



## Flower-bud formation in pome fruits as affected by fruit thinning

J. Tromp

Fruit Research Station, Brugstraat 51, 4475 AN Wilhelminadorp, The Netherlands

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### Abstract

Fruit thinning is commonly practiced in many fruit bearing woody perennials to improve fruit quality and to prevent 'biennial bearing', the severe alternation of fruit load in successive 'on' and 'off' years. Biennial bearing has its origin in the negative effect of the presence of fruits on flower production (return bloom), and, thus, the yield for next year. For reasons of labour cost, fruit thinning is usually done by using chemical compounds such as ethephon and ammonium thiosulphate at the blossoming stage, and for fruit thinning NAA, NAAm, carbaryl, and a few cytokinins. Apart from indirect effects of the various chemicals on return bloom via reduction of fruit load, they may also influence flower formation directly. In view of the supposedly negative relationship between flowering and shoot growth, chemical thinners may even affect bloom via interference with the vegetative development of the tree. In the present paper, in addition to a short discussion of the essentials of the flower-formation process in pome fruits, the effect of a number of chemical thinners on flower formation is reviewed. It is argued that in most experimental studies the data on the effect of thinning on return bloom is insufficiently detailed, and a better understanding especially of the early phases of the flower-formation process is badly needed.

### 1. Introduction

In commercial horticulture in many fruit bearing woody species part of the crop is removed early in fruit development to improve fruit quality of the remaining crop, in particular fruit size. However, the effect of 'fruit thinning' is not limited to improvement of fruit characteristics in the current season but may also interfere with three behaviour in the following year or even years. A heavy fruit load in one year is reflected in a strong reduction of flower production and fruit yield for the following season resulting in an alternation of 'on' and 'off' years with respect to fruit load. An important tool to prevent 'biennial bearing' is thinning of fruits in the on year. The safest way is thinning by hand, done at a time when the natural fruit drop is over (8 to 10 weeks after full bloom) and the size of the future yield can be estimated fairly accurately. However, manual thinning is labour-intensive which forces the grower to adopt chemical compounds to intensify fruit abscission. A serious drawback of using chemical thinners is that they are most effective early

in the season, from around bloom until about 4 weeks after full bloom, *i.e.* before the natural fruit drop has ceased and a reliable estimate of the final yield can be made. In view of the difference in timing of hand and chemical thinning, the effects on flowering may also be different. Flower-bud formation in fruit trees is a process of long duration, the greater part taking place in the preceding year. Finally, it must be recognized that thinning agents may affect flower-bud formation directly without any intervention of fruits.

In the following we will discuss the preceding considerations in some detail. Before doing so it seems appropriate to discuss briefly the essentials of flower-bud formation in pome fruits.

### 2. Process of flower-bud formation

The flower-formation process in fruit trees will be described here for so far as is relevant in the present context. For a more comprehensive discussion the reader is referred to [10, 22, 35, 44, 47, 59, 72].

In apple, flower buds are usually found terminally on spurs and shoots, but especially in modern cultivars they also occur laterally on one-year-old shoots. In the pear flower buds are formed almost exclusively on spurs. The beginning of floral differentiation, early in summer for spur buds, is seen in a flattening of the apical dome in the so far vegetative bud. During the rest of the season the actual flower parts are formed, and at the start of the dormant season the formation of the flower bud is largely completed. In winter, dependent on temperature and fruit species, bud development may continue at a slow pace. In early spring, activity is resumed. The final stage of development of pollen sacs and ovules occurs very late, shortly before bloom. Before there is any change of morphology, *i.e.* during induction, the meristem of the bud is programmed to form flowers by some unknown signal or some biochemical stimulus. The transition from the vegetative to the generative state is usually irreversible. This means that manipulation of the flower-bud formation process is mainly restricted to the induction phase occurring early in the growing season. After induction has occurred several treatments may affect flower differentiation as reflected in flower quality which is of paramount importance for fruit set, but the number of flower buds is usually not influenced.

In the present communication our attention will be mainly focussed on the induction process. As pointed out by Faust [22], mainly on the basis of older work [24], to receive the inductive stimulus the bud must be in a certain stage characterized by a critical number of nodes of 16–20. Additional prerequisites seem to be a certain minimum duration of the plastochron (probably 7 days in apple) and the presence of bracts [23]. In this reasoning, when an apex contains 6 nodes at the start of the season (end of April), to reach the 20-node stage about 100 days are needed before induction can occur. Although for the individual bud induction may take a very short time, throughout the tree the spread in the start of flower-bud formation is large, and for the tree as a whole induction is a long-term process. For example, in apple, flower-bud differentiation in lateral buds of current year's shoots may occur two months later than in spur buds.

Knowledge of the mechanism of flower-bud formation in fruit trees, *i.e.* the way that different physiological processes operate and interact causing flower initiation, is still speculative. In most theories the same factors are believed to play a role, *i.e.* nutrition, the leaves, the fruits and the growing shoot.

## 2.1 *Effect of nutrition*

The general idea in practical fruit growing that growth and flower-bud formation do not usually proceed in parallel, has formed the basis of the so-called C/N theory that has dominated research in this field in the first decennia of this century [44]. According this concept the ratio between the available carbohydrates and mineral nutrients (mainly nitrogen) determines which process prevails. Flower-bud formation occurs when the carbohydrate supply predominates, whereas shoot growth is stimulated when nitrogen supply is relatively more important. The absolute amounts of carbohydrates and nitrogen are of secondary importance although a certain lower threshold value must not be transgressed. At the optimal C/N ratio the tree is in a state of physiological balance at which each year a moderate shoot growth and a sufficiently high number of flower clusters go together. Especially in the USA between 1930 and 1940, the C/N hypothesis led to a number of elaborate studies on the chemical composition of fruit bearing and non-bearing spurs of apple with respect to nitrogen, sugars and starch [44]. However, no clear evidence was found that the C/N ratio is decisive for the formation of flowers.

## 2.2 *Effect of leaves*

The presence of leaves is a prerequisite for flower-bud production. Thus, in the pear cv. 'Bon Chrétien Williams' the percentage of flowering spurs is strongly related to leaf number per spur [40]. Defoliation and shading experiments confirmed the importance of leaves for flowering [38]. In itself these findings stress the role of assimilates in flower induction [38]. However, because of the lack of support from chemical analyses the conviction grew that either a hormonal factor produced in the leaf was vital for flower production or that leaves caused the redistribution of hormones from elsewhere via the transpiration stream.

## 2.3 *Effect of fruits*

The presence of fruits is antagonistic to flower formation leading to biennial bearing. This effect is known at best to be due to only a small extent to competition for nutrients or carbohydrates between fruits and developing buds, but is mainly determined by some hormonal factor produced in the seeds. This became very clear from the classical experiment with the apetalous apple cv. 'Spencer Seedless' that normally bears parthenocarpic fruits but that is able

to produce seeded fruits after hand pollination [17]. Three groups of flowering spurs were selected, one group not pollinated (parthenocarpic fruits), one group hand-pollinated (seeded fruits), and the last group deblossomed. When seeds were present hardly any return bloom was found in next spring but nearly all spurs that bore parthenocarpic fruits or that were deblossomed flowered abundantly.

There is little doubt that gibberellins (GAs) produced in the seeds are the main cause for the negative effect of fruits on flower-bud formation [22, 39, 57]. Gibberellin production in the apple cv. 'Emneth Early' started 4 to 5 weeks after full bloom and reached its maximum 4 to 5 weeks later [46]. Recently, a similar maximum was found for other cultivars during 4–6 weeks after bloom [56]. Weekly defruiting showed that the inhibiting effect was maximal when the fruits remained on the tree for about 8 weeks [46]. However, the time that fruits affect flowering is not undisputed. The inhibition of flower-bud formation may manifest itself much earlier, already within 3 weeks after bloom [17]. In pear that time was estimated as 4–6 weeks after bloom [40]. In another pear experiment, spurs bearing seedless fruits for 31 days after bloom formed more flower buds than spurs carrying seeded fruits, but thereafter no difference could be shown [34]. Studies where GAs were applied at different times supplied additional information [67]. Thus, in apple the adverse effect of applied GAs on flowering has been shown to be restricted mainly to the first few weeks after bloom (Figure 1). In similar trials GA applied 10 to 14 days after bloom also reduced flowerbud initiation [25, 48, 51]. Recently the view has been put forward that applied GAs inhibit flower-bud formation in apple via stimulation of auxin synthesis in the seeds and export from young fruits during the phase when flower buds are laid down [3, 16]. An earlier suggestion [46] was that the balance between GAs produced in the seeds of young fruits and cytokinins coming from the roots controls flower formation. Zeatin and benzyladenine applied to cut petioles of spur leaves of apple increased flowering on these spurs [57].

#### 2.4 Effect of shoot growth

In general, there is a negative correlation between growth vigour and the readiness to lay down flower buds. Since young leaves are rich sources of GAs, the idea is that as long as shoot growth continues and young leaves are present, these GAs inhibit flower-bud formation. Indeed, cultural treatments such as

*Table 1.* The effect of tree orientation and application of daminozide (1800 ppm) on shoot growth and flowering (percentage of flower clusters developing from the total number of buds) in one-year-old potted apple trees cv. 'Cox's Orange Pippin'. <sup>1</sup> stem and shoots vertical throughout; <sup>2</sup> horizontal throughout; <sup>3</sup> initially vertical, horizontal after termination of growth (mid-July); <sup>4</sup> June, <sup>5</sup> mid-July, after termination of growth

Treatment	Growth/tree (cm)	Flower clusters (%)
Vertical <sup>1</sup>	140.3a	34.1a
Horizontal <sup>2</sup>	75.8b	62.2b
Vertical/horizontal <sup>3</sup>	132.8a	59.2b
Vertical <sup>1</sup> , daminozide 'early' <sup>4</sup>	78.6b	59.1b
Vertical <sup>2</sup> , daminozide 'late' <sup>5</sup>	131.0a	53.1b

Means within a column followed by a different letter differ significantly ( $p = 0.05$ ).

shoot bending and application of growth inhibitors (daminozide, chlormequat) reduce growth and favour flowering [42, 66, 67]. However, evidence for a direct relationship between the two is not strong and an indirect relationship is likely since bending and growth inhibitors clearly stimulated flowering even when applied later in the season when shoot growth had already ceased (Table 1) [67]. A later study [22] provided no proof that shoot growth must stop before flower-bud initiation begins.

### 3. Effect of thinning

In view of the negative effect of fruit on flowering, probably the positive effect of thinning is due to the removal of fruits. However, this may be an oversimplification by ignoring the fact that removal of fruits, especially when carried out early, may stimulate shoot growth [7, 12, 31, 55], which may reduce return bloom. The effect of chemical thinning on flower-bud formation may also be due, at least partially, to the chemical agent affecting return bloom through interference with shoot growth. Thus, the effect of thinning on return bloom is the net result of several separate processes which may operate in opposite directions. Hence our understanding of the consequences of thinning for return bloom and biennial bearing is still very incomplete.

The literature on thinning [19, 52, 71, 74] reveals that most experimental efforts have been directed towards solving the practical thinning problem for a particular cultivar. Shoot growth data are usually not available and the consequences for return bloom are

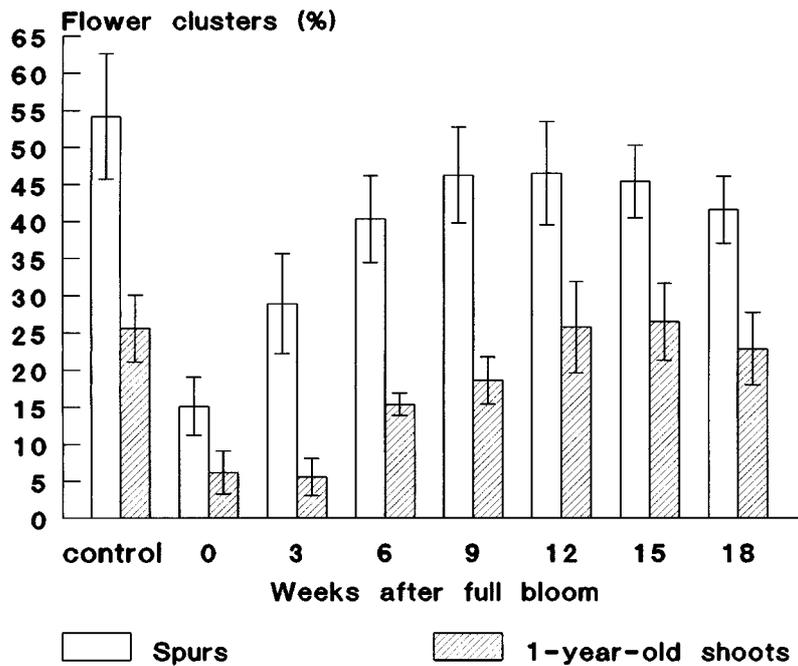


Figure 1. Flowering (percentage of flower clusters developing from the total number of buds) in three-year-old potted apple trees cv. Cox's Orange Pippin as affected by GA<sub>4+7</sub> (500 ppm) applied at three-weekly intervals throughout the growing season. Vertical lines denote SE.

mentioned only casually or not at all. To unravel the effect of a chemical thinner on return bloom would require an extra control treatment whereby the compound is applied to completely deblossomed trees. This has been done very rarely possibly since the absence of fruits will favour flowering to such a degree that any further stimulation could not be detected. Furthermore, in many trials seed number in the remaining fruits has not been recorded which would have been useful in understanding of the relationship between thinning and return bloom.

### 3.1 Thinning by hand

Hand thinning has proved to be a reliable way to improve fruit size and to control biennial bearing [6, 43, 55, 62, 63, 64]. Especially thinning at bloom is very effective as was shown for the severely alternately bearing apple cv. 'Boskoop' [62]. When hand-thinned at four dates between full bloom and 3 weeks thereafter return bloom at the last thinning date did not exceed the unthinned control. These results were confirmed in a later trial wherein hand-thinning at bloom, and 25 and 50 days thereafter were compared [6]. In contrast, in Asian pear return bloom responded positively to hand thinning as late as two months after

bloom, which was attributed to the fact that flower formation in Asian pear occurs later than in apple [50].

Since the production of GAs by fruits only starts several weeks after fruit set, it is unlikely that the pronounced effect of flower thinning on return bloom is entirely due to the removal of a (future) source of GAs. Production and distribution of assimilates may also play a role as shown for apple when a number of flower-thinning levels were applied [54]. Half-tree deblossoming resulted in much less return bloom on the untreated half than on the treated side which was explained as an only local competition of assimilates from the fruits on the untreated half or as a restricted translocation of GAs from these fruits [55]. In another trial deblossoming of one half of a tree favoured bloom on that half and also on the other half [64], which led to the conclusion that the number of fruits and not their distribution over the tree is decisive for flower-bud formation.

### 3.2 Chemical thinning

For an exhaustive overview of the chemical compounds that are being used in practice or tested in experiments the reader is referred to [71]. In the present context only those compounds will be

reviewed for which significant information on return bloom is available.

As flower thinner ethephon (2-chloroethylphosphonic acid) deserves to be mentioned firstly. It releases ethylene under alkaline conditions within the tissue. Its use is not restricted to thinning flowers; it remains effective for some days up to a few weeks after bloom. Its action usually goes together with stimulation of return bloom in apple [9, 12, 26, 41, 60, 68], pear [50], and plum [61]. There is no doubt that this stimulation is partly due to fewer fruits [41, 60]. A marked reduction of shoot growth also occurs especially when ethephon is sprayed a few weeks after bloom [12, 41, 68] which may indirectly have promoted return bloom [42, 73]. It cannot even be ruled out that ethephon favours flowering as shown in trials wherein it had no thinning action but nevertheless stimulated return bloom [8, 21]. Flowering promotion by ethephon has been reported for a number of plants including fruit trees [1, 10].

In the last 10–15 years a diversity of chemicals has been tried for flower thinning with varying success [71]. The fertilizer ammonium thiosulphate has been shown to thin apple [2, 71] and plum flowers [70] as well as promoting return bloom and for plum increasing shoot growth. The causal factor is likely to be the lower fruit load. In view of the usually good nutritional care of trial trees a nutritional effect of the very small amount of applied fertilizer is unlikely. Similarly, the promotion of return bloom of apple by urea sprayed just before full bloom is probably due to its thinning action [26]. Bloom-thinned peach trees by the desiccant endothall produced more flowers in the next season than the hand-thinned controls [14]. Endothall may directly affect flower initiation but the time difference between chemical and hand-thinning may be decisive as well.

The synthetic auxins naphthylacetic acid (NAA) and its amide (NAAm) are the most widely used thinners for apples and pears as well as the insecticide carbaryl. The thinning by the auxins is usually coupled with a promotion of flowering [26, 36, 37, 65]; when thinning fails to occur, return bloom is not affected [50, 58]. Nevertheless, the stimulation of return bloom by NAA or NAAm is not completely due to fewer fruits. Sometimes flowering abundance is greater than expected on the basis of thinning alone [36] suggesting a direct involvement of the auxin-type agents on flower initiation. This idea is supported by the observation that NAA may be able to favour return bloom without any thinning effect [36]. Furthermore, NAA

was able to stimulate flower-bud formation in biennially bearing apple trees in the off year [37]. How NAA or NAAm stimulate flower-bud formation is a matter of conjecture. Shoot growth may be involved since growth cessation can be advanced by NAA [36]. Furthermore, the number of viable seeds per fruit may be reduced which may have favoured flowering [45]. However, thinning by NAA or NAAm can occur without any clear effect on seed number [5]. Any direct promotion of flower initiation by auxin-like thinners is not in line with the view that the negative effect of fruits on flowering is due to auxins coming from the fruits [3, 16].

Generally consistent effects of carbaryl as a fruit thinner are recognized in most apple growing regions [71]. Its action is relatively little affected by concentration and time of application. Return bloom is enhanced in proportion to degree of thinning [5, 33, 50, 69], indicating that the lower fruit load is the main factor. However, stimulation of bloom without thinning may occur [58] suggesting a direct involvement of carbaryl in flower-bud formation. There seems to be an interaction with fruit load since its effect on return bloom was greatest on spurs that bore fruit [49]. In some experiments seed number per fruit was reduced by carbaryl [33] which may have enhanced flower-bud initiation.

The recognition of cytokinins as potent fruit thinning agents for apple is relatively new [71], including such synthetic chemicals as the N6-substituted purine benzyladenine (BA), and the phenylureas CPPU and thidiazuron [28]. The thinning effect of BA always results also in enhanced return bloom [4, 8, 9, 11, 20, 21, 28, 29, 31, 32, 33, 49, 75]. The relationship between number of fruits removed and flowering can be close [8, 29] and in proportion to the concentration of BA applied [20]. Apart from supraoptimal concentrations, BA did not increase flower initiation beyond a level that could not be explained solely based on the degree of fruit removal [29]. Seed number is probably important in explaining the effect of BA on return bloom. In a few BA trials on 'Delicious' apples BA clearly reduced seed number and covariance analyses showed that all variation in return bloom could be explained exclusively by seed number [32]. It has been suggested that, based on the view that flower-bud formation depends on an interaction between GAs and cytokinins, the promotion of flowering by BA is due to nullifying the inhibitive effect of GAs coming from the seeds [51]. This reasoning is supported by the observation that when all flowers were removed, BA had no effect on return bloom [51]. In thinning

apples by BA there is little evidence for a additional direct stimulation of return bloom. The concentration of BA used in chemical thinning usually is too low to have an effect on shoot growth [29]. At higher BA concentrations lateral branching may be enhanced [20, 21, 31]. This may lead to fewer flowers than expected when potential flower buds grow out into lateral shoots that remain vegetative [31], but, in contrast, promotion of bloom has been found to occur as well [20, 21, 29].

In a comparison of the three synthetic cytokinins CPPU, thidiazuron and BA, BA thinned least [28]. However, unlike BA, CPPU and thidiazuron both reduced return bloom, which has been confirmed in other studies with apple [18, 21, 27, 30]. Obviously, any positive effect of fruit removal on flower-bud formation was completely overcome by the inhibitory effect of the two phenylureas. Phenylurea is not a N6-substituted purine as zeatin and zeatin riboside (the most widespread occurring natural cytokinins) and BA. This might suggest that the N6-substitution is essential for flowering promotion [27], but, as mentioned in the foregoing, in thinning experiments a direct effect of BA on return bloom has not been shown.

Based on the observation that shading during a few days in the first few weeks after bloom causes fruit abscission, attempts have been made in apple [13] and peach [15] to mimick the shade treatments by applying the photosynthetic inhibitor terbacil. Terbacil was effective in reducing fruit set. Although in apple no effect could be shown, return bloom in peach was clearly greater than in the unthinned control. However, it was similar to the hand-thinned control, which suggests that the promotion of flowering by terbacil is due to the reduction of fruit load.

The fact that addition of surfactants to chemical thinners may increase their thinning potency leads to the question whether surfactants in their own right are able to thin. Indeed, Citowett applied alone induced fruit abscission; it stimulated return bloom when sprayed 4 days after full bloom but it inhibited flower-bud formation when applied 9 days later [53].

#### 4. Concluding remarks

Considering what is known of the effect of chemical thinning on return bloom in pome fruits, it is clear that the predominant causal factor is the reduction of fruit number. Any direct effect of the chemical used on flowering is of minor importance just as the influence

via shoot growth. As a consequence there is no essential distinction between hand and chemical thinning, at least when done at the same time. In general, the effect of thinning on return bloom decreases with time and is most pronounced when carried out at bloom or shortly thereafter. To understand the effect of fruits on flower-bud formation, a great deal of attention has been given to the fruit as site of synthesis of some factor relevant for flower formation. However, the mechanism of flower formation in pome fruits is not well understood. More effort should be warranted to clarifying the physiology of especially the early stage of the flowering process.

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