits had very few aborted seeds, whereas Cox's Orange Pippin had many.

3.2. The effect of growth regulators

3.2.1. Fruit drop

3.2.1.1. Fruit drop after treatment of individual fruitlets

Experiment 1968.2. Table 6 gives the results of experiment 1968.2. June drop was slight, and therefore it is difficult to draw any conclusions about the effect of the growth regulators involved. The very small first drop (columns F of Table 6) proves that the flowers had set very well, probably because all 5 styles were retained and pollinated. Only two treatments might have reduced June drop to some extent, viz. 10 ppm BA and 30 ppm GA_3 + 30 ppm NAAm, applied 21 days after full bloom. None of the treatments affected fruit drop after the actual June drop.

Table 6. Experiment 1968.2. Number of dropped fruits of Cox's Orange Pippin. F = first drop, J = June drop, P = pre-harvest drop. Starting number 25 fruits per treatment obtained from flowers of which 5 styles were hand-pollinated. Growth regulator treatment on individual fruitlets.

Treatment	Application time in days after full bloom								
	10			21			31		
	F	J	P	F	J	P	F	J	P
0 (water)	0	3	0	1	6	0	1	4	1
30 ppm GA_3	0	3	0	0	3	1	0	1	2
30 ppm NAAm	0	0	1	0	6	1	1	3	0
10 ppm BA	0	1	0	0	0	2	0	2	0
30 ppm GA_3 + 30 ppm NAAm	0	2	0	0	0	1	0	1	0
30 ppm GA_3 + 10 ppm BA	1	3	0	0	4	1	0	0	0
30 ppm NAAm + 10 ppm BA	0	4	2	0	3	0	0	2	2
30 ppm GA_3 + 30 ppm NAAm + 10 ppm BA	0	3	1	0	4	0	0	3	0

Experiment 1968.3. Table 7 shows the results of experiment 1968.3. As can be seen from column F, fruit set was very high since hardly any first drop occurred. As in the previous experiment, June drop was slight. Hence, conclusions about the effect of the growth regulators used and about the various concentrations cannot be drawn with certainty. GA_3 had little or no effect. NAAm did not affect June drop when used in concentrations of 3 or 100 ppm, but 10 and 30 ppm may have increased June drop to some extent. Low concentrations of BA had no effect, but 30 and 100 ppm may have enhanced June drop. Column P shows that none of the treatments caused pre-harvest drop.

TABLE 7. Experiment 1968.3. Number of dropped fruits of Cox's Orange Pippin. F = first drop, J = June drop, P = pre-harvest drop. Treatment 21 days after full bloom on individual fruitlets. Starting number 25 fruits per treatment obtained from flowers of which 5 styles were hand-pollinated.

Treatment	F	J	P
0 (water)	0	3	2
3 ppm GA_3	1	1	1
10 ppm GA_3	0	0	0
300 ppm GA_3	0	2	0
100 ppm GA_3	0	1	0
3 ppm NAAm	0	3	0
10 ppm NAAm	0	6	1
30 ppm NAAm	0	8	3
100 ppm NAAm	1	2	1
3 ppm BA	0	4	1
10 ppm BA	0	2	0
30 ppm BA	0	8	0
100 ppm BA	1	6	1

Experiment 1969.2. Table 8 gives the principal results of experiment 1969.2, which had the same treatments as experiment 1968.2 except that NAAm was replaced by NAA. Because of the light fruit drop obtained in 1968, fruits in this and following experiments were obtained by hand-pollination of only 2 styles per flower. Table 8 shows that both first drop and June drop were much heavier than in the 1968 experiments, possibly due to the pollination of fewer styles, or to the different pollinator variety used in 1969.

Application of GA_3, NAA, or BA, or their combinations did not reduce June drop when applied 10 or 21 days after full bloom. On the contrary, several treatments appeared to have enhanced June drop on both dates, for example GA_3 + BA applied 10 days after full bloom and almost all the treatments applied 21 days after full bloom. The two treatments of experiment 1968.2, which might have reduced June drop, did not have the same effect in this experiment.

It is very conspicuous that NAA reduced June drop when applied 30 days after full bloom, whether or not in combination with both other compounds. The effect of NAA alone appeared to be slightly stronger than that of NAA with GA_3, BA or both.

The drop patterns of the treatments applied 30 days after full bloom are given in Fig. 6, which clearly shows that NAA reduced the amount of June drop, whereas this was not the case with GA_3 or BA, whether used separately or in combination. Both Table 8 and Fig. 6 indicate that the reduction in June drop was not a transient effect.

TABLE 8. Experiment 1969.2. Number of dropped fruits of Cox's Orange Pippin. F = first drop, J = June drop, P = pre-harvest drop. Starting number 48 fruits per treatment obtained from flowers of which 2 styles were hand-pollinated. Growth-regulator treatment on individual fruitlets.

Treatment	Application time in days after full bloom								
	10			21			30		
	F	J	P	F	J	P	F	J	P
0 (water)	9	21	0	3	24	2	2	20	1
30 ppm GA_3	0	27	0	2	29	1	1	23	0
30 ppm NAA	1	23	1	4	29	0	0	4	0
10 ppm BA	6	24	4	2	33	2	3	18	2
30 ppm GA_3 + 30 ppm NAA	5	27	0	2	31	0	3	9	0
30 ppm GA_3 + 10 ppm BA	0	34	0	1	24	0	3	15	1
30 ppm NAA + 10 ppm BA	7	23	1	2	28	1	3	8	3
30 ppm GA_3 + 30 ppm NAA + 10 ppm BA	5	20	1	4	26	1	2	6	1

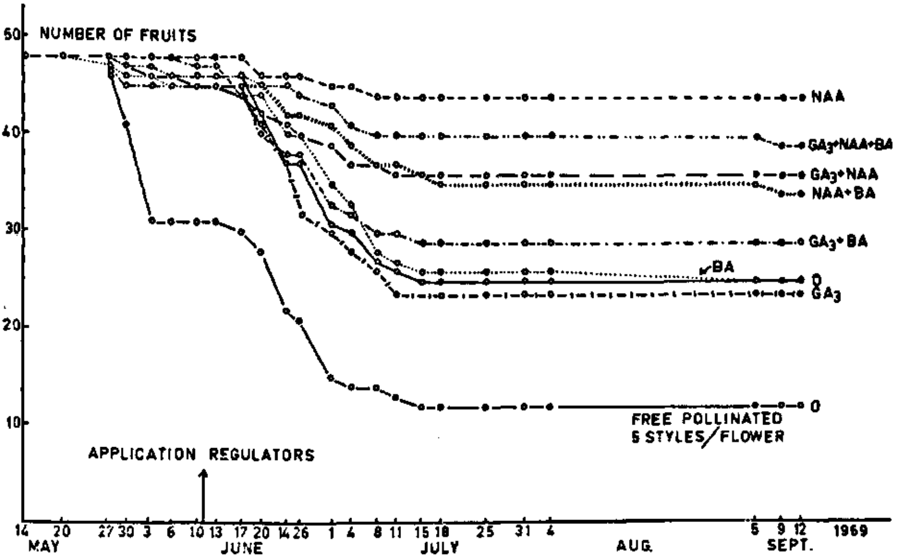


Fig. 6. Experiment 1969.2. Drop patterns of Cox's Orange Pippin ovaries and fruits as affected by the application to the fruitlets of 30 ppm NAA, 30 ppm GA_3, or 10 ppm BA, or combinations of these, 30 days after full bloom. Fruits obtained from hand-pollinated flowers with 2 styles (48 fruits followed per treatment).

Experiment 1969.3. Table 9 gives the results of experiment 1969.3. The amount of first drop and June drop was considerable. GA_3 reduced June drop, expecially in the two highest concentrations. GA_{4+7} was the most effective compound in reducing June drop in this experiment. With increasing concentrations, June drop was increasingly suppressed. After the use of 1000 ppm GA_{4+7}, hardly any drop occurred. The interesting effect of this gibberellin mixture on fruit drop is also given in Fig. 7.

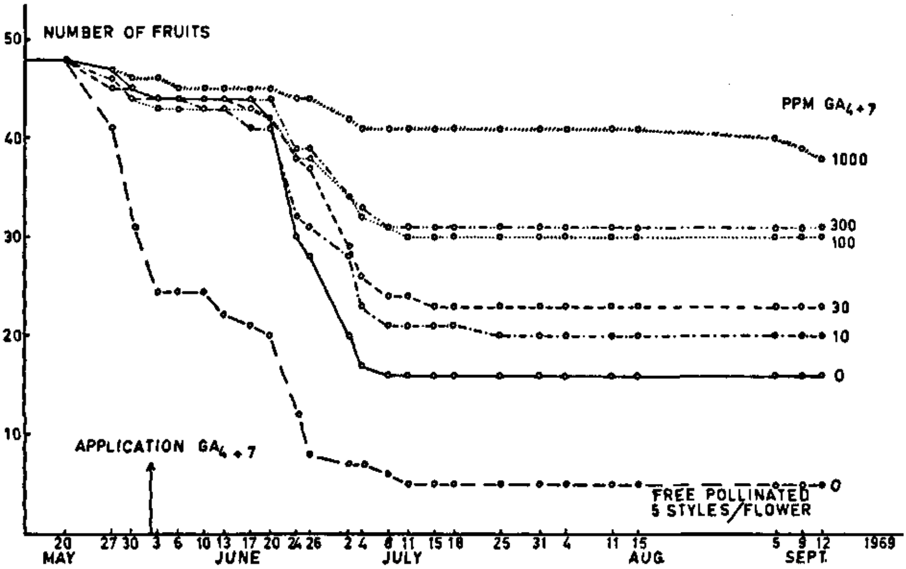


Fig. 7. Experiment 1969.3. Drop patterns of Cox's Orange Pippin ovaries and fruits as affected by the application to the fruitlets of various concentrations of GA_{4+7}, 21 days after full bloom. Fruits obtained from hand-pollinated flowers with 2 styles (48 fruits followed per treatment).

To return to Table 9, NAA increased the amount of June drop when used in concentrations $\leqslant$ 100 ppm, but higher concentrations reduced it. BA also enhanced the amount of June drop slightly, but here only in concentrations $\geqslant$ 100 ppm, lower concentrations having no effect. ABA had no clear effect.

None of the treatments had a significant effect on pre-harvest drop.

Experiment 1970.1. In experiment 1970.1 only GA_{4+7} was applied to the individual fruitlets in various concentrations 21 days after full bloom. The results of this experiment are given in Table 10 and Fig. 8. First drop and June drop were slight. Fruit drop occurred more or less gradually throughout the season, without sharply defined drop periods. However, GA_{4+7} was definitively effective in diminishing fruit drop.

TABLE 9. Experiment 1969.3. Number of dropped fruits of Cox's Orange Pippin. F = first drop, J = June drop, P = pre-harvest drop. Treatment 21 days after full bloom on individual fruitlets. Starting number 48 fruits per treatment obtained from flowers of which 2 styles were hand-pollinated.

Treatment	F	J	P
0 (water)	4	28	0
10 ppm GA_3	4	21	2
30 ppm GA_3	4	24	1
100 ppm GA_3	6	23	2
300 ppm GA_3	7	16	1
1000 ppm GA_3	4	18	2
10 ppm GA_{4+7}	5	22	1
30 ppm GA_{4+7}	4	20	1
100 ppm GA_{4+7}	5	13	0
300 ppm GA_{4+7}	4	13	0
1000 ppm GA_{4+7}	3	3	3
10 ppm NAA	2	34	0
30 ppm NAA	1	29	3
100 ppm NAA	1	30	2
300 ppm NAA	3	23	1
1000 ppm NAA	3	21	3
10 ppm BA	1	24	1
30 ppm BA	4	28	1
100 ppm BA	2	33	5
300 ppm BA	3	32	1
1000 ppm BA	6	31	1
10 ppm ABA	3	27	2
30 ppm ABA	5	18	0
100 ppm ABA	3	25	2
300 ppm ABA	2	27	2

TABLE 10. Experiment 1970.1. Number of dropped fruits of Cox's Orange Pippin. F = first drop, J = June drop, P = pre-harvest drop. Treatment 21 days after full bloom on individual fruitlets. Starting number 48 fruits per treatment obtained from flowers of which 2 styles were hand-pollinated.

Treatment	F	J	P
0 (water)	0	7	5
10 ppm GA_{4+7}	0	3	5
30 ppm GA_{4+7}	0	4	2
100 ppm GA_{4+7}	0	2	3
300 ppm GA_{4+7}	0	1	2
1000 ppm GA_{4+7}	0	3	0

Fig. 8 shows that higher concentrations were somewhat more effective than lower ones. It also shows that the free-pollinated treatment showed a considerable first drop, which occurred later than normal but was not followed by further drop. As in the previous experiments, free-pollination of flowers with 5 styles caused less fruit set than hand-pollination of only 2 styles per flower.

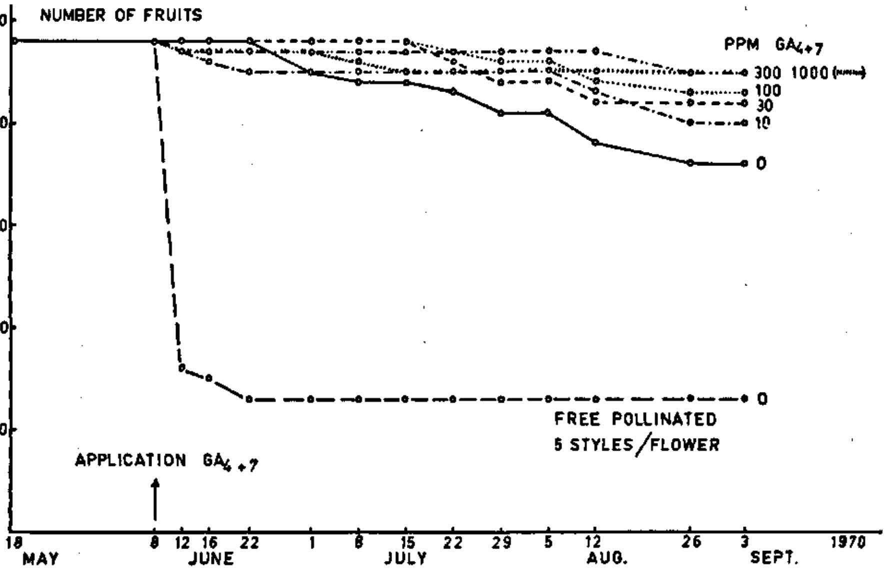
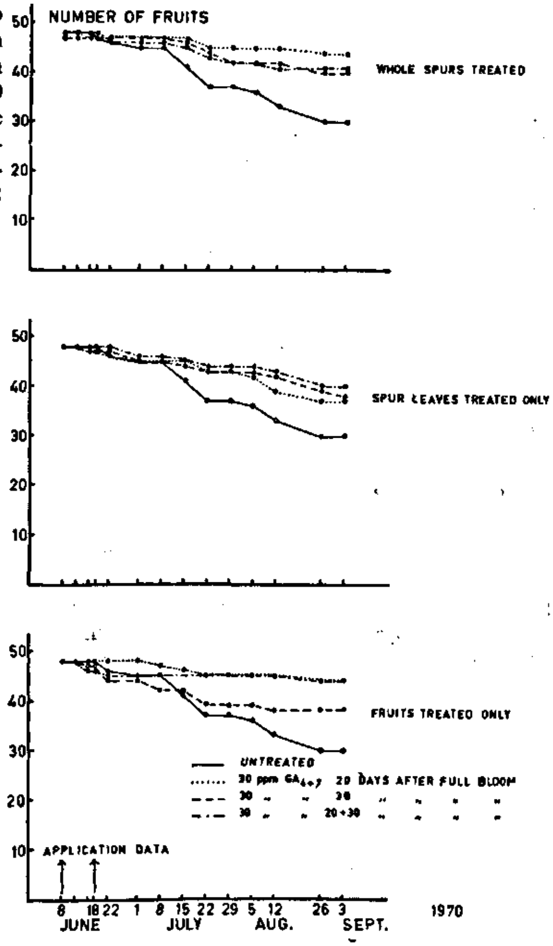


Fig. 8. Experiment 1970.1. Drop patterns of Cox's Orange Pippin ovaries and fruits as affected by the application to the fruitlets of various concentrations of GA_{4+7}, 21 days after full bloom. Fruits obtained from hand-pollinated flowers with 2 styles (48 fruits followed per treatment).

3.2.1.2. Fruit drop after treatment of fruitlets, spur leaves, or whole spurs

Experiment 1970.2. The results of experiment 1970.2 are shown in Fig. 9. Fruit drop was light, but GA_{4+7} did reduce it. Although the differences between the various treatments were small, the application 20 days after full bloom was somewhat more effective than that made 30 days after full bloom. Two applications carried out 20 and 30 days after full bloom were not more effective than a single treatment 20 days after full bloom. Spraying whole spurs did not give better results than treating fruitlets alone. The differences in actual June drop between the treatments on spur leaves or fruits were negligible. However, when total fruit drop is considered, application to the fruitlets might have been more effective. Neither in this treatment nor in the ones mentioned before did the growth regulators affect the time at which the fruits dropped. Only the amount of drop was influenced.

Fig. 9. Experiment 1970.2. Drop patterns of Cox's Orange Pippin fruits as affected by the application of 30 ppm GA_{4+7}, 20 and/or 30 days after full bloom to the whole spurs, the spur leaves, or the fruitlets. Fruits obtained from hand-pollinated flowers with 2 styles (48 fruits followed per treatment).



3.2.1.3. Fruit drop after treatment of whole branches or trees

Experiment 1968.4. The results of experiment 1968.4 (first column of Table 11) show that NAAm reduced June drop considerably. This effect was not enhanced by the addition of either GA_3 or BA, their combined addition gave further reduction. This is also to be seen in Fig. 10. Neither GA_3 nor BA affected June drop. The chemicals had no detrimental effect upon the leaves. In this experiment no further data were gathered after June drop.

Experiment 1969.4. Table 11 also gives the results of experiment 1969.4. All substances tended to increase June drop slightly when applied 11 or 21 days after full bloom. Thirty days after full bloom, GA_3 and BA possibly also enhanced June drop somewhat. NAA, however, clearly diminished June drop when applied at that time. Later, i.e. 39 days after full bloom, NAA had the

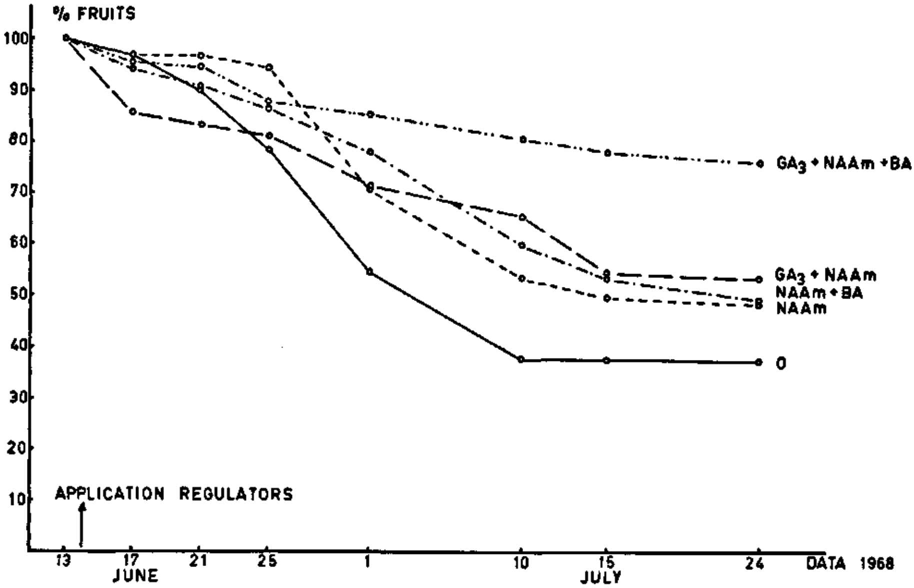


Fig. 10. Experiment 1968.4. Drop patterns of Cox's Orange Pippin fruits as affected by the spraying of 30 ppm NAAm, whether or not combined with 30 ppm GA_3 and/or 10 ppm BA, 42 days after full bloom on whole branches. (Means of 2 branches per treatment).

same effect, but now GA_3 and BA also had a slight reducing effect, though far less than NAA.

Table 11 also shows considerable percentages of fruit drop occurring after the actual June drop was over. Several treatments affected this late drop, either positively or negatively.

Conspicuous effects in this respect were caused by applications of all three regulators; applications made 11 and especially 30 days after full bloom increased the rate of fruit drop after June drop, but applications made 21 or 39 days after full bloom reduced it. It is clear that all treatments carried out 39 after full bloom reduced this late fruit drop to some extent.

Experiment 1970.3. In this experiment whole trees were sprayed with various concentrations of GA_{4+7} or, at various times after flowering, once or several times with 30 ppm GA_{4+7}. The first counting of the fruits was carried out on 25 June, i.e. 19 days after the first treatment and 9 days after the second one. On this date the differences in numbers of fruits between the treatments observed at picking time, were already present. Therefore, GA_{4+7} must have taken effect rapidly. After 25 June, only a very slight fruit drop occurred; 2% to 7% of the fruits was dropped between this date and 22 September, the day of picking. The results of these treatments are included in Table 12. Except for 30 ppm applied 20 or 40 days after full bloom, all treatments with GA_{4+7} increased the number

TABLE 11. Experiments 1968.4 and 1969.4. Percentage of dropped fruits of Cox's Orange Pippin during June drop and in 1969 also thereafter ( ), after treatment of branches.

Treatment	Application in days after full bloom 1968	1969			
	42	11	21	30	39
0 (water)	63.1	68.2 (14.4)	66.4 (17.1)	64.9 (21.8)	70.9 (23.9)
30 ppm GA_3	64.3	75.7 (15.8)	74.4 (18.8)	68.2 (19.4)	62.5 (10.5)
30 ppm NAAm [1]	51.7	71.8 (11.6)	69.5 (12.8)	56.0 (21.7)	57.5 (13.1)
10 ppm BA	69.6	70.0 (9.1)	72.2 (20.3)	68.3 (21.5)	66.7 (16.3)
30 ppm GA_3 + 30 ppm NAAm [1]	48.1	73.8 (16.9)	73.0 (9.6)	54.4 (15.2)	51.8 (16.7)
30 ppm GA_3 + 10 ppm BA	66.3	70.9 (22.8)	71.9 (21.3)	67.1 (15.1)	66.7 (13.9)
30 ppm NAAm [1] + 10 ppm BA	51.4	76.3 (15.9)	69.1 (23.2)	59.0 (17.5)	58.7 (13.1)
30 ppm GA_3 + 30 ppm NAAm [1] + 10 ppm BA	25.6	74.3 (21.8)	70.6 (5.6)	53.0 (47.5)	57.5 (12.3)

[1] In 1969 NAA was used.

TABLE 12. Experiment 1970.3. Data on yield, fruit size, shape, seed content and occurrence of bitter pit of Cox's Orange Pippin fruits after application(s) of various concentrations of GA_{4+7} on whole trees.

Treatment.	Time of application in days after full bloom	Number of trees	Flower clusters/tree (Flower clusters in 1971 in % of 1970)	Fruits/tree at harvest	Fruits/100 flower clusters	kg/tree	Mean fruit weight (g)	Height/diameter	Seeds/fruit		% of fruits with bitter pit
								25 fruits/tree	Normal	Deaf	
0 (water)	20	8	543.6 (229.5)	160.3	29.5	23.9	149	0.85	2.1	0.8	13.2
30 ppm GA_{4+7}	20	7	528.3 (172.7)	158.7	30.1	24.2	152	0.88	1.6	0.8	14.0
100 ppm GA_{4+7}	20	8	532.8 (178.8)	196.3	36.9	29.4	149	0.88	1.8	0.6	11.4
300 ppm GA_{4+7}	20	7	515.4 (189.8)	179.0	34.8	27.4	153	0.89	2.2	0.9	27.7
1000 ppm GA_{4+7}	20	8	488.5 (131.7)	171.3	35.0	27.0	157	0.90	1.5	0.9	24.7
30 ppm GA_{4+7}	30	7	494.7 (206.1)	179.0	36.2	25.6	143	0.86	2.0	0.5	10.8
30 ppm GA_{4+7}	40	9	491.6 (268.2)	137.6	29.3	22.0	160	0.86	2.2	0.7	9.8
30 ppm GA_{4+7}	20 + 30	7	442.3 (264.1)	195.6	44.2	28.6	147	0.88	1.9	0.5	11.5
30 ppm GA_{4+7}	20 + 40	9	463.9 (220.7)	213.4	43.0	28.6	134	0.88	1.9	0.5	9.1
30 ppm GA_{4+7}	30 + 40	8	484.5 (236.4)	203.4	42.0	28.2	139	0.86	1.8	0.7	8.9
30 ppm GA_{4+7}	20 + 30 + 40	9	493.0 (192.6)	175.3	36.4	27.1	155	0.88	2.4	0.6	14.5

of fruits per 100 flower clusters and the yield in kg per tree, in some cases to a considerable extent. None of the treatments appeared to be phytotoxic. As can be seen from the percentage of flower clusters in 1971 as compared to 1970, some GA_{4+7} treatments affected flower-bud formation negatively, especially 1000 ppm applied 20 days after full bloom. Two applications with 30 ppm did not suppress flower-bud formation. The negative effect on amount of bloom was, for a great part, caused by the abscence of flower clusters on the long one-year-old twigs. The other data of Table 12 are dealt with on p. 39 and 40.

3.2.2. *Fruit size, shape, and seed content*

3.2.2.1. Fruit size, shape, and seed content after treatment of individual fruitlets

Experiment 1968.2. The picked fruits of experiment 1968.2 showed great variability in size (Table 13), possibly due in part to the small numbers of

TABLE 13. Experiment 1968.2. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape and seed content. Treatment of individual fruitlets with 30 ppm GA_3 or NAAm or 10 ppm BA or their combinations.

Treatment	Days after full bloom	Number of picked fruits	Average fruit				Height/ diameter	Seeds/fruit	
			weight (g)	volume (cm³)	diameter (mm)	height (mm)		Normal	deaf
0 (water)	10	22	158	176	72.0	62.6	0.87	1.9	5.5
GA_3		22	144	173	71.2	61.6	0.87	1.3	5.3
NAAm		24	177	211	75.5	63.0	0.86	1.4	6.0
BA		22	149	177	72.3	61.5	0.85	1.2	6.0
GA_3 + NAAm		23	156	184	72.5	62.0	0.86	1.7	6.0
GA_3 + BA		21	177	209	75.9	66.0	0.87	1.3	5.2
NAAm + BA		18	146	166	70.4	61.7	0.87	1.1	5.5
GA_3 + NAAm + BA		20	164	183	74.3	64.0	0.86	1.4	5.4
0 (water)	21	17	143	169	70.0	56.5	0.81	1.5	5.3
GA_3		20	151	181	71.2	58.3	0.83	1.6	5.6
NAAm		17	178	212	75.5	61.7	0.82	1.4	6.1
BA		22	177	207	75.3	62.0	0.82	1.6	5.5
GA_3 + NAAm		23	181	209	74.9	63.1	0.85	1.8	5.0
GA_3 + BA		20	149	189	72.8	60.5	0.83	1.1	6.7
NAAm + BA		20	133	153	67.7	59.4	0.84	1.1	5.8
GA_3 + NAAm + BA		21	149	175	71.7	59.3	0.83	1.0	6.5
0 (water)	31	19	196	202	74.8	63.5	0.85	1.9	5.1
GA_3		22	170	199	74.7	64.3	0.86	2.0	5.4
NAAm		22	159	180	72.8	63.0	0.86	1.2	5.8
BA		22	176	208	75.9	66.2	0.87	1.8	5.7
GA_3 + NAAm		24	150	172	71.1	62.2	0.87	1.9	5.3
GA_3 + BA		25	156	180	71.7	62.5	0.87	2.5	5.4
NAAm + BA		21	170	194	72.9	64.6	0.89	1.7	5.4
GA_3 + NAAm + BA		22	172	197	74.4	64.3	0.87	1.6	5.5

fruits, In view of the differences in fruit size between the three control treatments, it is clear that none of the growth regulators clearly affected fruit size. The same holds for height: diameter ratio and seed content. It is remarkable that the height: diameter ratio of all treatments carried out 21 days after full bloom differed from those of the treatments 10 or 31 days after full bloom. Further, it was noteworthy that so many deaf seeds occurred in the fruits.

Experiment 1968.3. Table 14 shows the determinations on the picked fruits of experiment 1968.3. The average fruit size in most treatments was smaller than that of the untreated material. On the average, GA_3 appeared to be least inhibiting. Neither GA_3 nor NAAm affected the height: diameter ratio of the fruits, but high concentrations of BA (30 and 100) gave slightly flatter fruits. Most treatments led to a lower number of good seeds as compared to the control, and in all treatments the fruits contained a high average number of aborted seeds.

TABLE 14. Experiment 1968.3. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape and seed content. Treatment of individual fruitlets with various concentrations of growth regulators 21 days after full bloom.

Treatment	Number of picked fruits	Average fruit				Height/ diameter	Seeds/fruit	
		weight (g)	volume (cm$_3$)	diameter (mm)	height. (mm)		Normal	Deaf
0 (water)	20	163	193	74.0	65.5	0.89	1.7	5.5
3 ppm GA_3	23	143	162	68.9	59.4	0.87	1.0	6.3
10 ppm GA_3	25	160	186	73.0	63.0	0.87	1.6	5.8
30 ppm GA_3	23	149	170	70.8	62.8	0.89	1.5	6.0
100 ppm GA_3	24	150	182	71.0	62.7	0.89	1.4	6.1
3 ppm NAAm	22	142	161	70.3	57.6	0.85	0.7	5.9
10 ppm NAAm	18	118	131	65.2	56.3	0.86	0.8	5.6
30 ppm NAAm	14	140	161	68.6	59.3	0.86	1.6	5.8
100 ppm NAAm	22	140	159	68.5	60.1	0.88	1.0	5.7
3 ppm BA	20	144	212	69.4	59.2	0.86	0.9	6.5
10 ppm BA	22	140	172	69.4	59.0	0.85	1.8	5.8
30 ppm BA	17	147	177	71.2	60.4	0.80	0.9	5.7
100 ppm BA	18	131	156	68.5	58.4	0.81	0.8	6.1

Experiment 1969.2. Table 15 gives the results of all determinations on picked fruits except for the very few fruits obtained from free-pollinated flowers. As the values in Table 15 show, none of the treatments affected fruit size or shape. Several treatments may have decreased the number of normal seeds, especially the application of NAA 10 days after full bloom. For later application dates, the picture is not so clear: sometimes a combination of growth regulators had a detrimental effect, but this was not the case for the regulators separately, for example, GA_3 + NAA applied 21 days after full bloom.

TABLE 15. Experiment 1969.2. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape and seed content. Treatment of individual fruitlets with 30 ppm GA_3 or NAAm or 10 ppm BA or their combinations.

Treatment	Days after full bloom	Number of picked fruits.	Average fruit				Height/ diameter	Seeds/fruit	
			weight (g)	volume (cm^3)	diameter (mm)	height (mm)		Normal	Deaf
0 (water)	10	18	126	142	66.8	57.9	0.87	2.6	4.1
GA_3		21	121	135	66.6	55.7	0.84	1.4	4.9
NAA		23	128	144	67.2	55.9	0.83	1.2	5.2
BA		14	119	132	65.4	55.9	0.85	2.5	4.1
GA_3 + NAA		16	117	130	65.6	55.7	0.85	1.8	4.9
GA_3 + BA		14	127	142	67.1	56.4	0.84	2.2	3.6
NAA + BA		17	113	127	63.9	53.6	0.84	1.8	4.3
GA_3 + NAA + BA		22	117	128	65.5	55.7	0.84	1.4	4.5
0 (water)	21	19	118	132	65.2	55.6	0.85	2.1	4.3
GA_3		16	121	154	68.5	57.9	0.85	2.1	4.3
NAA		15	118	132	65.9	55.5	0.84	2.1	3.9
BA		11	118	132	65.4	55.2	0.84	1.9	4.2
GA_3 + NAA		15	121	134	65.2	56.4	0.86	1.1	5.2
GA_3 + BA		21	143	161	69.8	58.3	0.84	1.8	4.0
NAA + BA		17	128	142	67.5	57.3	0.85	1.4	4.9
GA_3 + NAA + BA		17	129	143	67.1	56.9	0.85	1.9	5.3
0 (water)	30	25	134	149	68.3	58.2	0.85	2.4	3.6
GA_3		24	138	156	68.9	59.0	0.86	2.6	3.3
NAA		44	134	151	68.0	58.2	0.86	2.0	2.3
BA		25	138	156	69.5	58.9	0.85	1.8	4.1
GA_3 + NAA		36	126	141	66.2	57.3	0.86	2.0	3.2
GA_3 + BA		29	132	147	67.3	57.7	0.86	3.1	3.3
NAA + BA		34	133	148	67.8	57.8	0.85	1.8	3.6
GA_3 + NAA + BA		39	130	145	66.9	57.2	0.85	1.6	4.0

Experiment 1969.3. Table 16 gives the results of the determinations done on harvested fruits of experiment 1969.3. GA_3 had no effect on fruit size in concentrations $\leqslant$ 300 ppm, but 1000 ppm clearly promoted fruit growth. GA_{4+7}, when used in concentrations $\geqslant$ 100 ppm also had a positive effect on fruit growth. NAA, on the contrary, had an inhibitory effect in the same concentrations (Figs. 11 and 12).

Neither GA_{4+7} nor NAA had any effect when used in concentrations of 10 and 30 ppm (Table 16). BA promoted fruit growth in concentrations $\geqslant$ 100 ppm, but these results are less reliable, because of the low number of fruits. ABA did not appear to affect fruit growth.

As can be seen from the height: diameter ratio in Table 16, high concentrations of GA_3 (1000 ppm) and GA_{4+7} ($\geqslant$ 30 ppm) gave more elongated fruits. High concentrations of NAA ($\geqslant$ 300 ppm), BA ($\geqslant$ 100 ppm), or ABA (1000 ppm) caused flattening of the fruit shape.

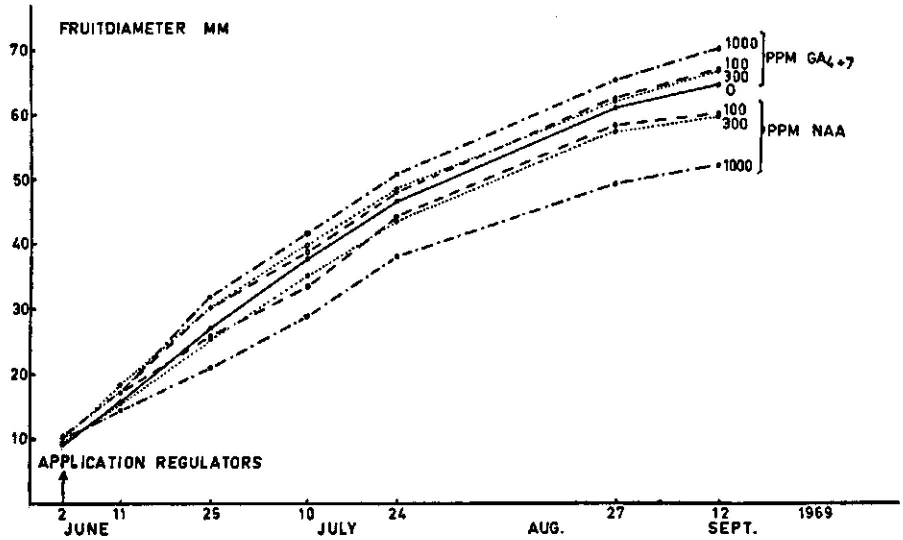


Fig. 11. Experiment 1969.3 Growth curves of Cox's Orange Pippin fruits as affected by the application of various concentrations of NAA and GA_{4+7}, 21 days after full bloom. (Means of 12 fruits per treatment). Compare Fig. 12.

Fig. 12. Experiment 1969.3. Picked fruits of Cox's Orange Pippin. Notice differences in fruit size. The four fruits on the left had been treated with 1000 ppm GA_{4+7}, 21 days after full bloom, the four on the right with 1000 ppm NAA on the same date. The four fruits in the middle had been treated with water only. Compare Fig. 11.

The data on seed content in Table 16 indicate that all treatments except 1000 ppm GA_{4+7} affected normal seed development negatively. Especially 1000 ppm BA appeared to have been detrimental in this respect.

TABLE 16. Experiment 1969.3. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape and seed content. Treatment of individual fruitlets with various concentrations of growth regulators 21 days after full bloom.

Treatment	Number of picked fruits	Average fruit				Height/ diameter	Seeds/fruit	
		weight (g)	volume (cm^3)	diameter (mm)	height (mm)		Normal	Deaf
0 (water)	16	116	127	65.4	55.0	0.84	2.8	3.8
10 ppm GA$_3$	21	110	118	63.2	53.1	0.84	2.3	3.9
30 ppm GA$_3$	19	111	123	64.3	53.6	0.84	1.4	4.6
100 ppm GA$_3$	17	117	132	65.3	55.1	0.85	1.9	4.4
300 ppm GA$_3$	23	111	125	64.3	54.5	0.85	2.3	3.7
1000 ppm GA$_3$	23	138	159	69.1	60.1	0.87	2.0	3.6
10 ppm GA$_{4+7}$	20	114	129	64.9	55.0	0.85	1.0	5.3
30 ppm GA$_{4+7}$	23	121	138	65.3	57.3	0.88	1.6	3.6
100 ppm GA$_{4+7}$	30	138	155	68.1	59.5	0.88	1.7	3.6
300 ppm GA$_{4+7}$	31	145	161	68.6	60.8	0.89	1.9	2.8
1000 ppm GA$_{4+7}$	39	143	164	69.3	61.4	0.89	2.7	2.2
10 ppm NAA	11	119	133	65.6	55.2	0.84	1.9	4.2
30 ppm NAA	15	112	126	64.6	55.6	0.86	1.1	5.0
100 ppm NAA	15	99	111	61.1	51.2	0.85	1.5	4.2
300 ppm NAA	21	92	94	58.5	47.3	0.81	1.2	4.4
1000 ppm NAA	21	60	62	51.8	42.4	0.82	1.9	2.2
10 ppm BA	21	112	125	64.4	54.0	0.84	1.9	4.4
30 ppm BA	15	118	132	65.4	54.3	0.83	1.8	4.5
100 ppm BA	7	141	160	69.9	54.6	0.81	1.5	3.2
300 ppm BA	12	129	144	68.8	54.8	0.80	1.3	3.7
1000 ppm BA	10	142	156	70.2	55.7	0.79	0.8	5.3
10 ppm ABA	16	108	122	63.4	54.7	0.86	2.1	4.1
30 ppm ABA	25	110	124	63.6	54.0	0.85	1.4	5.1
100 ppm ABA	18	114	127	64.5	54.8	0.85	1.7	4.5
300 ppm ABA	17	114	121	63.7	52.7	0.82	1.8	4.4

Experiment 1970.1. Table 17 contains the results of the determinations on picked fruits for experiment 1970.1. It is clear that GA$_{4+7}$ promoted fruit growth. Except with 300 ppm, an increase in concentration had an increasingly strong effect. In this experiment GA$_{4+7}$ did not induce a more elongated fruit shape as in experiment 1969.3. The fruits were rather small because, standing close to a windscreen of poplars, the experimental trees suffered temporarily from drought, due to little rainfall in the first part of the growing season. Nevertheless, fruit growth was promoted. The effect of this gibberellin mixture on fruit development is also shown in Fig. 13.

The drought led to some cracking in untreated fruits, viz. in 7 of the 36 picked fruits. GA$_{4+7}$ apparently prevented the formation of drought cracks,

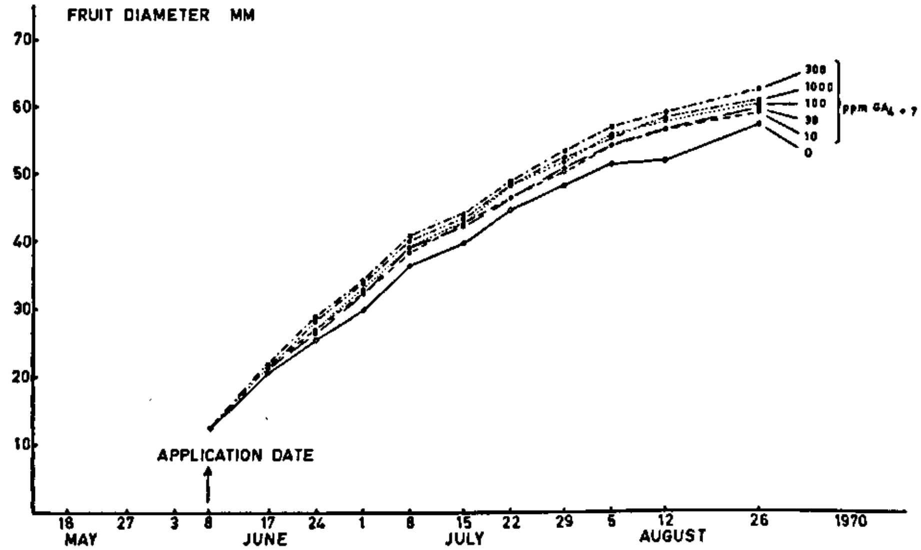


Fig. 13. Experiment 1970.1. Growth curves of Cox's Orange Pippin fruits as affected by the applications to the fruitlets of various concentrations of GA_{4+7}, 21 days after full bloom. (Means of 12 fruits per treatment).

because not a single GA_{4+7}-treated fruit showed them. The 13 picked fruits of the free-pollinated treatment (not mentioned in Table 17) included 3 with cracks. Cracking also occurred on fruits not included in the experiment.

The data on seed content in Table 17 clearly indicate that GA_{4+7} promoted normal seed development. This effect was greater, the higher the concentration, except with 300 ppm. Table 17 shows that GA_{4+7} in concentrations $\geqslant 100$ ppm affected flower-bud formation negatively, and the more severly the higher the concentration. Between 300 and 1000 ppm, however, the differences were

TABLE 17. Experiment 1970.1. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape and seed content. Treatment of individual fruitlets with various concentrations of GA_{4+7}, 21 days after full bloom.

Treatment	Number of picked fruits	Average fruit				Height/ diameter	Seeds/fruit		% bourses with flower bud(s) in 1971
		weight (g)	volume (cm³)	diameter (mm)	height (mm)		Normal	Deaf	
0 (water)	36	84	92	58.1	49.4	0.86	1.4	4.7	84.6
10 ppm GA_{4+7}	40	103	115	62.8	53.7	0.86	1.9	3.9	91.5
30 ppm GA_{4+7}	42	115	129	65.3	56.0	0.86	2.6	3.6	85.1
100 ppm GA_{4+7}	43	121	138	67.8	56.8	0.86	2.9	3.1	67.4
300 ppm GA_{4+7}	45	111	126	64.7	54.7	0.85	2.4	3.8	55.0
1000 ppm GA_{4+7}	45	129	147	68.0	58.3	0.86	3.6	2.3	51.2

small. Treatments with 10 or 30 ppm had no effect on flower-bud formation. The negative effect of high concentrations may be due not solely to the GA_{4+7}, since there were more spurs with fruits after treatment than without treatment; the fruits may therefore have also played a role.

3.2.2.2. Fruit size, shape, and seed content after treatment of fruitlets, spur leaves, or whole spurs

Experiment 1970.2. The results of experiment 1970.2 are summarized in Table 18. In this experiment, as in the previous one, the trees suffered from drought. Again, GA_{4+7} prevented the occurrence of drought cracks in the fruits when applied to fruitlets or whole spurs. Table 18 also shows that when applied to the fruitlets GA_{4+7} had a greater effect on fruit growth than when brought onto the leaves. When whole spurs were treated, the effect on fruit growth was similar to that of treating the fruits. The growth curves of all treatments are given in Fig. 14.

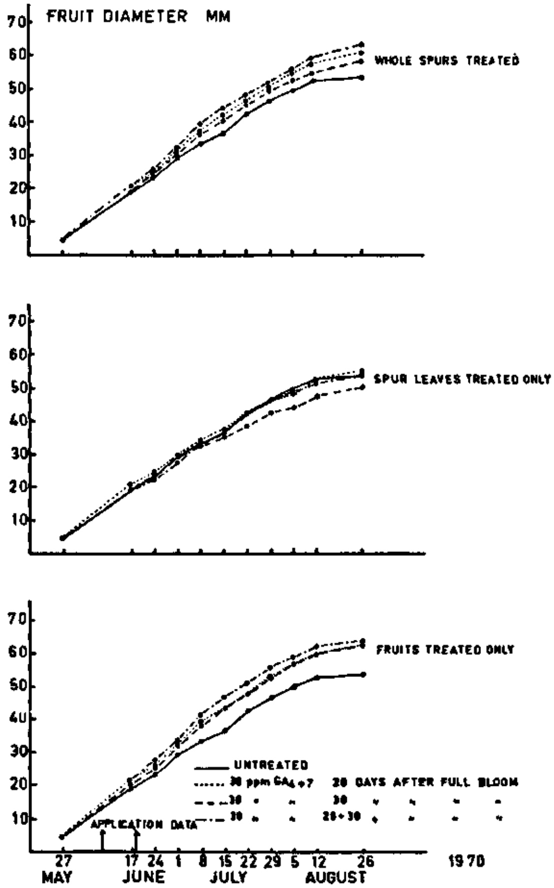


Fig. 14. Experiment 1970.2. Growth curves of Cox's Orange Pippin fruits as affected by the application of 30 ppm GA_{4+7}, 20 and/or 30 days after full bloom to whole spurs, spur leaves, or the fruitlets only. (Means of 12 fruits per treatment.

TABLE 18. Experiment 1970, 2. Determinations on picked fruits of Cox's Orange Pippin concerning fruit size, shape or seed content. Treatment with 30 ppm GA_{4+7}, 20 and/or 30 days after full bloom on fruitlets, spur leaves or whole spurs.

Treatment on	Days after full bloom	Number of picked fruits	Number of fruits with drought cracks	Average fruit				Height/ diameter	Seeds/fruit		% bourses with flower bud(s) in 1971
				weight (g)	volume (cm^3)	diameter (mm)	height (mm)		Normal	Deaf	
0	–	30	11	80	89	57.4	49.1	0.86	1.3	4.7	89.7
Fruitlets	20	44	1	101	113	61.6	52.4	0.87	1.8	3.5	87.5
Fruitlets	30	38	1	102	119	62.3	53.2	0.85	2.3	2.9	69.2
Fruitlets	20 + 30	44	0	117	134	65.5	56.5	0.87	2.9	3.0	76.7
Spur leaves	20	37	7	83	91	58.0	49.9	0.87	1.5	4.4	86.1
Spur leaves	30	38	8	86	97	58.0	50.4	0.87	1.6	3.5	95.0
Spur leaves	20 + 30	40	6	85	93	58.5	49.5	0.85	1.4	4.6	81.1
Whole spurs	20	44	3	102	112	62.2	53.5	0.86	2.3	4.2	82.5
Whole spurs	30	40	3	104	118	62.5	53.8	0.88	2.6	3.0	87.2
Whole spurs	20 + 30	41	2	109	124	63.7	55.0	0.86	2.2	2.5	82.9

In Table 18 the height: diameter ratio is not varying much between the treatments. Hence, the shape of the fruits was not altered. The data on seeds indicate that GA_{4+7} supported normal seed development, since the treated fruits had fewer deaf seeds, and especially after treatment of fruitlets, whether or not together with the spur leaves. The only two treatments that affected flower-bud formation negatively were those in which the fruitlets were treated with GA_{4+7} 30 days after full bloom. Strangely enough, this was not the case when fruits and leaves were treated at the same time. Since GA-treated spurs had more fruits than the untreated ones, the reduction in flower-bud formation may also have been caused by the extra number of fruits.

3.2.2.3. Fruit size, shape, and seed content after treatment of whole branches or trees

Experiment 1969.4. Table 19 gives the mean fruit weights of the picked fruits of experiment 1969.4. Untreated fruits were among the largest, except in the last series treated 39 days after full bloom. Furthermore, on the average all regulators slightly decreased fruit weight, NAA most of all, although the effects were not large.

TABLE 19. Experiment 1969.4. Mean fruit weight (g) of picked Cox's Orange Pippin fruits. Treatment of whole branches with 30 ppm GA_3 or NAA or 10 ppm BA, or their combinations at various times after full bloom.

Treatment	Application in days after full bloom				
	11	21	30	39	Average
0 (water)	120	108	109	96	109
GA_3	96	96	99	109	100
NAA	107	105	86	94	98
BA	107	100	98	100	101
GA_3 + NAA	97	109	89	96	97
GA_3 + BA	96	109	103	97	101
NAA + BA	98	104	92	104	99
GA_3 + NAA + BA	98	105	86	89	94

Experiment 1970.3. The results of experiment 1970.3 are shown in five columns at the right in Table 12 (p. 30). As indicated by a higher mean fruit weight, some of the GA_{4+7} treatments gave larger fruits, viz. 300 and 1000 ppm applied 20 days after full bloom, 30 ppm applied 40 days after full bloom, and also 30 ppm sprayed three times, 20, 30, and 40 days after full bloom. It is not clear why the other two treatments, in which applications were made 40 days after full bloom, had smaller fruits than the control treatment, but the fruit-size variability occurring on the experimental trees may be responsible. Therefore, it is difficult to draw any definite conclusions about the effect of GA_{4+7} on fruit size in this experiment.

The height: diameter ratios in Table 12 indicate that GA_{4+7} may have induced taller fruits, especially after the use of 300 and 1000 ppm. There was no clear effect on seed content. Compared to the trials at Wilhelminadorp, fruits of this experiment at Oudelande had a low total seed content. This was perhaps caused by the triploid cultivar Schone van Boskoop, which was the pollinator at Oudelande. Trees in this experiment did not suffer from drought.

The data on bitter pit in Table 12 show that two of the treatments induced more bitter pit, viz. 300 and 1000 ppm. Most of the treatments with 30 ppm may, however, have slightly suppressed this disorder.

3.2.3. Conclusions

– Application of various growth regulators, viz. NAA, NAAm, GA_3, GA_{4+7}, BA, and ABA, applied at various times after flowering showed that various concentrations of NAA or NAAm and GA_{4+7} were effective in reducing June drop of Cox's Orange Pippin fruits.

– NAA or NAAm reduced June drop when applied 30 to 42 days after full bloom, whereas GA_{4+7} gave this effect when used as early as 20 to 30 days after full bloom, and 20 days actually appeared to be slightly more effective. GA_{4+7} was already active in low concentrations (30 ppm).

– When NAA or NAAm were applied 10 or 21 days after full bloom, June drop was enhanced after the use of low concentrations, but diminished after use of high concentrations ($\geqslant$ 300 ppm).

– GA_3 only reduced June drop when used in high concentrations ($\geqslant$ 300 ppm) 21 days after full bloom. Low concentrations sometimes increased June drop after application up to 30 days after full bloom.

– BA increased June drop when used in high concentrations ($\geqslant$ 100 ppm) 21 days after full bloom and sometimes also when used in lower concentrations up to 30 days after full bloom. Still later, i.e. 39 days after full bloom, BA may have diminished June drop.

– ABA had no clear effect on June drop when used 21 days after full bloom in concentrations of up to 300 ppm.

– NAA(m), GA_3, and BA were not more active in combination than separately except in one case, in which NAAm + GA_3 + BA used 42 days after full bloom reduced June drop more effectively than the regulators used separately or two of them combined.

– Application of GA_{4+7} to the fruitlets or to whole spurs was more effective in reducing fruit drop than spraying the spur leaves only.

– None of the chemicals affected the time of June drop; only the amount of June drop was influenced.

– When June drop was reduced by a growth regulator or a combination of regulators, no extra fruit drop occurred later in the season except in one case, viz. when NAA + GA_3 + BA were used 30 days after full bloom on whole branches.

– The fruit-drop reducing effect of 2 or 3 sprays with 30 ppm GA_{4+7} applied 20, 30, and/or 40 days after full bloom to whole trees was equal to or even higher than that of one application with $\geqslant 100$ ppm.

- Fruit size was affected positively by high concentrations of GA_3 (1000 ppm), GA_{4+7} ($\geqslant 100$ ppm), and BA ($\geqslant 100$ ppm), and negatively after the use of NAAm or NAA, especially after the treatment with $\geqslant 100$ ppm on the fruitlets. ABA showed no effect on fruit size.
- Fruit shape also was affected by some treatments. Flatter fruits were induced by NAA ($\geqslant 300$ ppm), BA ($\geqslant 100$ ppm), and ABA (300 ppm). More elongated fruits were caused by applications of GA_3 (1000 ppm) and GA_{4+7} ($\geqslant 30$ ppm in 1969, $\geqslant 300$ ppm in 1970).
- Most of the treatments affected seed development negatively when used up to 21 days after full bloom, the only exception being 1000 ppm GA_{4+7}. Later applications were less detrimental. Under conditions of water stress, GA_{4+7} promoted normal seed development in all concentrations used ($\geqslant 10$ ppm), and prevented the occurrence of drought cracks in the fruits.
- After spraying of whole spurs, branches, or trees, no phytotoxicity was observed for 30 ppm NAA (m), 30 ppm GA_3, 10 ppm BA, combinations of these, or $\geqslant 30$ ppm GA_{4+7}.

4. DISCUSSION

4.1. FIRST DROP

As mentioned in Chapter 1, first drop is ascribed to lack of sufficient pollination and/or fertilization or to early seed abortion.

Pollination. Lack of pollination indeed causes a heavy first drop as can be inferred from experiments 1968.1 and 1969.1, in which virtually all the ovaries 'without styles' dropped soon after flowering (Figs. 2 and 3). SCHANDERL (1949) similarly observed that preventing pollination of apple flowers led to drop of undeveloped flowers. Theoretically, the style-stumps left after excision of the free styles could have been pollinated. NAMIKAWA (1923) found that after hand-pollination of style-stumps, pollen germination, pollen tube growth and fertilization are possible. Hand-pollination was not carried out in the present experiments in these particular treatments, however, and it is not likely that pollination of the flowers without styles occurred, since even open pollination of intact flowers failed to induce a reasonable fruit set (Fig. 2). Since hand-pollination caused a high fruit set of the same kind of flowers, flower sterility could not have been the cause of the heavy flower abscission following free-pollination. Therefore, pollen transfer must have been the limiting factor. The same defect was observed by WILLIAMS (1970a). It is likely that in experiment 1968.1 only a few flowers were pollinated by free-pollination and probably also only a few stigmas per flower. The former can be deduced from the similarity in first-drop pattern between free-pollinated flowers and flowers without styles (also open-pollinated) (Fig. 2). The latter is probable because first drop following free-pollination was heavier than that of flowers from which only 1 or 2 stigmas were hand-pollinated. This also held for Cox's Orange Pippin (Figs. 3, 6, and 7). Pollen density on the stigmatic surface may, however, have been involved for it is known that this affects fruit set (LEOPOLD, 1964). It is likely that hand-pollination of one stigma brought more pollen to the flower than free-pollination of five stigmas. This may also be the reason why there was slightly more first drop after hand-pollination of one or two stigmas than after hand-pollination of three or more styles per flower (Figs. 2 and 3).

Because open pollination may fail to give good fruit set – although to achieve this it is only necessary for one stigma to be well pollinated (Figs. 2 and 3) – poor pollen transfer should be considered one of the first causes of poor set. Improvement of pollen transfer can be achieved by increasing the number of honeybees, the main pollinating insect for apple, by placing bee hives in the orchard (SMITH, 1970). Increasing the possibilities for air-borne pollen should also be considered, since bee activity is low under adverse weather conditions (SMITH, 1970; LANGRIDGE and JENKINS, 1970) and considerable quantities of air-borne pollen are present in apple orchards (BURCHILL, 1963; WERTHEIM, 1968; LANGRIDGE, 1969). 'Making wind' with the spray equipment several times during blossoming has therefore been recommended (SAURE, 1967; WERTHEIM, 1968).

Fertilization. The presence of pollen grains on the stigmas gives no certainty as to whether the flower will set. In spite of thorough hand-pollination in the present trials, a few of the flowers still dropped. Lack of fertilization may have been involved here. Pollen tubes could have come too late in these flowers to reach the egg apparatus in a viable state. WILLIAMS (1970b) found that the egg cell has a limited life-span and therefore the time of pollination or the rapidity of pollen tube growth can be critical for fertilization. However, since hand-pollination was carried out as early as in the balloon stage, the time of pollination could hardly have been limiting. Another possibility to explain flower drop after hand-pollination is to assume that fertilization did occur, but that the embryo or some other essential seed tissue degenerated very soon afterward. This might be caused by a short in food supply, which is one of the reasons for poor set (TAYLOR, 1969). But in any case, since OSTERWALDER (1909) found embryos in dropped pear 'flowers', fertilization does not give complete certainty about retention of the ovary.

Nutrient supply. Concerning the nutrient supply, ABBOTT (1960) even stated that it is not pollination that is crucial for fruit set, but rather the nutrient supply from the reserves present in the branches and/or roots. POSSINGHAM (1970) similarly postulated that in grape carbohydrate nutrition of the inflorescence is of primary importance for fruit set. Fruit set may be limited by the ability of the developing cluster to command organic foods. Therefore, bark ringing may increase fruit set (HEINICKE, 1923) because it raises the level of assimilates above the ring. Bark ringing may, however, involve more changes, for instance the gibberellin metabolism, as found in grape (SACHS and WEAVER, 1968), which may also affect fruit set. HOWLETT (1926) showed that set apple flowers withdraw nitrogen to such an extent that despite their rapid growth there is no change in total nitrogen content on the basis of percentage of dry weight; set flowers also accumulated carbohydrates. Fruit set therefore depends to a considerable extent on the presence of nutrients.

In the present trials a few fruits indeed reached maturity without any sign of seed development (Table 4), which points to the possibility of fruit growth without stimuli from fertilization and seed development. Apparently, these fruits survived all drops only on the basis of a good supply of nutrients, although a stimulus from pollination alone cannot be ruled out. Thinning of the flowers to one per cluster may have contributed to a good nutritional status of the flowers.

Competition. At anthesis, flowers generally do not appear to be strong sinks, although there may be exceptions like the lemon flower (KRIEDEMANN, 1969). During anthesis development stops abruptly in apple flower. There is no cell multiplication or cell enlargement (SMITH, 1950), and the fruitlet also grows slowly the first few days after pollination (DENNE, 1960), probably because the most important stimulus for growth, which comes from fertilization is still lacking. A real strong sink is only created after fertilization (HALE and WEAVER, 1962; KRIEDEMANN, 1968b; WEAVER et al., 1969; STÖSSER, 1970a). Because the flower itself is such a weak sink, the presence of other sinks will decrease the chances of fruit set, especially those closely situated to the flower cluster. In the 1969 experiments first drop was heavier from spurs with a developing shoot than from spurs without such a shoot (Table 3). The tips of growing shoots form sinks (HANSEN, 1967b). ABBOTT (1965) also observed that fruit set on a bourse without a shoot was higher than on a bourse with a shoot. Similarly, TROMP (1968) found that fruit set on apple trees with weak growth was higher than on more vigourously growing trees. QUINLAN and PRESTON (1968) obtained an increase in the number of shoots – also bourse shoots – after early thinning of fruitlets. They concluded that the competition for substrates between above ground parts is most severe during the time of blossoming. Early removal of shoot tips can therefore increase fruit set, probably because the fruitlets no longer compete with the demanding young leaves, as found in grape (SKENE, 1969) and pear (WERTHEIM, 1971). Treatment of grape inflorescences with the growth retardant CCC (chloromequat) before anthesis increases fruit set, probably by retarding shoot growth so that more organic foods can go to the developing ovaries (COOMBE, 1970).

Probably also the competition between the ovaries plays a role in fruit set. A slight start in fruit development of one fruit may check fruit set of an adjacent flower – as found in pear (WAUCHOPE, 1968), cucumber (DE STIGTER, 1969), and citrus (KRIEDEMANN, 1969) – probably because the flow of substrates from the leaves is stimulated by rapidly growing fruits (HALE and WEAVER, 1962) at the expense of the fruits that have not yet started to grow. That such competition also occurs in apple can be deduced from the fact that early thinning, i.e. in the pink bud stage or one week after full bloom, increases the ultimate size of the remaining fruits (QUINLAN and PRESTON, 1968). It is conceivable that besides the rate of inter-fruit competition in first drop, rapidly growing fruits may produce substances leading to the acceleration of abscission tendencies of later flowers, as found in lupines (VAN STEVENINCK, 1959). It will be clear that because there is a heavy competition between the above ground parts of the tree for all kinds of nutrients, the nutritional status of the tree is of extreme importance for fruit set (TAYLOR, 1969).

Role of hormones. The capacity of the fertilized flower to command nutrients is thought to be governed in particular by a raised auxin level (JACKSON, 1968), just as has been supposed for growing shoot tips by LUCKWILL (1968, 1970). Indeed, the auxin content of ovaries, which is low at anthesis, rises after pollination or fruit set, as found in tobacco (MUIR, 1942; LUND, 1956), Fritillaria (KALDEWEY, in LEOPOLD, 1964), and grape (ITO et al., 1969). The import capacities of flowers of parthenocarpic cultivars is thus probably attributable to their higher auxin content as compared with non-parthenocarpic cultivars.

The increased auxin content after pollination and fertilization may at the same time be responsible for the prevention of abscission of the pedicle of the flower. Removal of tobacco ovaries accelerates the abscission of the flower pedicle, which can be counteracted by application of auxin indoleacetic acid on the cut surface (YAGER, 1960). These phenomena may clarify why application of auxin raises fruit set in various plant species. For fruit crops this has been found, for instance, in pear (OSBORNE, 1949; DETAR et al., 1950; DECOURTYE, 1963; LIEBSTER, 1968), grape (WEAVER et al., 1969), fig and avocado (LEOPOLD, 1958), orange (STEWART and KLOTZ, 1947), strawberry (THOMPSON, 1967) and peach (HIBBARD and MURNEEK, 1950). LUCKWILL (1953 a, b) also attributed first drop of apple to a shortage of auxin in the developing seeds; therefore first drop ends when the auxin content in the seeds rises at the time that the endosperm passes from the free nuclear to the cellular state.

Although all these facts point to auxin as the decisive factor in fruit set, it is highly probable that this hormone is not solely responsible, since not all plant species can be forced to set fruit with auxin applications (LEOPOLD, 1964). Moreover, other hormones such as gibberellins, and cytokinins, may enhance fruit set as well. Gibberellins for example, are known to have this effect in apple (see Chapter 1), pear (VARGA, 1964, 1965, 1968; UITTERLINDEN, 1966; MODLIBOWSKA, 1966), grape (WEAVER et al., 1969), cherry (REBEIZ and CRANE, 1961), peach (CRANE et al., 1961), plum (JACKSON, 1968), and blueberry (MAINLAND and ECK, 1969). Cytokinins may induce fruit set in apples (LETHAM and WILLIAMS, 1969; VARGA, 1969), pear (VARGA, 1969), and grape (WEAVER et al., 1969). JONES (1965) stated that application of a cytokinin to young melon fruits enhanced their competitive power with respect to other plant parts. LETHAM (1967) mentioned that developing fruits of various species, including apple, are rich sources of cytokinins, their presence being not dependent on fertilization. They may play an important role in the regulation of cell division in these fruits and appear, for example, to be important in the morphogenesis of the embryo.

It is, however, quite possible that gibberellins and cytokinins exert their effect on fruit set via auxin, for example, by enhancing auxin production or transport (JACKSON, 1968). SASTRY and MUIR (1963) found that gibberellin A_3 can augment the amount of diffusible auxin by young tomato fruits. They even postulated that the stimulus of pollination in fruit growth arises from gibberellin in the pollen, which results in the production of diffusible auxin in the ovary tissue. ITO et al. (1969) found that a pre-bloom dip of grape clusters in a gibberellin solution increases the auxin level at bloom. A raise in diffusible auxin after gibberellin treatment is not restricted to flowers or fruits (VALDOVINOS and ERNEST, 1967; SKYTT ANDERSON and MUIR, 1969), and seems therefore to be a fairly general reaction to gibberellin treatment (see also CLELAND, 1969: p. 71-77). According to HARRIS et al. (1969), gibberellins together with auxins have a function in the control of carnation flower development up to anthesis and in the distribution of assimilates between flower and shoot. In bean, auxin induces transport of labelled P and C assimilates towards the region of application, whereas gibberellin and cytokinin do not (SETH and WAREING, 1967). They found, however, that combinations of these hormones were more active than auxin alone. Similarly, KOTOB and SCHWABE (1971) found that fruit set could be induced in Cox's Orange Pippin apple only when a combination of an auxin, a gibberellin, and a cytokinin was applied to emasculated and effeminated flowers. A synergism of auxin and gibberellin has also been observed in cherry fruit set (REBEIZ and CRANE, 1961; CRANE and HICKS, 1968), and the same holds for the strawberry (THOMPSON, 1967) and for the tomato (WITTWER and TOLBERT, 1960).

In the present trials the growth regulators were used to affect not fruit set but June drop, and were therefore applied rather late, i.e. 10 days after full bloom at the earliest. With respect to fruit set the results of these early treatments were inconclusive. In one trial the growth regulators applied at that time had no effect (Table 6), in another trial all regulators decreased first drop slightly (Table 8), but in a third experiment the same treatments increased first drop (Table 11). It therefore seems difficult to affect fruit set reliably with the treatments involved.

Conclusion. In conclusion, fruit set is probably controlled by the combined action of several growth-promoting hormones, emanating in all likelihood from the seeds, these hormones, in an unknown way, directing the supply of nutrients to the fruit and thus enabling their growth. At the same time, the auxin component prevents the start of abscission processes. Only when all competition from other sinks is eliminated, can fruit set be obtained without any stimulus. Fruit set can only be improved artificially by application of growth regulators if the limiting hormone(s) can be supplied, whether directly or indirectly, at the right moment in the complex interplay of the endogenous hormones.

4.2. JUNE DROP

Apple fruits that have set continue to grow but some of them only temporarily. About 14 days before June drop the fruitlets that will drop suddenly show diminished growth (SCHUMACHER, 1962). So, although June-drop fruitlets are clearly more than simply ovaries and reach diameters up to 30 mm (Table 2, see also HEINICKE, 1917), they are on the average smaller than the remaining fruitlets (compare Table 2 with Fig. 5 for the same dates). This difference was also found by TYDEMAN (1938), VON RAUSSENDORFF-BARGEN (1963) and SIMONS (1965).

Seed number. Fruitlets of various fruit crops shed during June drop have been fertilized, since many of them contain embryos in the seeds (SRIVASTAVA, 1938; BRADLEY, 1962; VON RAUSSENDORFF-BARGEN, 1963). Seed formation occurred in most of the shed fruitlets of the present trials. Still, a number of these fruitlets did not show even a single sign of seed development (Table 4, upper part). These have survived first drop and such fruits can even survive June drop, since some of the picked fruits too contained no seeds at all (Table 4, lower part). On the average, June drop fruitlets contained fewer seeds per fruit than the remaining ones (Table 4), as has long been known (HEINICKE, 1917; LUCKWILL, 1948; VON RAUSSENDORFF-BARGEN, 1962). Thus although they are apparently not indispensable it is justified to suppose that seeds can help the fruit through a critical period. This is supported by the observation that abscised fruitlets of the first part of the June-drop period contained fewer seeds as compared to the fruits shed during the second part of this period (Table 2). The higher the number of seeds, the longer the fruits can be retained.

Seed quality. It is higly probable that not only seed number is involved in June drop but also seed quality. In dropped cherry fruits it was observed by BRADBURY (in: BRINK and COOPER, 1947) that the endosperm was less well developed than in retained ones. DORSEY (in: BRINK and COOPER, 1947) found that in plum the cross Compass x Yellow Egg gave little endosperm development and only a few fruits reached maturity, in spite of good fruit set. Similarly, peach fruits about to abscise and those considered potential drop fruits have seeds without endosperm or with degenerating endosperm and/or no embryo or an aborting one (LEUTY and BUKOVAC, 1968a). Non-functinal endosperm might be the reason why TYDEMAN (1944) found more drop in certain apple crosses than in others. This might also be true for the differences in June drop of Cox's Orange Pippin in 1969 (Tables 8 and 9) and 1970 (Table 10, Fig. 9), since in 1969 James Grieve pollen was used and in 1970 Benoni pollen. The differences in amount of drop between a cultivar like Golden Delicious (Fig. 2) and Cox's Orange Pippin (Fig. 3) may also be due to differences in endosperm development. It would be interesting to investigate this further. Since the endosperm tissue is so important for the embryo, embryo abortion is a secondary phenomenon, one of several factors originating in abnormal endosperm development (BRINK and COOPER, 1947). Varieties that drop easily should show more signs of embryo abortion than varieties less inclined to drop. Indeed, in the heavily dropping pear cultivar Doyenné du Comice much embryo abortion occurs (JAUMIEN, 1968). In apple VON RAUSSENDORFF-BARGEN (1963) also found fewer and smaller embryos in the seeds of dropped fruitlets than in remaining ones. The importance of the endosperm in fruit retention may also be derived from the fact that chemical thinning of certain peach cultivars is only achieved when auxin or an ethylene-delivering compound like Ethrel (2-chloroethylphosphonic acid) is applied during the transition from the free nuclear to the cellular stage of the endosperm (BUCHANAN et al., 1970). From the work of CRANE and NELSON (1970) with apricot it is clear that embryo abortion does not necessarily lead to fruit abscission. When all competition exerted by growing shoots is eliminated by a spray with a growth retardant, no abscission occurs. Abscission is delayed until regrowth occurs. If shoot growth induces fruit abscission, it appeared to be progressively worse the higher the percentage of fruits with aborted seeds. Therefore, in the normal compettive relations of a fruit tree normal seeds are important for fruit retention. For apple this was shown to be the case by ABBOTT (1959), who found that seeds are essential for fruit retention up to the end of the June-drop period and that the stimulus from the seeds could be replaced by synthetic auxin. Thus, seeds probably act via auxin in this respect. The work of LUCKWILL (1948, 1949, 1953a, b) supports this view. He found that when the embryo enters a phase of rapid growth at the expense of the endosperm, the auxin level decreases and the June drop begins. When the embryo has reached its ultimate size, the auxin level rises again and June drop ends. Hence, June drop is caused by the periodicity in auxin content of the seeds. It seems logical to conclude that in periods with a decreasing auxin level, fruits with few seeds have a greater chance to drop than those with many seeds. Total hormone content will be lower in the former case.

It is also understandable that induction of seed abortion will cause extra fruit drop. Chemical thinning of apples with auxins shortly after flowering has such an effect (MURNEEK and TEUBNER, 1953; NITSCH, 1953; HARTMAN and HOWLETT, 1962). Other authors believe, however, that induction of seed abortion by auxins or other chemical thinners and extra fruit drop are independent phenomena (WILLIAMS and BATJER, 1964; BATJER, 1965; CROWE, 1965; TESKEY and KUNG, 1967). They think that interference with the endogenous hormone metabolism or transport in the fruit causes fruit abscission. Seed abortion, namely, does not always occur when extra fruit drop is achieved. In peach, where NAA causes fruit abscission, no embryo nor endosperm degeneration due to NAA is observed, although this degeneration is the cause of natural abscission (LEUTY and BUKOVAC, 1968a). Still, seed metabolism, including hormone synthesis, may have been modified by the auxin application, leading in turn to fruit abscission (LEUTY and BUKOVAC, 1968b).

In the present experiments Cox's Orane Pippin fruits contained many more aborted seeds than did Golden Delicious fruits (Table 5), which may be one of the reasons for their divergent June-drop behaviour (Figs. 2 and 3). The differences in amount of June drop after application of the various regulators to the fruitlets could not, however, be related to differences in seed abortion. Tables 9 and 16 show that a decrease and an increase in June drop can both be accompanied by an increase in seed abortion (compare for example the effect of GA_{4+7} concentrations $\leqslant$ 300 ppm with BA concentrations $\geqslant$ 100 ppm). It is remarkable that so many growth-regulator treatments caused seed abortion (Tables 13 to 16). Apparently application of the compounds involved readily disturbed early seed development. It is also remarkable that when a regulator favours seed development, as in the case of GA_{4+7} in some of the present trials (Tables 17 and 18), June drop is diminished (Figs. 8 and 9). It is inexplicable that in 1969, GA_{4+7} induced seed abortion (Table 16), at least in concentrations $\leqslant$ 300 ppm, whereas in 1970 all concentrations favoured seed development (Tables 17 and 18). The latter effect might have been caused by the fact that in 1970, under the conditions of temporary drought, the leaves and fruits competed for water, leading to increased seed abortion. GA_{4+7} application may have lessened this competition for water by enabling the fruitlets to become a more active sink for water, possibly by enhancing starch hydrolysis – a gibberellin effect according to VAN OVERBEEK (1966) – which increases the osmotic value of the fruit. As a result the fruits would have suffered less from the competition for water, and more seeds could maintain their development normally. The gibberellin effect is then indirect.

Role of hormones. In the present trials, both gibberellins and auxins were able to diminish June drop. Among the gibberellins, GA_4+_7 was far more active than GA_3 (Table 9). GA_3 was also found to decrease June drop in apple by SRIVASTAVA and AGARWAL (1966) and GROCHOWSKA (1968). VARGA (1969), however, found GA_3 to increase June drop in apple when used in a low concentration (25 ppm). Such a treatment (30 ppm) also increased June drop in some of the present experiments (Tables 8 and 11). For GA_{4+7} this drop reducing effect has been, as far as known, not reported previously. VARGA (1969), namely, obtained no reduction after use of 25 ppm and other reports are lacking. The marked effect of GA_{4+7} on June drop, especially when applied to the fruitlets (Fig. 9), might be explained by assuming that the applied gibberellins replenish the amount of endogenous GA_{4+7} occurring naturally in the seeds. These endogenous gibberellins first appear four to five weeks after flowering, when the embryo is full grown (LUCKWILL et al., 1969; LUCKWILL, 1970). Because the applied GA_{4+7} was already active after application 20 to 30 days after full bloom, it must apparently be supplied well before or at the same time as its first natural occurrence. In plum, JACKSON (1968) also found GA_{4+7} effective in reducing drop of non-pollinated and hence non-fertilized ovaries. He stated that the gibberellin produced by the nucellus, which is formed irrespective of fertilization, is responsible for ovarian growth during and immediately after flowering, and the supplied gibberellin partially replaces the effect normally exerted by the gibberellin formed in the endosperm and embryo of fertilized fruits. Fruit growth then proceeds and abscission is prevented. With respect to the effect of gibberellins on fruit drop, it might be that the applied gibberellin plus the endogenous auxin sustain the movement of growth factors to the fruit, the endogenous auxin level quite possibly also being raised by the gibberellin application. This would lead to an extra growth stimulus, because both growth-promoting hormones occur in higher concentrations than normal. Fruit size would therefore be positively affected, as will be discussed below (p. 52). The increased auxin level might then be responsible for the reduced fruit abscission, since gibberellins are not active in inhibiting abscission processes, at least not in leaf abscission (BÖTTCHER, 1970a). For cotton, VAN OVERBEEK (1961) mentioned that young fruits could also be prevented from dropping after use of gibberellin, whereas auxin promoted drop. He therefore thought that in apple the anti-drop hormone, called auxin by LUCKWILL (1957b), might also be a gibberellin. He argued that when June drop is brought about by a drop in this gibberellin, it becomes clear why auxin-induced fruit thinning can occur, because gibberellin-controlled processes are antagonized by auxin. If this hypothesis is true, it could explain the effect of GA_{4+7} on June drop in the present trials. Thus, there are two explanations for the activity of gibberellins in reducing fruit drop. The first of these – gibberellin diminishing fruit drop via an increased auxin level – appears more probable, since it allows for the well-known abscission retarding effect of auxin.

As for auxins, the effect on fruit drop is a complex one: auxin sometimes reduces drop and sometimes enhances it (see, for example Tables 7, 8, 9, and 11). This has been explained by supposing that auxin supplied at certain stages causes seed abortion, which in turn leads to more fruit abscission. At the same time, however, auxin retards abscission processes. What will happen depends on the degree of both effects (MURNEEK and TEUBNER, 1953). Therefore, an auxin application can also temporarily reduce drop but later on enhance it (STRUCKMEYER and ROBERTS, 1950; HARTMAN and HOWLETT, 1962). In the apple cultivar Delicious, early NAA applications cause seed abortion, but the fruitlets arrested in growth remain attached to the tree (HOFFMANN et al., 1955). Here, apparently, the effect on abscission dominates.

Time of application and concentration of auxin are also clearly involved. Late applications do not thin, for example, 35 days after petal fall (HARTMAN and HOWLET, 1962), probably because they can no longer disturb seed development. In the present trials auxins even reduced drop when used 30 days or more after full bloom (Tables 8 and 11; Figs. 6 and 10). Here, the auxin apparently only prevented abscission. Still later applications such as are used against preharvest drop, also work only against abscission. Tables 7 and 9 show that concentration may be involved. Low concentrations can increase June drop, high concentrations can decrease it when applied on the same dates. With high concentrations the effect on abscission apparently dominates. That low auxin concentrations applied at certain stages can increase fruit drop, may be due, apart from an abortive action on the seeds, to enhanced ethylene production by the fruit (MAXIE and CRANE, 1967; BUCHANAN et al., 1970), the ethylene accelerating the abscission. With high concentrations of auxin, ethylene production would also be increased, but the greater amount of auxin can better counteract the abscission-accelerating effect of ethylene (see also Section 4.5, p. 56).

The role of other hormones in fruit retention is obscure. OHKUMA et al. (1963) found that maximum quantities of abscisic acid occur in young cotton fruits about to drop. Since abscission is induced by ABA in many plant species (SMITH et al., 1968), this hormone could well be involved in fruit abscission, although the data of RUDNICKI and PIENIAZEK (1970) do not suggest that its role in apple June drop is important. BÖTTCHER (1970b) postulated that in leaf abscission the increase in ABA output in the senescent leaves and the decrease in auxin content induce leaf abscission. ABA might be active via an increase in ethylene production (SCOTT and LEOPOLD, 1966; CRACKER and ABELES, 1969) or by raising the sensitivity to ethylene (LEWIS et al., 1968). Besides acceleration of ethylene production CRACKER and ABELES (1969) mentioned an increase in cellulase activity and this enzyme is important in abscission (ABELES, 1969). In the present trials ABA was ineffective with respect to June drop (Table 9), perhaps because the hormone is easily inactivated in certain tissues (SMITH et al., 1968).

Cytokinins may also be involved in fruit drop, because they counteract degradation processes by preventing the formation of degradative enzymes (ABELES et al., 1968) and by maintaining gradients for nutrients. Rather unexpectedly, therefore, BA promoted June drop in several treatments (Table 7: ⩾ 30 ppm; Table 8: applied 21 days after full bloom; Table 9: ⩾ 100 ppm; Table 11 applied 11, 21, or 30 days after full bloom). Other cytokinin treatments either did not show any effect or slightly decreased June drop. The only explanation that can be offered for the promotive effect of BA is that it counteracted the effect of other hormones necessary for fruit retention.

Combination of auxins with either GA_3, BA, or both, did not give consistent results. According to Fig. 6, NAA alone gave the best reduction in June drop, whereas according to Fig. 10 the triple combination with GA_3 and BA was most successful. It is difficult to explain these discrepancies. A decrease in auxin effect might be the result of counteraction of auxin by GA_3 and BA. An increase in the auxin effect could be due to a situation in the fruit such that auxin is not the only limiting factor for retention.

Competition. It is known that mobile elements are drawn back into the tree from the fruitlets predestined to drop (QUINLAN, 1969). When elements leave the fruit, this can no longer be considered a metabolic sink. In all likelihood, this inability to serve as a sink must be ascribed to an inadequate hormone content. It will be clear that the availability of nutrients required for growth will have a strong influence on fruits that are weak sinks or not sinks at all. This nutrient availability is determined by the sink-source relations within the tree. Competing bourse shoots were found to increase June drop in apple (ABBOTT, 1960, 1965). In the present trials, however, the opposite effect occurred (Table 3). Possibly, when shoot growth is moderate, as in the present experiments, shoots may even contribute to fruit growth by drawing more nutrients to the spur where both fruit and shoot are situated. Indeed, when the shoots were vigourous, they tended to increase drop in the present trials too (p.14). That bourse shoots are more harmful for fruit set than for later fruit retention, may be explained by the fact that during fruit set shoots consist mainly of demanding young leaves, whereas later on mature exporting leaves are present as well.

That shoots and fruits compete can be deduced from the increase in shoot growth after deblossoming or defruiting (MAGGS, 1963; QUINLAN, 1969). Conversely, a heavy crop leads to a weak shoot growth (HANSEN, 1967a), notwithstanding the fact that the leaves show greater photosynthetic activity when fruits are present (MAGGS, 1963; HANSEN, 1967a). The finding that growth retardants sometimes decrease June drop in apple and pear (VARGA, 1969), can also be considered an indication of the competition between shoots and fruits.

Not only shoot-fruit but also inter-fruit competition is involved in June drop. More June drop can be expected after a heavy fruit set than after a light set or after early thinning (HEINICKE, 1917; HOWLETT, 1931). Table 3 shows that after a varying degree of first drop, an equally heavy June drop may still occur. Thinning of the flowers to one per cluster may have changed the competitive relationship here, leaving June drop only dependent on other factors. The existence of inter-fruit competition is also reflected in the greater fruit size due to more and larger cells with a decreasing number of fruits per tree (DENNE, 1961).

Of course, vegetative growth is not only competitive, but also contributive for fruit growth, because leaves form the necessary assimilates (MAGNESS et al., 1931). Indeed, on the average fruits on spurs with a long shoot were slightly greater at harvest than those of spurs with a short shoot (p. 18). After premature leaf drop (ROBERTS, 1946) or early removal of spur leaves (LLEWELYN, 1968), more June drop occurs, which is in accordance with a contributive effect of the leaves. The same holds for the data of MURNEEK and SCHOWENGERDT (1936), showing good correlation between fruit weight and the weight of spur leaves. In the present trials, June drop occurred first on the spurs with the fewest leaves (Table 2), certainly due to shortage of assimilates. Therefore, increasing this level of assimilates, by bark ringing, decreases June drop (DENNIS and EDGERTON, 1966).

Conclusion. It may be concluded that many factors are involved in June drop, i.e. the number and 'quality' of seeds, the level and periodicity of their hormones, and the competitive relations between the various growing organs. HEINICKE (1917) summarized the situation when he stated that both the number of seeds and the position of the fruit on the tree, determine the chance on June drop. Theoretically a fruit without seeds favourably positioned, may survive June drop and another fruit with many seeds in an unfavourable situation may still abscise. The promising ability of GA_{4+7} to reduce June drop may be regarded as artificially raising the competitive power of the fruit, exerted by the seeds, via supplementing hormones normally produced by the seeds during a certain developmental stage.

4.3. FRUIT GROWTH

The seeds play not only a hormonal role in fruit retention but also in fruit growth.

Fruit size and shape. Developing seeds determine the rate of early fruit growth (TYDEMAN, 1944; MURNEEK, 1952; DENNE, 1963). Table 5 shows that when there are great differences in seed content, Golden Delicious fruits differ in size. When there are small differences in seed numbers, fruit size does not vary markedly (Golden Delicious, Cox's Orange Pippin).

Asymmetric fruits are caused by uneven seed distribution in the fruit, growth being most pronounced on the side where the seeds are situated (HEINICKE, 1917), probably because the conducting vessels are less well developed on the seedless side (MC ALPINE, 1911). This points to a shortage of endogenous hormones, since the development of a good vascular system is under control of hormones (NITSCH, 1970). Golden Delicious fruits were more asymmetric, the fewer seeds they contained, Cox's Orange Pippin fruits showed no differences in symmetry, but here all fruits had equally few normal seeds (Table 5). KOBEL (1954) stated that uneven seed distribution in the fruit does not always show up in the fruit shape, perhaps because asymmetric fruits, with their locale ovule abortion (SIMONS, 1965), preferentially drop during the June drop (HEINICKE, 1917). Support for a relationship between presence of seeds and growth of adjacent fruit tissue was also provided by BUKOVAC and NAKAGAWA's (1968) discovery that asymmetry in apple can be induced by local application of gibberellins $A_4 + A_7$ to the fruit. Both these gibberellins occur naturally in apple seeds, as already mentioned (DENNIS and NITSCH, 1966). The same gibberellins promoted seed development in some of the present trials and also stimulated fruit growth (Tables 17 and 18, Figs. 13 and 14). These are strong indications that the seeds play a role in fruit growth via these gibberellins. The enhanced growth after application of gibberellins $A_4 + A_7$ can be explained by assuming that these hormones, together with an increased auxin level, cause the fruit to become a more active metabolic sink. This assumption is strenthened by the observation that GA_{4+7} suppressed the occurrence of drought cracks in the fruits (Tables 17 and 18). Apparently, the fruits supplied with extra GA_{4+7} could better withstand the competition for water under dry conditions. This effect is perhaps to be traced to an enhanced starch hydrolysis by the gibberellins, thus increasing the osmotic value of the fruit (VAN OVERBEEK, 1966). In addition, this enhanced conversion of starch into sugars also gives more substrates for respiration, the process which delivers the energy necessary for growth (NITSCH, 1953).

THOMPSON (1969) stated that for strawberry the actual growth promotion throughout the second developmental phase might be a function of the gibberellin component of the hormone complex, whereas the transport of the metabolities to support the growth is dependent on the presence of auxin. In view of the results obtained by SETH and WAREING (1967) with bean and by KOTOB and SCHWABE (1971) with apple, however, the latter activity can also be attributed to a combined action of auxin plus gibberellin and/or cytokinin. A role of cytokinin in increasing the import abilities of the fruit can be derived from work of KRIEDEMANN (1968a). The fact that LUCKWILL (1957b) found no 'auxin no. 2' in 'chat' fruit apples, which do not grow beyond a certain small size, and considerable quantities in normal apples, points to the importance of auxin, unless this auxin actually is a gibberellin, as VAN OVERBEEK (1961) suggested. CRANE et al. (1961) made it plausible that in unfertilized and hence under-developed peach fruits, the so-called 'buttons', gibberellins are the missing hormones. GA-treated branches did not bear a single button, whereas these were abundantly present on untreated branches. GROCHOWSKA (1968) also obtained promotion of fruit growth in apple after application of 1000 ppm GA_3 in May, and inhibition of fruit growth with some auxin treatments, which was also the case in some of the present trials (Table 16, Figs 11 and 12). LAVEE (1960) found in grape berries that a GA_3 application can replace the effect of seeds. The fewer seeds the greater the effect of GA_3 on fruit size. All these facts suggest that gibberellin is the main promotor of fruit development, although it is certainly not gibberellin alone that is involved.

In the present trials GA_3 was only promotive in a high concentration (1000 ppm), GA_{4+7}, however, promoted fruit growth in some cases in doses as low as 10 or 30 ppm (Tables 16, 17 and 18)). In other cases only high concentrations of GA_{4+7} were active ($\geqslant$ 300 ppm, Table 12). If the applied gibberellins take effect by supplementing natural endogenous gibberellins, this difference between GA_{4+7} and GA_3 may be due to the greater natural role of the former in the apple fruit.

The negative effect of high auxin concentrations on fruit growth is difficult to explain. High auxin concentrations appear to inhibit may plant growth processes (LEOPOLD, 1964: p. 104–106), which has been ascribed to auxin-stimulated ethylene production (GALSTON and DAVIES, 1969), ethylene being the actual growth inhibitor.

During the growth seasons of 1969 and 1970 it became apparent that GA_3 and GA_{4+7} also affected fruit shape. In some experiments GA-treated fruits were more elongated (Tables 12 and 16). This phenomenon, which was also observed by VARGA (1966), WILLIAMS and STAHLY (1969), NAKAGAWA et al. (1969), and WEBSTER and CROWE (1969), is not restricted to apple, since a greater length-to-width ratio has also been found in grape (WEAVER et al., 1966; SACHS and WEAVER, 1968), peach (CRANE et al., 1961) and pear (KEIPERT, 1970). The effects of gibberellins on fruit size and shape possibly are to be attributed to the well-known promotive effect of these hormones on cell elongation. The several reasons for this latter effect of gibberellins are discussed by VAN OVERBEEK (1966; p. 728).

Auxins, BA and ABA sometimes caused flattening of the fruits (Table 16). For BA this is in agreement with work of LETHAM (1969), who obtained flat Cox's Orange Pippin fruits as well after use of zeatin, another cytokinin. In Delicious, however, cytokinin induced a taller fruit (WILLIAMS and STAHLY, 1969), hence varietal differences exist. The effect of ABA may be explained by its general counteraction effect on gibberellins (WAREING et al., 1969), and the same might be true for auxin.

The effect of external conditions on fruit shape is perhaps also caused by an effect on hormone metabolism. Apple fruits are more elongated when temperatures are low during the early developmental period and flattened when higher temperatures prevail (ROEMER, 1966; WILLIAMS and STAHLY, 1969). A light crop and a vigourous rootstock also lead to a more elongated fruit shape (WESTWOOD and BLANEY, 1969), and top fruits are more elongated than lateral ones (DENNE, 1963). All this might be explainable in terms of gibberellins, for example by assuming that these hormones enter the fruit more abundantly under low temperatures and vigourous growth and further the top fruits more easily than lateral fruits, thanks to the better vascular connections of the former. The gibberellins might have their origin in the roots (JONES and LACEY, 1968), although the occurrence of gibberellins in the xylem sap coming from apple roots is disputed (LUCKWILL and WHYTE, 1968). It is also possible that the gibberellins involved come from the shoots. It is not likely that the gibberellins determining fruit length are seed-borne, since Table 5 shows that fruits with few seeds were more elongated than those with more seeds. This is in accordance with measurements of WESTPHAL-STEVELS (1970). ROBERTS (1946), however, observed that seedless Wealthy apples flatter than seeded ones. Therefore, it is difficult to decide for the origin of the gibberellins determining fruit length. The data from ROBERTS plead for seed-borne gibberellins, the data in Table 5 suggest that gibberellin enters the fruit from elsewhere, which led to the assumption that in the latter case the fruits with few seeds were more dependent on imported gibberellin for growth than were fruits with many seeds.

Flower bud formation. Another factor which makes it likely that gibberellin is normally an important hormone in apple fruit development, is the detrimental influence of the seeds on flower-bud formation (CHAN and CAIN, 1967). This effect is in all probability caused by the gibberellins coming from the seeds (LUCKWILL, 1970). When in the present trials extra GA_{4+7} was brought onto the fruits, this treatment gave a further reduction of flower-bud formation (Tables 17 and 18), which is in agreement with LUCKWILL's hypothesis. The effect of the fruits on flower-bud formation was not very marked in the present trials, probably because only one fruit per cluster was allowed and the seed content was not high due to the limited pollination of only two stigmas per flower. GROCHOWSKA (1968) too found an inhibiting action of GA_3 on flower-bud formation, but only with 1000 ppm and not with 500 ppm. Apparently, GA_{4+7} is also more active in this respect, because even 100 ppm exerts an effect. This argues that GA_{4+7} and not GA_3 is normally involved in the suppression of the flower-bud formation by apple seeds. The promising effect on yield of two sprayings of 30 ppm GA_{4+7} (Table 12) and the fact that these low concentrations do not (Table 18) affect flower-bud formation, or to a limited extent only (Table 12) mean that such applications may be used without any danger and may become of practical value, at least if the favourable effects prove to be consistent in future experiments.

Conclusion. Fruit size and shape are determined to a large extent by hormones in all likelihood principally orginating in the seeds. The data on fruit shape, however, indicate that hormones formed elsewhere and transported into the fruit may be involved in fruit development as well. Applications of the gibberellins A_4 and A_7 – naturally occurring during certain stages of seed development – appear to be effective in promoting fruit growth. These hormones also induce a more elongated fruit shape. The two gibberellins mentioned are in all probability also responsible for the well-known reduction in flower-bud formation exerted by the fruits.

4.4. PRE-HARVEST DROP

Pre-harvest drop was not important in the present trials (Tables 6–9). In cases where fruit drop was pronounced after the actual June drop (Tables 10 and 11), this was not due solely to a real pre-harvest drop but also to a more or less gradual fruit drop from the end of the June drop onward (Figs. 8 and 9). Only in one case was a chemically reduced June drop followed by marked late drop, i.e. after treatment with 30 ppm GA_3 + 30 ppm NAA + 10 ppm BA, 30 days after full bloom (Table 11). Most often, however, there was no compensatory late drop. Some treatments, for example with GA_{4+7}, not only reduced June drop but this late drop as well (Table 11, last two columns, Figs. 8 and 9).

Role of hormones. Pre-harvest is ascribed to both a reduced auxin level in the fruit and an increased ethylene production by the fruit (Chapter 1). The pre-harvest drop reduction attained with various auxins (MURNEEK, 1950;

Batjer et al., 1954; Hatton, 1955) may be regarded as dipping the auxine-ethylene balance (section 4.5.) to the auxin side, i.e. the side of abscission prevention. Possibly auxin also limits ethylene production of apple fruits (Abeles and Rubinstein, 1964), although auxin sprays generally appear to increase ethylene production (Maxie and Crane, 1967; Hallaway and Osborne, 1969). Cooper et al. (1968) put forward the following hypothesis: auxins promote the enzymatically regulated ethylene formation and at the same time retard abscission through their effect on the cells of the abscission layer. The latter rapid effect initially masks any abscission-promoting effect of the ethylene. Therefore, it is possible that in apple, pear, and citrus fruit drop can be checked with synthetic auxin sprays, whereas the extra ethylene production is expressed in the accelerated fruit coloration. That ethylene indeed accelerates fruit abscission is proved by the results of applications of 2-chloroethanephosphonic acid (Ethrel) an ethylene-delivering compound (Bukovac et al., 1969; Edgerton and Hatch, 1969; Schumacher, 1969; Wertheim, 1970). Ethrel can even induce formation of complete abscission layers in places where these normally do not occur, i.e. in the transition zone of pedicle and fruit of the sweet cherry (Stösser, 1970b). Combined sprays of Ethrel and auxin admit the promotive effect on ripening, but the stimulation in abscission is suppressed to a large extent (Edgerton and Blanpied, 1968, 1970). All this goes far to prove that abscission is regulated by an auxin-ethylene balance.

4.5. COMPARISON OF FRUIT AND LEAF ABSCISSION

Fruit abscission. In considering the abscission phenomenon, Barlow (1953) may have been right when he stated that cells able to separate always tend to do so, enforced by het ever present ethylene, which stimulates the formation of the enzymes necessary for the separation processes. This tendency, however, is countered by a continuous stream of auxin from the distal organ. When the auxin level, for whatever reason, drops below a critical level, abscission occurs. Therefore it must be an auxin-ethylene balance that determines whether abscission is going to occur.

Ethylene can indeed induce fruit abscission in apple at quite different developmental stages, e.g. such as shortly after fertilization (Edgerton and Greengalgh, 1969) and shortly before picking (Section 4.4.). Combined treatments of ethylene-delivering compounds and auxins do indeed give much less or no abscission (Section 4.4.). This was also found in grape, where ethylene has a thinning effect in the fruit set stage but not after an auxin treatment has been given (Weaver and Pool, 1969). Fruit abscission would then not only be set in motion by a drop in the auxin level in the fruit but also by enhanced ethylene production. It is known that in parallel with the respiration climacterium, more ethylene is produced (Rhodes et al., 1970), so that this, together with a low auxin level in mature fruits, may cause fruit drop. In early fruit drop the same may be true, but exact data about ethylene production in these stages are not available. POLLARD and BIGGS (1970) found that in citrus species an increase in cellulase activity is associated with both natural and chemically accelerated abscission, and that ethylene shortened the time, required for attaintment of measurable increases in cellulase activity prior to separation. Ethylene also shortened the time between the onset of detectable increases in cellulase activity and attaintment of high cellulase activity. When cellulase activity is inhibited (by cycloheximide), abscission is also inhibited. Similary, acceleration of citrus fruit abscission by aquous solutions of $CuCl_2$ and $FeCl_3$ is accompanied by promotion of ethylene production, whereas these ions also seem to inactivate auxin. The abscission acceleration can therefore be attributed to enhancement of ethylene production or direct auxin inactivation, or both (BEN-YEHOSHUA and BIGGS, 1970). It is also known that enhancement of ethylene formation itself can reduce auxin levels (BURG, 1968). Consequently it is highly probably that ethylene and auxin determine whether or not abscission of fruits occurs, as suggested by BARLOW (1953).

Leaf abscission. For leaf abscission a similar course of events has been proposed (ABELES et al., 1968; ABELES, 1968). Ethylene is thought to be responsible for the formation of cell-wall degrading enzymes, such as cellulase (ABELES, 1969). The action of ethylene depends on the sensivity of the cells of the abscission layer to the gas. These cells are not sensitive to endogenous ethylene as long as there is a supply from distal adjacent cells of 'juvenility factors' or 'aging retardants', such as auxins and cytokinins. These aging retardants repress the synthesis of catabolic enzymes as well as the sensitivity of the separation layer to the ethylene. When these factors drop below a certain level, catabolic enzymes are formed and the tissue becomes sensitive to ethylene. Cell-separation enzymes are then formed. When the threshold between insensitivity and sensitivity is crossed, every increase in ethylene causes an acceleration in abscission. Both ethylene and auxin have a mutiplicity of effects, all of which may be involved in abscission (ABELES, 1969). Ethylene, for example, may help degrade enzymes necessary for maintaining the cell walls and it can accelerate auxin-inactivation. The latter causes a drop in the level of diffusible auxin, which may also be caused by an inhibition of auxin synthesis or transport (BURG, 1968). Auxin, in its turn, besides retarding aging, may maintain membrance integrity, through which the cells remain intact, and it prevents the formation of a cell-division layer. JACKSON and OSBORNE (1970) stated that large quantities of ethylene are produced shortly before leaf fall in tissues adjacent to the separation zone. This is only the case in a particular stage of senescence; which may be induced by abscisic acid (VEEN, 1970). The ethylene sets in motion the biochemical sequential processes responsible for separation. Therefore, ethylene must be the triggering substance in abscission (ABELES et al., 1971).

Conclusion. The data concerning leaf drop and fruit drop are in agreement. A drop in aging retardants (such as auxin) in flowers and fruits may occur, either because such processes as pollination, fertilization, and normal seed development remain in abeyance, or if they occur, a drop in auxin content may be caused by a varying amount of endosperm tissue. This may allow aging and abscission processes to occur, because the continuously produced ethylene is no longer counteracted. Gibberellins, which reduced fruit drop in the present experiments, in all probability did so through their effect on auxin metabolism. i.e. by raising the endogenous auxin level. Increased levels of both gibberellins and auxin may cause an extra growth stimulus; the increased auxin level may prevent the initiation of aging and abscission processes.

4.6. THE PRACTICAL ASPECTS OF GIBBERELLIN TREATMENTS AGAINST JUNE DROP

The results with GA_{4+7} applications to diminish June drop were promising. With fairly low concentrations June drop was reduced and yield was increased, phytotoxicity did not occur, fruit size was not reduced or promoted and flowerbud formation was only negatively affected to a limited extent. Whether the use of these gibberellin applications have any value for practical fruit growing, will depend on the possibilities for predicting the amount of June drop and on the cost of such applications. June drop reduction, is of course not always necessary and before the amount of June drop can be predicted, more studies will have to be done to determine whether correlations prove to exist between the average seed content shortly after flowering and the amount of June drop. If such correlations prove to exist, i.e. a low average seed content invariably leads to a heavy drop of fruits and vice versa, and GA_{4+7} sprays prove to give consistent results in future experiments, application of GA_{4+7} could be recommend when seed content is low and fruit set light or moderate.

SUMMARY

To study possibilities for increases of yield of the apple cultivar Cox's Orange Pippin, relevant information was gathered about fruit set and fruit drop, in particular about June drop. The information concerned pollination intensity, amount of fruit set, seed content of the fruit, number of leaves per spur, and the influence of the bourse shoots. Several growth regulators were tested to see whether these can reduce June drop.

The main conclusions drawn from the results of these observations are given in Section 3.1.3. (p. 18). The growth regulators examined were NAA, NAAm, GA_3, GA_{4+7}, BA and ABA. The experimental results are given in Section 3.2.3 (p. 40). The most interesting finding in the latter part of this work was the promising ability of GA_{4+7} to reduce June drop.

The factors underlying fruit set, fruit drop, and fruit growth and the possible role of the applied regulators under study are discussed, whereby fruit drop was related with leaf abscission.

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SAMENVATTING

De vruchtopbrengst van de appelcultivar Cox's Orange Pippin kan teleurstellend zijn als gevolg van onvoldoende vruchtzetting, maar ook door een te sterke vruchtval enkele weken na de bloei; de zogenaamde junirui. Om meer inzicht te krijgen in de vruchtzetting maar vooral in de junirui van deze voor Nederland belangrijke cultivar, werden in de jaren 1968 tot en met 1970 terzake waarnemingen verricht. Tevens werd nagegaan of de junirui op eenvoudige wijze is tegen te gaan met behulp van groeiregulatoren. Opbrengstverhoging bij Cox's Orange Pippin – hetzij door een hogere vruchtzetting, hetzij door een verminderde junirui – is te meer welkom omdat dit kan bijdragen tot vermindering van de zogenaamde Cox's ziekte en van kurkstip. Beide afwijkingen treden namelijk vooral op bij geringe aantallen vruchten per boom.

De waarnemingen en behandelingen werden gedeeltelijk verricht aan individuele vruchten aan gemerkte kortloten – verkregen uit handbestoven of vrij bestoven bloemen – en gedeeltelijk aan vruchten aan hele takken of bomen. De voornaamste resultaten van de waarnemingen inzake de vruchtzetting en junirui volgen eerst. Daarna worden de resultaten van de behandelingen met de groeiregulatoren samengevat.

Bloemen waarvan alle stijlen in het ballonstadium werden weggeknipt, vielen bijna allen kort na de bloei af, de resterende tijdens de junirui. Dit gold zowel voor de cultivar Cox Orange Pippin als voor Golden Delicious, hetgeen wijst op de noodzaak van bestuiving ter verkrijging van de vruchtzetting bij appel. Werd slechts één met de hand bestoven stijl per bloem aangehouden, dan bleek de vruchtzetting zeer goed te zijn. De vruchtzetting van bloemen met één tot vijf handbestoven stijlen per bloem was ongeveer gelijk met slechts een iets sterkere nabloeival van bloemen met één of twee handbestoven stijlen. Vrije bestuiving van normale bloemen had een geringere vruchtzetting tot gevolg dan wanneer slechts één handbestoven stijl per bloem werd gehandhaafd. Dit wijst op een grote mate van ondoeltreffendheid bij de vrije bestuiving hetgeen hoogstwaarschijnlijk moet worden toegeschreven aan een onvoldoende stuifmeeloverdracht.

De mate van junirui van Cox's Orange Pippin bleek per jaar zeer verschillend. De invloed van bestuivingsintensiteit op de rui bleek het meest uitgesproken bij vruchtjes ontstaan uit bloemen met één handbestoven stijl per bloem. Handhaving van twee of meer handbestoven stijlen veroorzaakt een ongeveer even sterke junirui, welke ook gelijk was aan de rui na vrije bestuiving.

Het bleek dat vruchtjes, die tijdens het eerste deel van de juniruiperiode afvielen, kleiner waren, minder zaden bevatten en afkomstig waren van kortloten met minder bladeren dan later afvallende vruchtjes. In tegenstelling tot de nabloeival bleek de junirui iets minder sterk aan kortloten met scheutontwikkeling, dit laatste uitgezonderd bij zeer lange beursscheuten, die de rui in de hand werkten.

De grootste diameter van tijdens de rui afgevallen vruchtjes bedroeg ongeveer

30 mm. De afgevallen vruchtjes waren gemiddeld kleiner dan de blijvende gemeten op hetzelfde tijdstip, en bevatten gemiddeld ook minder zaden.

De grootte van geplukte vruchten was bij Golden Delicious het kleinst wanneer de vrucht ontstaan was uit een bloem met slechts één handbestoven stijl; na handhaving van twee of meer stijlen per bloem was er geen onderscheid in vruchtgrootte meer. Bij Cox's Orange Pippin was er in het geheel geen verschil in grootte van vruchten ontstaan uit bloemen met één tot vijf handbestoven stijlen per bloem.

Bij een afnemend aantal stijlen per bloem was er bij Golden Delicious een afnemend aantal goed ontwikkelde zaden per vrucht, een steeds wat meer langere vruchtvorm en een vaker voorkomen van asymmetrie in de vruchtvorm. Bij Cox's Orange Pippin echter was er geen verband tussen het aantal stijlen en de hoeveelheid zaad of de symmetrie van de vruchtvorm. De vruchtlengte vertoonde echter globaal eenzelfde beeld als bij Golden Delicious.

Er waren bij beide cultivars maar weinig vruchten met een zaadinhoud, die aan de verwachting voldeed, dat wil zeggen dat het aantal bestoven stempels geen zekerheid gaf omtrent het aantal gevormde zaden. Verwacht werd dat bestuiving van één stempel zaadvorming in één hokje zou veroorzaken. Dit was echter niet het geval. Evenmin bleek dat slechts 2 zaden per hokje voorkwamen. Hierdoor kwam het, dat méér zaden voorkwamen dan verwacht werd bij Golden Delicious na handhaving van één tot drie stijlen, en bij Cox's Orange Pippin bij handhaving van één tot vier handbestoven stijlen. Werden meer handbestoven stijlen per bloem aangehouden dan was de zaadhoeveelheid per vrucht juist lager dan verwacht kon worden. Opvallend was tenslotte dat Golden Delicious vruchten weinig geaborteerde zaden bevatten, terwijl deze bij Cox's Orange Pippin veelvuldig voorkwamen. Mogelijk is dit de reden waarom eerstgenoemde cultivar een veel geringere rui kent dan laatstgenoemde.

Wat betreft de toetsing van groeiregulatoren op hun werking tegen de junirui kan het volgende opgemerkt worden. Onderzocht werden de auxinen α – naftylazijnzuur (NAA) en α – naftylaceetamide (NAAm); de gibberellinen gibberellazuur (GA_3) en het gibberellinemengsel $A_4 + A_7$ (GA_{4+7}); de cytokinine benzyladenine (BA) en tenslotte abscisinezuur (ABA). Deze regulatoren werden daarom onderzocht, omdat zij, al of niet synthetische, vertegenwoordigers zijn van groepen hormonen die van nature in de appelvrucht voorkomen. De regulatoren werden in uiteenlopende doseringen op verschillende tijdstippen na de bloei vaak ook gecombineerd getoetst op de cultivar Cox's Orange Pippin. Van alle gebruikte regulatoren bleken alleen NAA, NAAm en GA_{4+7} de rui doeltreffend te kunnen tegengaan. NAA en NAAm deden dit na toepassing 30 tot 42 dagen na de volle bloei; GA_{4+7} 20 tot 30 dagen na volle bloei. Bij het laatste middel bleek eerstgenoemd tijdstip wat betere resultaten te geven. De drie genoemde regulatoren bleken al werkzaam in lage doseringen (30 dpm). Het middel GA_{4+7} was het meestbelovend; na gebruik van 1000 dpm werd de junirui bijna geheel onderdrukt. De werking van dit gibberelline-mengsel tegen de val van gedeeltelijk ontwikkelde vruchtjes wordt toegeschreven aan het aanvullen van de natuurlijke gibberellen A_4 en A_7, die in bepaalde stadia van de zaadontwikkeling in de zaden voorkomen. Dit aanvullen van natuurlijk voorkomende gibberellinen zou indirekt ook de auxinehoeveelheid in de vrucht kunnen opvoeren. Beide verhoogde niveaux aan groeibevorderende hormonen zouden de vrucht dan tot een meer actief verbruikscentrum van allerlei groeifaktoren maken, beter bestand tegen concurrentie uitgeoefend door andere groeiende delen van de boom, zoals scheuten. Inderdaad bleken met GA_{4+7} behandelde vruchten dan ook vaak groter te zijn. De verhoogde auxine-component van het hormonencomplex wordt verantwoordelijk geacht voor het tegenhouden van de reeks processen die vruchtval tot gevolg hebben. Dit laatste dreigt altijd te gebeuren onder invloed van het altijd aanwezig gasvormige hormoon ethyleen.

Werden NAA of NAAm vroeg toegepast, namelijk 10 of 21 dagen na de volle bloei dan trad een versterking van de junirui op na gebruik van lage concentratie, maar juist een vermindering na gebruik van hoge doseringen ($\geqslant$ 300 dpm). Dit tweedledige effekt wordt toegeschreven aan het feit dat toediening van lage concentraties van synthetische auxinen mogelijk via een opgewekte zaadabortie en een verhoogde ethyleenproduktie vruchtrui in de hand werkt. Bij hoge concentraties van dergelijke auxinen worden deze effekten echter overvleugeld door het bekende abscissievertragende effekt van auxinen. Combinaties van regulatoren waren niet werkzamer dan de regulatoren alleen, met uitzondering van één duidelijk geval, waarin de drievoudige combinatie; GA_3 + NAAm + BA gebruikt werd 42 dagen na de volle bloei en waardoor de rui meer werd beperkt dan na gebruik van de regulatoren apart of de tweevoudige combinaties.

Uit het onderzoek met GA_{4+7} bleek verder dat toediening aan de vrucht meer effekt had dan wanneer alleen het blad werd behandeld. Behandeling van vrucht èn blad had evenveel resultaat als behandeling van de vruchten alleen.

Geen van de gebruikte verbindingen beïnvloedde de tijd waarop de junirui plaats had, alleen de mate van rui werd beïnvloed. Extra vruchtval na een aanvankelijk beperkte val trad slechts in één geval duidelijk op, namelijk na gebruik van GA_3 + NAA + BA 30 dagen na de volle bloei op gehele takken.

Twee of drie bespuitingen met 30 dpm GA_{4+7}, uitgevoerd 20, 30 en/of 40 dagen na de volle bloei op gehele bomen, bleken de rui te beperken en wel evenveel of meer als één bespuiting met concentraties van 100 tot 1000 dpm op 20 dagen na de volle bloei.

De vruchtgrootte werd behalve door GA_{4+7} ook positief beïnvloed door hoge concentraties GA_3 (1000 dpm) en BA ($\geqslant$ 100 dpm). Een negatieve invloed hadden NAAm en NAA, vooral na gebruik van $\geqslant$ 100 dpm NAA op de vruchten. ABA had geen effekt op de vruchtgrootte. Gezien het verschil in invloed op de vruchtgrootte tussen de auxinen en GA_{4+7} is de laatste interessanter voor gebruik tegen de rui.

De vruchtvorm werd door enkele behandelingen eveneens beïnvloed. Een meer afgeplatte vrucht werd verkregen na gebruik van NAA ($\geqslant$ 300 dpm), BA ($\geqslant$ 100 dpm) en ABA (300 dpm). Een langere vruchtvorm was het gevolg van toediening van GA_3 (1000 dpm) en GA_{4+7} ($\geqslant$ 30 dpm in 1969, $\geqslant$ 300 dpm in 1970).

De zaadontwikkeling werd door de meeste behandelingen negatief beïnvloed en wel na gebruik tot 20 dagen na de volle bloei; uitgezonderd door 1000 dpm GA_{4+7}. Latere toepassingen waren in dit opzicht minder nadelig.

In geval van tijdelijke droogte bleken concentraties vanaf 10 dpm GA_{4+7} de zaadontwikkeling te stimuleren en het voorkomen van droogtescheuren in de vrucht te voorkomen. Dit zijn sterke aanwijzingen dat deze gibberellinen de vrucht inderdaad tot een krachtiger verbruikscentrum maken.

Schade aan het gewas werd in geen enkel geval waargenomen. De bloemknopvorming – alleen nagegaan voor GA_{4+7} – bleek nadelig beïnvloed te worden na gebruik van 30 dpm of hogere doseringen. Het gebruik van 30 dpm, één maal of meerdere malen toegepast, bleek echter niet erg schadelijk. Duidelijke vermindering van de bloemknopvorming trad op na gebruik van 1000 dpm GA_{4+7}.

De rol van de gebruikte regulatoren en van de van nature voorkomende hormonen bij de bloem- en vruchtval en bij de vruchtgroei werd besproken, alsmede de concurrentieverschijnselen die zowel bij de vruchtzetting als bij de junirui een rol spelen. De achtergronden van de bloem- en vruchtval werden in verband gebracht met literatuurgegevens inzake bladval.

Alles overziende kan gesteld worden dat GA_{4+7} het meest veelbelovende middel tegen de junirui bleek van de onderzochte regulatoren. GA_{4+7} bleek namelijk niet alleen de rui te beperken maar ook geen nadelige invloed te hebben op de vruchtgrootte – wat bij auxinen vaak wel het geval kan zijn – soms bleek GA_{4+7} zelfs de vruchtgrootte te bevorderen. Bovendien bleek GA_{4+7} niet fytotoxisch – wat auxinen wel kunnen zijn – en ontstond pas bij hoge doseringen een sterk nadelige invloed op de bloemknopvorming. Het lijkt nuttig dit middel op grotere schaal te toetsen, om na te gaan in hoeverre het hier gevondene voldoende betrouwbaar is onder verschillende omstandigheden. Bij gebleken geschiktheid zouden enkele bespuitingen met een lage dosering (bijvoorbeeld 30 dpm) 20 tot 30 dagen na de volle bloei voor de cultivar Cox's Orange Pippin aanbevolen kunnen worden, echter alléén in die gevallen waar, bij een lichte tot matige vruchtzetting verwacht wordt, dat de vruchtdracht door junirui nog verder zou worden verminderd. Nader onderzoek over de kansen op junirui is gewenst.

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