REPRODUCTIVE BUD DEVELOPMENT IN PEARS

 $\mathbf{B}\mathbf{y}$

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Thesis presented in partial fulfilment of the requirements for the degree Masters of Sciene in Agricultural Science in the Department of Horticultural Science at the University of Stellenbosch

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously, in its entirely or in part, submitted it at any university for a degree.

Summary

Reproductive bud development is the first step of sexual reproduction of plants and is a major factor determining yield. For consistent yields in pears, knowledge of the development of the reproductive bud is required.

The development of the reproductive bud with emphasis on the primordial bourse shoot was studied. The bourse shoot is important because of the ability of a bourse shoot to become reproductive, which can lead to bourse-overbourse bearing. The progression of reproductive bud development in 'Forelle' and 'Rosemarie' was studied from primordial bourse shoot initiation until dormancy the following season. The primordial bourse shoot was initiated in January 2003. The primordial bourse shoot progressed during dormancy with a plastochron length of 60 days in June. The rate of preformed leaf formation increased rapidly until August when the plastochron was 5 days. 'Rosemarie's' primordial bourse shoot development was more advanced at full bloom, which is a possible reason for the higher bourse-over-bourse bearing habit of the cultivar. The number of leaves of the bourse shoot was more than with the 'Forelle', which has a low tendency for bourseover-bourse bearing. Flower initiation of the terminal bourse shoot bud was 56 and 77 d.a.f.b. for the 'Forelle' and 'Rosemarie', respectively. Initiation was well correlated with bourse shoot growth cessation. An increase in mitotic activity occurred during flower differentiation of the terminal bourse bud with a peak of floral appendage formation during December and January. From February until dormancy enlargement of the floral parts took place.

The influence of severe dormant pruning and the quality of 2-year-old wood, on reproductive bud sink strength of 'Packham's Triumph' trees were investigated. The sink strength of primary growth increased by 40 % for short bearing units (SBU's) and 140 % for thick bearing units (BU's) as compared to long bearing units (LBU's) and thin BU's respectively. The increase in primary growth was due to better fruit set and larger fruit in the SBU's and the thick BU's. Since the increase in primary growth is less for SBU's compared to thick BU's the conclusion, which can be made, is that branch diameter influenced sink strength more than branch length. With increase in branch diameter the size of the xylem transport system increases more than that of the phloem. The increase in xylem transported

metabolites, in particular root derived cytokinin seems to predominantly influence the magnitude of the sink strength.

The influence of scoring and 6-benzyladenine (BA) application, during the flower induction phase on 'Doyenne du Comice' and 'Rosemarie', were studied. Scoring caused a 50 % increase in fruit number of 'Doyenne du Comice', which resulted in a 38 % increase in yield compared to the control. The increase in fruit number was due to higher percentage reproductive buds and improved bud quality. For the 'Rosemarie' scoring at the correct time resulted in a 40 % increase in reproductive buds. Scoring disrupts basipetal transport in the phloem, which results in the removal of apical dominance and an increase in root derived cytokinin's. More meristems can respond to inductive conditions and high quality reproductive buds develop. The combination of BA and scoring, lead to more flowers per inflorescence in 'Doyenne du Comice'.

OPSOMMING

Reproduktiewe knopontwikkeling by die peer

Reproduktiewe knopontwikkeling is die eerste fase van reproduktiewe voortplanting in plante en is belangrik, want dit bepaal die oesgrootte. Vir konstante oeste in peerproduksie moet reproduktiewe knopontwikkeling verstaan word.

Die ontwikkeling van die reproduktiewe knop, meer spesifiek die primordiale beursloot is bestudeer. Die beursloot is belangrik a.g.v. die beurs-oorbeurs drawyse. Die ontwikkeling van die reproduktiewe knop van 'Forelle' en 'Rosemarie' is gevolg. Die primordiale beursloot is Januarie 2003 geinisieër en ontwikkel tydens die boom se dormante fase met 'n plastochron van 60 dae gedurende Junie. Preformeerde blaarvormingstempo neem toe tot Augustus waar die plastochron 5 dae is. 'Rosemarie' se primordiale beursloot ontwikkeling was meer gevorderd teen volblom, met meer beurslootblare reeds teenwoordig. Dit is dalk die rede vir die hoër tendens van beurs-oor-beurs drag van die kultivar in vergelyking met 'Forelle'. Die terminale beurslootknop is 56 en 77 dae na volblom geïniseer vir 'Forelle' en 'Rosemarie' respektiewelik. Inisiasie was goed gekorreleerd met beeindiging van beurslootgroei. Blomdifferensiasie het inisiasie gevolg met 'n toename in mitotiese aktiwiteit, blomaanhangsel vorming het 'n piek bereik in Desember en Januarie. Vanaf Februarie tot dormansie het ontwikkeling hoofsaaklik in vergroting van blomorgane plaasgevind.

Die invloed van strawwe dormante snoei en die kwaliteit van 2-jaar-oue dra-eenhede op sinksterkte van reproduktiewe knoppe van 'Packham's Triumph' pere is ondersoek tydens die 2002/03 seisoen. Die sinksterkte van primêre groei het 40 % toegeneem vir kort dra-eenhede en 140 % vir dik dra-eenhede in vergelyking met lang dra-eenhede en dun dra-eenhede respektiewelik. Die toename in primêre groei vir kort en dik dra-eenhede kon toegeskryf word aan beter vrugset en groter vrugte. Omdat die toename in sinksterkte minder is vir kort dra-eenhede in vergelyking met dik dra-eenhede kan die afleiding gemaak word dat dra-eenheiddikte sinksterkte meer beïnvloed as dra-eenheidlengte. Met 'n toename in dra-eenheiddikte,

neem xileemvaatweefsel meer toe as floeëmvaatweefsel. 'n Toename in xileem getranslokeerde metaboliete, meer spesifiek wortel vervaardigde sitokiniene beïnvloed die sinksterkte van die reproduktiewe knoppe.

Die invloed van ringelering (ringsnit deur floeëm sonder bas verwydering) en 6-bensielaldenien (BA) toediening tydens reproduktiewe knopinduksie van 'Doyenne du Comice' en 'Rosemarie' is ondersoek. Ringelering het 'n 50 % toename in vrugaantal veroorsaak wat die oes met 38 % laat toeneem het in vergelyking met die kontrole, vir 'Doyenne du Comice'. Die toename in vrugte was a.g.v. 'n hoër persentasie reproduktiewe knoppe en toename in blomkwaliteit. By 'Rosemarie' het ringelering 'n 40 % toename in reproduktiewe knoppe bewerkstellig. Ringelering onderbreek die basipetale vervoer in die floeëm, verwyder dus apikale dominansie, met die gevolg dat daar 'n toename in wortel geproduseerde sitokiniene is. Meer meristeme reageer op induktiewe toestande en reproduktiewe knoppe van hoë kwaliteit vorm. Die kombinasie van ringelering en BA-toediening het meer blomme per reproduktiewe knop veroorsaak.

Dedicated to my parents, Percy and Annamarie who gave me the opportunity and support to complete my studies.

ACKNOWLEDGEMENTS

I am grateful to:

My Heavenly Father for the strength and wisdom to complete my degree.

My supervisor, Prof. K.I. Theron for guidance, constructive criticism, encouragement and her invaluable assistance with the statistical analyses of the data.

Prof. G. Jacobs my co-supervisor for his guidance, constructive criticism and help with interpretation of the data.

Messrs. Johan Dippenaar, Bernhardt du Toit, Marco du Toit, Albie Venter, Petro Wiese and the Du Toit-Group for making sites available and for their assistance.

The Deciduous Fruit Producers Trust and the National Research Foundation for their generous financial support.

The lectures and staff of the Department of Horticultural Science, University of Stellenbosch for their assistance, advice and encouragement throughout my study.

My fellow students and friends for their encouragement.

My parents and family for their support throughout my studies.

Sanri Rossouw for her motivation and support.

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INTRODUCTION

Regular and substantial yields of superior quality are the most important parameters for successful fruit growing. With a broader knowledge of the development of the reproductive buds these parameters should be easier to achieve. In the past, numerous scientists studied the development of the reproductive bud, but minor emphasis was placed on the primordial bourse shoot. The bourse shoot is important to obtain regular yields because it is a potential bearing site.

The aim of the first paper was to determine when the bourse meristem and the primordial shoot develop and to follow its procession over time. The two cultivars, which were used 'Forelle' and 'Rosemarie', are different in there bearing habit with both of them bearing mainly on spurs on two-year-old wood, but 'Rosemarie' has the ability to bear fruit on one-year-old shoots, which can lead to bourse-over-bourse bearing (Du Plooy *et al.*, 2002). By comparing the two cultivars it should be possible to get a better understanding of the bourse shoot development and the possible factors that increase bourse-over-bourse bearing.

The profitable commercial production of pears in South Africa has become increasingly difficult over the last decade. This is explained by the costs of production increasing at a much faster rate than compensatory increases in yield or market returns to the grower. To justify investments in pears it is essential to increase market returns by improving the fruit size and quality. Fruit size of pears is dependent on the sink strength of the fruit. Sink strength influences the amount of assimilates utilised by the fruit. Sink strength can be conceptualised as the product of two components, sink activity, which is a measure of the potential flux of assimilate accumulation, and sink size which is a measure of a potential volume for biomass gain (Patrick, 1988). Both of these characteristics are subject to hormonal regulation.

The second paper is about the effect of bearing unit (BU) length and diameter on sink strength of the reproductive bud. With emphasis on the difference in the number of fruit and fruit size between the BU's.

A prerequisite for a large crop is the presence of a sufficient number of reproductive buds at the start of the season, but the quality of the flower cluster is equally important.

Flower quality is measured in terms of their ability to set, retain and size fruit until harvest (Webster 2002). To improve flower quality you

need to increase the inflorescence size. Flower quality can be improved by earlier initiation, which will lead to a longer period of differentiation, or by increasing the rate of differentiation.

The third paper is about improving the inductive conditions for initiation and thereby increasing the number of reproductive buds initiated and also enhancing the process of initiation, which will result in better quality of buds.

Two strategies were evaluated, viz. scoring and applying exogenous cytokinin (6-benzyladenine, BA). The thought being that by scoring the tree at the start of flower initiation, the basipolar transport of auxin will be disrupted, which will lead to an increase in root-derived cytokinin (Li et al., 1995). It is well known that foliar thinning sprays of BA cause return bloom to increase the following season in apple cultivars (Mclaughlin and Greene 1984). BA sprayed trees have more flowers within an inflorescence compared to the unsprayed trees (Bubán, 2000).

This root-derived cytokinin, as well as that applied exogenously should stimulate cell division in the developing reproductive bud and thereby raising the metabolic activity of the bud. Furthermore the cytokinin can release meristems from apical dominance and therefore allow them to react to inductive conditions and becoming reproductive (Bangerth *et al.*, 2000).

Literature cited:

- Bangerth, F., Li, C. and Gruber, J. 2000. Mutual interaction of auxin and cytokinins in regulating correlative dominance. *Pl. Gr. Regul.* **32:** 205-217.
- Bubán, T. 2000. The use of benzyladenine in orchard fruit growing: a mini review. *Pl. Gr. Regul.* **32:** 381-390.
- Du Plooy, P., Jacobs, G. and Cook, N.C. 2002. Quantification of bearing habit on the basis of lateral bud growth of seven pear cultivars grown under conditions of inadequate winter chilling in South Africa. *Sci. Hort.* **95:** 185-192.
- Li, C.J., Guevara, E., Herrera, J. and Bangerth, F. 1995. Effect of the apex excision and replacement by 1-naphtylacetic acid on cytokinin concentration and apical dominance in pea plants. *Physiol. Plant.* **94:** 465-469.

- Mclaughlin, J.M. and Greene, D.W. 1984. Effects of benzyladenine and daminozide on fruit set, fruit quality, vegetative growth, flower initiation, and flower quality of 'Golden Delicuos' apple. *J. Amer. Soc. Hort. Sci.* **109(1):** 34-39.
- Patrick, J.W. 1988. Assimilate partitioning in relation to crop productivity. *Hort. Sci.* **23(1):** 33-40.
- Webster, A.J. 2002. Factors influencing the flower, fruit set and fruit growth of European pears. *Acta Hort.* **596(2):** 699-709.

1. LITERATURE REVIEW: REPRODUCTIVE BUD DEVELOPMENT OF PEARS

Introduction

Flowering, the first step of sexual reproduction of plants is of paramount importance to agriculture, horticulture and plant breeding, as it is a major factor in determining yield. Not only for economic, but also for scientific reasons, the morphological and physiological changes occurring during the transition of the meristem from vegetative to reproductive has been the topic of much research. In unravelling the mechanism involved in the control of generative development, the conclusion is that in woody species, including pears, flowering is not triggered by a single factor but a wide range of factors, such as nutrition, plant hormones and different environmental factors, which all may determine the response. Additionally, not all potential flower sites (buds meristem) respond to the prevailing conditions, as only some of the meristems actually become reproductive. The inability to predict where and when a flower bud is likely to form has been a major handicap to better understand flowering in trees (Crabbé, 1984). Furthermore, reproductive bud development in fruit trees is a process of long duration, the greater part taking place in the ten months preceding bloom (Tromp, 2000). This means that the different stages of the flowering process occur under changing environmental conditions and coincide with other developmental activities occurring in the tree.

These factors make woody species a complex research topic. The aim of this review is to get a better understanding of the mechanism by which flowering of woody species is controlled and therefore how to manipulate these mechanisms to ensure a sustainable yield and to improve product quality.

1. Developmental stages in pear buds

Pear buds and inflorescences are similar to those of apple with two distinct differences. The pear inflorescence contains seven or eight flowers and is indeterminate; that is, the lateral blossoms open first and the terminal bloom opens last (Westwood, 1978). In the pear, reproductive buds are formed almost exclusively terminally on spurs (Tromp, 2000). The initial phase of bud development is similar irrespective of whether buds remain vegetative or become reproductive and is characterised by the initiation of bud scales, transition leaves and true leaves by the meristem (Bijhouwer, 1924).

1.1. Floral induction

In pears floral induction denotes the process by which the meristem becomes committed to form flower buds. It does not involve visible modification of the meristem, but only changes at the biochemical or genetic level (Bubán and Faust, 1982).

The inhibition of flower bud induction causes severe alternate bearing (Tromp, 2000; Jonkers, 1979). For better flower induction, the induced flower must be a strong sink during the time of induction. Floral induction occurs from around the time of bloom until several weeks after full bloom and from the start of the inductive phase to anthesis takes approximately a year (Bubán and Faust, 1982). For minimum competition, flower induction must occur before the predominance of the inhibiting effect exerted by the gibberellins produced by the seeds of fruits (Bubán and Faust, 1982).

1.2. Floral initiation

Floral initiation is the first visible change in the meristem. The first morphological change that occurs is the broadening of the apex, which also becomes convex, followed by its lengthening into a cylindrical shape (Carrera, 1982). Verheij (1996) observed a rapid increase in appendage formation with floral initiation in the apple, which afforded Huet (1974) (cited by Tromp, 2000) to state that an increase in mitotic activity is an indispensable condition for flower initiation.

The start of floral initiation occurs about sixty days after full bloom, at the time of shoot growth cessation (Pratt, 1988; Van Zyl, 1979; Westwood, 1978). The appearance of the dome-shaped meristem does not occur in all reproductive buds at once but is spread over weeks (Verheij, 1996). It generally occurs several weeks earlier terminally in spur buds than on shoots (Walters, 1968) and initiation on lateral buds may occur two months later compared to terminal spur buds (Tromp, 2000; Wertheim, 1990).

1.3. Floral differentiation

Floral differentiation refers to the morphological transformation of the apex following initiation leading to the formation of an inflorescence (Verheij, 1996). Differentiation is characterised by an increase in mitotic activity and cell division (Bubán and Faust, 1982). In addition the rate of primordia production by the apex increases and bracts (leaf-forms in which the lamina and stipules are entirely suppressed) are formed (Bubán and Faust, 1982).

Differentiation follows directly after initiation. Verheij (1996) observed in apples, that one week after the appearance of the dome shape flower initials could be distinguished in the axils of the uppermost five to six primordia.

Walters (1968) studied the reproductive development of 'Bon Chretien' and 'Kieffer' and observed four flowers at the end of April and more recently this was confirmed by Tromp (2000) who stated that the formation of the reproductive bud is largely completed at the start of the dormant season. Data of the northern hemisphere confirm the above and Zeller (1983, cited by Bubán, 1996) stated that flower initiation of pears begins in July. By the middle of August there are inflorescence primordia in the buds. Whorls of sepals, petals, stamens and capels are initiated in rapid succession, and differentiation then proceeds at a slower rate throughout the winter period. At the end of September the pistil primord ia appear in the terminal flowers and by winter morphologically differentiated anther primordia are found. During this slower period enlargement of organs proceed (Tromp, 2000). With apple inflorescences, the diameter of the apical and lateral flower primordium increased by 23 to 46 % between October and early December (Northern Hemisphere). By middle February the growth was slower, 16 to 17% and 6 to 18% respectively, but following this from mid-February until the middle of March the flower primordia doubled in size (Bubán, 1996). Walters (1968) found the same growth curve for 'Bon Chretien' and 'Kieffer' pear flower parts, where there is a slow period of growth from the end of May until the beginning of August, followed by a large increase in the length of the different flower parts until bloom. The sudden growth in the middle of February makes it probable that by then, the bound water in the tissue of flower buds is already converted to free water (Faust, 1989). By the middle of March there are developing ovules in the ovary and pollen grains in the anther (Zeller, 1983 cited by Bubán, 1996). Just before and during bud opening in the spring the last developmental processes, i.e. development of pollen sacs and ovules take place (Tromp 2000). The number of flowers per cluster for apple varied slightly under diverse extreme conditions suggesting that this number is mainly genetically determined (Verheij, 1996). Wertheim (1990) found similar results for pears and furthermore found a variation in start of flower initiation between cultivars. Early cultivars like Conference and Bon Chretien Williams flower initiation occurring earlier compared to 'Beurré Hardy' and 'Doyenné du Comice'.

1.4. Anthesis

Anthesis is the cumulative stage of the flowering process, during which the stamens release pollen and the pistil is receptive to pollination and fertilisation. It occurs in the spring of the year following induction when the temperature becomes sufficiently high to support growth activity. Leaves and flower parts in the bud expand, resulting in bud opening. Upon bud opening, flower buds give rise to a rosette of leaves and flowers. In the axils of one or more leaves a bourse bud is found which can form a bourse shoot (Bijhouwer, 1924; Luyten and De Vries, 1926; Wertheim, 1990). The sepals and petals of the flowers enlarge and move apart to expose the stigmas and stamens. After pollination the flowers may set fruit or abscise.

1.5. General

It is not yet clear to what extent induction is a reversible process but it generally assumed that once a meristem has reached the differentiation phase it is irreversibly committed to produce flowers (Tromp, 2000). It is generally assumed that any bud on the tree is capable of becoming reproductive. However, only some of the buds do become reproductive. The tendency of buds to become floral depends on a complex of factors, which will be discussed in the following sections. It also varies with morphological aspects of bud development and bud position. Spur buds have a high tendency to become floral. The tendency for terminal and /or lateral buds on long shoots to become reproductive varies with cultivar, age and vigour of the tree (Bubán and Faust, 1982). Along the shoot there is also a gradient in flowering potential. Middle buds have a higher tendency to become floral than basal or distal buds (Bubán and Faust, 1982).

2. Factors affecting flower quality

The quantity and quality of reproductive buds reaching anthesis are important factors determining yield. The number of reproductive buds setting fruit is only a small part of the total number that reached anthesis, as many abscise. The factors affecting flower quality of apples are thoroughly researched, but research on the factors affecting pear flower quality is not. It is highly likely that the same factors, which affect apple flower quality, will affect pear flower quality, but this can't be said with absolute certainty.

Flower quality of apples is generally defined in terms of fertility, i.e. the capacity of flowers to respond to fruit setting stimuli. Good quality flowers are those in which the stigmas remain receptive and the embryo sac stays viable for a long period of time, thereby increasing the chance for successful pollination (Pratt, 1988; Williams, 1965). A good quality cluster has many flowers with short stalks and a high tendency to set fruit. Flower pedicle length and dry weight as well as flower dry weight are positively related to harvest fruit weight and fruit set for apples (Ferree et al., 2001). Lauri and Térouanne (1999) found a positive relation between the number of flowers and fruit set for apples. A low quality apple blossom has clusters with long flower pedicles, a reduced number of flowers and well-developed leaves in comparison to the flowers. These buds were of poor quality, as they rarely set fruit (Williams, 1965). The morphological features are associated with the time in the season that the flower formed, strong blossoms are old, i.e. they were formed early in the previous season, while weak blossom are young, i.e. formed late in the season. Early bud development of apple is characterised by an increase in the number of appendages, i.e. bud scales, transition leaves and true leaves in the bud (Bijhouwer, 1924). The number of leaves per cluster is determined by the rate at which appendages are formed in the period preceding floral differentiation, and by the time in the season that floral differentiation starts (Verheij, 1996; Wertheim, 1990). The stronger (old) buds are also the buds which emerge early.

3. Physiological factors affecting bud formation

There are a large number of theories concerning factors affecting reproductive bud formation. Before the discovery of plant hormones flowering of pears was explained on a nutritional basis whereby a relatively high

C/N ratio was said to promote flower induction whereas a relatively low C/N ratio promoted vegetative development (Verheij, 1996). With the discovery of hormones from the 1930's onwards, the nutrient theory was largely abandoned in favour of a hormone theory. Today a theory with a complex of participators is considered, in which the previous nutrient and hormone theories are reconciled, as both groups of factors are essential for the flowering process (Verheij, 1996).

3.1. Nutrients and assimilates

The general idea 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 the previous century. According to this concept the ratio between the available carbohydrates and nitrogen determines which process prevails. Flower bud induction occurs when the carbohydrate (C) supply predominates, whereas shoot growth is stimulated when nitrogen (N) supply is more important. No clear evidence was found that the C/N ratio is decisive for the formation of flowers (Tromp, 2000).

Contrary to earlier reports, nitrogen fertilisers often increase flower initiation and development. Williams (1965) found that late summer applications of N resulted in much stronger flowers the following spring. Since leaf senescence and abscission were postponed by late application of N, it was suggested that the promotive effect of N may be mediated through enhanced levels of assimilates for meristematic activity in the bud. Which leads to an increase in the number of flowers per bud and the number of appendages per bud and results in better flower differentiation. Alternatively, enhanced production of cytokinin in the roots may be responsible for the enhanced flower quality (Verheij, 1996).

Normal flower development requires adequate mineral elements in a proper balance. Any severe imbalance or deficiency of an element can hinder proper development. For example, boron deficiency causes flower to wither and die just before and during anthesis (Westwood, 1978).

3.2. Hormones

A wealth of data obtained with exogenous applications of hormones and synthetic growth regulators suggest that endogenous hormones have a regulatory role. Plant hormones play a dominant role in determining the direction of

movement of organic metabolites and in the establishment of sink/source relationships (Verheij, 1996).

3.2.1. Gibberellins

Of the hormones gibberellin (GA) is most frequently negatively associated with reproductive bud formation of the pear. The functions of gibberellins at the cellular level include cell elongation and expansion as well as stem elongation at the whole plant level (Taiz and Zeiger, 1998).

GA's alone or in combination with other plant growth regulators are applied commercially to induce parthenocarpic fruit development, to reduce fruit russeting and to enhance fruit size (Westwood and Bjornstad, 1974). An undesired effect of GA spray application to fruit trees, especially of GA₃ and GA₇, is the inhibition of flower induction (Tromp, 1982; Wertheim, 1990). This effect seems to be closely related to biennial bearing of fruit trees. Biennial bearing seems to be mainly due to a reduction in the induction of reproductive buds (Jonkers, 1979).

The two main sources of endogenous GA in the tree seems to be the terminal regions of rapidly elongating shoots, particularly the young, rapidly expanding leaves and developing seeds during the period of rapid embryo growth which occurs over the period of four to nine weeks after fertilisation (Luckwill, 1970). The synthesized GA's can be transport through both xylem and phloem and is non-polar.

It is speculated that seed-produced GA's are involved in the signal transduction to the spur buds, resulting in suppression of reproductive bud induction (Bubán and Faust, 1982; Gill et al., 1973). Stephan et al. (2001) tried to prove this hypothesis, by applying radioactive GA's to fruit and de-fruited pedicle's and then monitored the amount of GA's transported to the bourse shoot (where reproductive bud induction was expected to occur). In no case, not with application to the fruit or the de-fruited pedicle, did the applied GA's accumulate in the bourse shoot. These results may lead to the conclusion that the administered GA's were unable to enter the relevant transport system, possibly due to injuries caused by the application mode (Stephan et al., 2001).

Application of GA inhibits flower formation in apple, peach and pear. Although it is often claimed that GA represses flowering by enhancing shoot growth, it is largely assumed that the effect of GA is direct, as GA may inhibit reproductive bud formation without a large effect on growth (Tromp, 1982; Verheij, 1996). Application of chemical growth retardants which may interfere with GA-action or biosynthesis, such as daminozide (Alar), chloromequat chloride (CCC) and paclobutrazol generally promote reproductive bud formation (Du Plessis *et al.*, 1998), suggesting that induction of flowering may require low levels of endogenous GA.

3.2.2. Cytokinins

Cytokinins (CK's) are associated with promotion of reproductive bud formation and flower differentiation (Roitsch and Ehne, 2000; Wertheim, 1990). Zeatin or benzyladenine (BA) introduced into the transpiration stream promoted flowering of pear and apple (Bubán, 2000). Spraying apple trees with BA soon after anthesis resulted in an increase in return bloom (Bubán, 2000; Bubán and Lakatos, 2000; McLaughlin and Greene, 1984). CKpromotes flower formation by ensuring sufficient meristematic activity for the differentiation of flower parts, which lead to high quality reproductive buds. Reproductive buds generally contain more appendages than vegetative buds (Wertheim, 1990).

Investigations into the early drop of apple fruits, Fukui *et al.*, 1985 (cited by Bubán, 2000) found that in seeds of fruit with the potential to drop early, the CKactivity was only 1/40 to 1/15 of that in seeds of persistent fruit. This confirms the role of CKin increasing the sink strength of an organ for carbohydrates and amino acids.

The major function of CK's is to promote cell division thereby enhancing sink strength. Luckwill (1970) showed that the concentration of CK's emanating from the roots was at it's highest at full bloom, when buds are most responsive to induction, and the levels subsequently decrease to a low level in August, 150 d.a.f.b.. Luckwill (1970) assumed that a balance of CK's and GA is critical to flower induction.

To summarise, high levels of CK's during flower induction will increase the number of reproductive buds induced and high levels of CK's during the time of flower initiation and differentiation will improve flower quality. CKwill stimulate cell division, which will raise the metabolic activity and ultimately increase the sink strength and the degree of dominance of the developing bud.

3.2.3. Auxins

The effect of auxin on reproductive bud development is not clear, as both inhibition and promotion of reproductive bud development has been reported. Auxins applied early tend to inhibit flower indution, yet if they are applied later they can enhance reproductive bud development (Westwood, 1978).

Auxin produced in seeds reaches a maximum four to five weeks after flowering (Luckwill, 1970), which is followed by a second auxin peak probably originating from the embryo seven weeks later. The auxins are able to intensify the effect of the GA's (Bubán, 1996). GA's start appearing in the seeds four to five weeks after full bloom and they reach a peak at the ninth week after bloom. This is the time of flower induction and the interaction of auxin and GA's will inhibit induction (Callejas and Bangerth, 1997).

Luckwill (1970) and Bubán (2000) suggested that flower induction requires the release from apical dominance before buds reach a dormant state. As buds age they gradually pass into a state of para-dormancy. Basal buds are under strong apical dominance which may prevent the accumulation of appendages and reproductive bud formation. By the time apical dominance ceases due to the cessation of shoot growth, dormancy may have proceeded too far for generative development to proceed, while middle, top and terminal buds are still sufficiently active to enable the enhanced metabolic activity associated with flower initiation and differentiation. Several experiments support the suggestion that both the rate of appendage and reproductive bud formation are under apical control. In pear, sprays of paclobutrazol, thought to reduce apical dominance, increased the number of appendages per bud as well as reproductive bud formation (Browning *et al.*, 1992).

Furthermore apical dominance plays an important role in determining the start and rate of flower differentiation. The distinction between the dominance of fruit sinks and apical dominance is that in the earlier it is not the morphological position of the fruit sinks that determine their degree of dominance or inhibition but, rather, their sequence of development relative to each other. Usually the earlier developed organ dominates over later developed ones, which is called primigenic dominance (Bangerth, 1989; Gruber and Bangerth, 1990). There is some evidence that suggest that indoleacetic acid (IAA) could be involved in the transfer of the dominance signal.

- 1.) The rate of diffusible IAA from dominant apple fruit is higher than that from inhibited fruits on the same plant (Bangerth, 1989).
- 2.) Manipulating the dominance relationship is quickly reflected in an altered rate of IAA diffusion (Bangerth, 1989). This relationship also exists between fruits and vegetative sinks. For instance, when the shoot tip of an apple is removed, nearby fruit show higher fruit set and start to export more IAA (Li and Bangerth, 1999; Quinlan and Preston, 1971).
- 3.) The possible role of the IAA export rate in dominance also follows from the importance of seeds in the dominant fruits. Without the stimulative effects of hormone applications, in some species parthenocarpic fruit set can be obtained only when competition with vegetative sinks is eliminated (Carbonell and Garcia-Martinez, 1980). Even when phytohormones are used to induce parthenocarpic fruit set, the simultaneous presence of competing seeded fruits restrict or even prevent their further development (Retamales and Bukovac, 1986). Competition for assimilates cannot be the sole reason for this, because a similar number of seeded fruits can be supported. This suggests a dominance effect of shoot tips and/or seeded fruit on the growth of parthenocarpic fruit. The rate of export of IAA from a fruit is also closely related to the presence and number of seeds (Bangerth, 2000). Bubán (1996) found an average of five seeds in fruits of apple trees bearing annually and in alternately bearing trees there was an average of eight, and the intensity of the diffusion of auxin in the latter was 60 % higher.

Furthermore, auxin produced in the leaves may inhibit appendage formation. Young leaves are a major source of auxin. In apple, Fulford (1966) showed that regrowth of buds was greater if the young leaves (rich in auxin) rather than the old leaves were removed, and after leaf removal regrowth could be prevented if lanolin paste containing auxins was applied to the petioles (Fulford, 1966).

To summarise, a developing bud dominated by a fruit or shoot with high auxin export will develop slowly and will lead to the formation of flowers of poor quality. On the other hand if a bud develops with low inhibition of other fruits or shoots its development will start earlier and occur at a higher rate than a strongly inhibited bud and will lead to flowers of superior quality. The assumption is thus made that polar IAA export is essential for a growing organ. If this IAA export does not take place or is inhibited, for instance because of the proposed auto-

inhibition, the growth of the specific organ may be reduced or it may abscise (Bangerth, 1989).

Auxin's role is still unclear in flower formation because auxin intensifies the effect of GA, which will cause a negative effect on flower formation, but on the other hand a certain amount of auxin must be exported out of developing fruits and buds to avoid abscission and maintaining an active sink. Terminal flower initiation follows shoot growth cessation, which may imply that growing shoots exported IAA levels are too high for initiation to occur and only when shoot growth ceased levels of exported IAA dropped to such a level that initiation can take place.

3.3. The importance of shoot growth, leaves, fruits and roots on reproductive bud development

3.3.1. Shoot growth

In fruit trees there is an antagonistic relationship between shoot growth and reproductive bud development (Du Plooy *et al.*, 2002). Where shoots, adjacent to fruit, are growing vigorously, their high levels of IAA export results in correlative inhibition of IAA export from young fruit (Bangerth, 2000; Du Plooy *et al.*, 2002). Corresponding with this assumption, IAA export from shoot tips is increased by the application of GA's which stimulate shoot growth, while application of growth retardants such as diaminozide or prohexadione-Ca will have the opposite effect (Callejas and Bangerth, 1997).

Treatments which stimulate vegetative growth often reduce flowering, while conversely, treatments curbing vigour tend to enhance it (Miller, 1988). The duration of growth may also affect reproductive bud initiation and differentiation. Treatments leading to early cessation of shoot growth tend to stimulate reproductive bud induction, while prolonged vegetative growth inhibits it (Luckwill, 1970). The inhibitory effect of excessive shoot growth on reproductive bud induction is ascribed to the production of GA in terminal regions of rapid elongating shoots. Early cessation of shoot growth may be conducive to flowering by enabling flower initiation and differentiation to proceed at a time when CK levels are still sufficiently high (Luckwill, 1970). CK's may be required to induce the enhanced metabolic activity associated with flower initiation and differentiation. According to Luckwill (1970) both GA and CK's reach a maximum in the xylem sap early in the season and decrease as the season progresses. Actively growing extension shoots

provide a continuing though likely declining supply of GA until extension growth ceases. Cessation of shoot growth of spurs in pears occurs in the beginning of October (two to four weeks after flowering), and long shoots at the end of November (Walters, 1968). These observations support the theory that as long shoot growth continues and young leaves are present, these young leaves produce GA's which inhibit reproductive bud induction (Luckwill, 1970). A detailed analysis has shown (Huet, 1974, cited by Tromp, 2000) that the relative growth rate of shoots of pear cultivars, in the month before growth is completed, is inversely related to the number of reproductive buds per shoot.

Not only excessive vegetative development but also too weak vegetative development may inhibit reproductive bud development. Too weak vegetative development will lead to a small leaf area, leaves are important for reproductive bud development as discussed in the following section (Verheij, 1996). Furthermore, too weak vegetative growth will reduce the number of sites for potential reproductive buds. 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 has already ceased (Tromp, 1976).

3.3.2. Leaves

The inhibitory effects of treatments such as defoliation, shading and leaf injury have established that the presence of leaves is a prerequisite for reproductive bud induction (Fulford, 1966; Tromp, 2000). Lauri and Térouanne (1999) as well as Ferree *et al.* (2001) found a positive correlation between the number of leaves and flowers of the inflorescence (spur leaves, bourse-shoot and flower cluster) and fruit set for apples. Removal of cluster leaves before or after bloom severely reduced fruit set or increased fruit drop (Ferree and Palmer, 1982). The number of cluster leaves is also positively related with bourse buds/shoots per reproductive bud (Verheij, 1996). In the pear cv. Bon Chrétien Williams the percentage of flowering spurs is strongly related to leaf number per spur (Huet and Lemonine, 1972, cited in Tromp, 2000). Spur leaf area has been shown to be strongly correlated to fruit set, size and fruit Ca levels at harvest (Feree and Palmer, 1982). Quinlan and Preston (1971) and Lauri and Térouanne (1999) concluded that competition between fruits and bourse shoots, occurring during blossoming and the

following two to three weeks may limit fruit set, but the presence of bourse shoot leaves was beneficial in the latter part of the season by enhancing fruit growth. Proctor and Palmer (1991) reported that return bloom of a spur was dependant on the presence of the bourse shoot and not on the amount of spur leaf area. The requirements for leaves has been explained in terms of their acting as a source of both assimilates and hormones. Leaves also are of direct importance by sustaining the transpiration stream, ensuring that promotive substances produced elsewhere in the plant reach the site of reproductive bud development. However, because of the lack of chemical support from chemical analyses the conviction grew that leaves produce a hormonal factor that is vital for reproductive bud development (Tromp, 2000).

3.3.3. Fruits

The presence of a large crop is also well known to have an inhibitory effect on reproductive bud development. Initially this was thought to be due to competition for assimilates. However, Chan and Chain (1967) demonstrated that deseeded fruit did not reduce flower number, indicating that the seeds present in the fruit were the source of inhibition. Developing seeds are a rich source of GA₄ and GA₇, which appear four to six weeks after full bloom and reach a maximum after nine weeks. The concentration, measured in GA₃ units at this time was 15-500 times higher than in leaves and shoots (Luckwill, 1970). Recently the view has been put forward that applied GA's inhibit reproductive bud induction in apple via stimulation of auxin synthesis in the seeds and export from young fruits during reproductive bud induction (Callejas and Bangerth, 1997).

3.3.4. Root growth

A root system is essential to flower development, by ensuring a supply of CK's, as the roots are the major source of CK's in the plant (Verheij, 1996).

4. Environmental factors influencing reproductive bud induction and initiation

Flower induction and initiation of apple and pear is not triggered by a single environmental factor such as day length or temperature, but many environmental factors may affect the response. Flower induction is enhanced by high levels of light in comparison with low levels, and by moderately low temperatures rather than high temperatures (Tromp, 1976). The inhibiting effect of

high temperature on flower induction can be explained, because more GA's are produced in the young leaflets at high temperatures (Tromp, 1982). Low relative air humidity (RH) and conditions leading to moisture stress generally enhances flower initiation (Tromp, 1984).

5. Manipulations affecting induction, initiation and differentiation

The transition from vegetative to generative is usually irreversible. This means that manipulating the number of reproductive buds is mainly restricted to the induction phase, which occurs early in the growing season. After induction has occurred several treatments may affect flower differentiation as reflected in flower quality, which is important for fruit set, but the number of reproductive buds is not influenced (Tromp 2000).

5.1. Girdling

Girdling is the complete removal of a bark cylinder around the trunk, while scoring is the severing of the bark tissue with a thin cut completely encirciling the trunk, without removing the bark. Redistribution of assimilate supply between different plant organs appears to be the predominant effect of girdling or scoring, with the growth of fruit being favoured over the growth of vegetative organs (Dann *et al.*, 1984). Girdling after fertilisation and petal fall gives improved fruit set in apples (Noël, 1970). Reduced leaf area per unit fruit number, together with reductions in leaf size, limb circumference growth, lateral length and internode length reflects this change on peach trees girdled one week after harvest (Dann *et al.*, 1984).

Girdling's effect is due to the disruption of the phloem transport system. Scoring is a less severe disruption with the same result. Auxin moves primarily in phloem in a basipetal direction in plants (Goldsmith, 1977) and is thought to be a principle factor in correlative growth control (Bangerth, 1989). Girdling would disrupt this basipetal hormone signal (Noël, 1970; Wertheim, 1990). Dann *et al.* (1984) found a sharp increase in IAA concentration in the bark above the girdle in peach trees and a 75% reduction in the IAA concentration below the girdle. Girdling consistently decreased shoot tip IAA export while considerably increasing export from fruit (Bangerth, 2000). A possible role of IAA in apical dominance is to control the distribution and metabolism of CK's (Bubán, 2000). This disruption of the basipetal transport of IAA would lead to an increase in xylem transported CK's

presumably from the roots (Bangerth et al., 2000; Li et al., 1995). Although to date these CK effects on IAA transport and biosynthesis have only been demonstrated for exogenously applied CK's another auxin/CK interaction was detected which seems to be regulated by endogenous factors. Within six to ten hours of decapitating bean plants a very substantial increase in presumably root-derived CK concentration in the xylem was observed (Li et al., 1995). Application of the auxin transport inhibitor napthylphthalamic acid (NPA) to the stem of intact bean plants also lead to a CK increase, although considerably less so than after decapitation (Bangerth et al., 2000). The effect of decapitation or NPA treatment seems good evidence that it is the endogenous polar IAA transport, which controls CK-production in the root, or it's loading into the xylem (Bangerth et al., 2000).

The increase in xylem transported CK's after decapitation is detected before a measurable growth response of lateral buds is observed (Bangerth *et al.*, 2000; Li *et al.*, 1995). This suggests that the CK concentration participates in the release from apical dominance and is possibly caused by the stimulation of the cell cycle by CK and/or by the stimulation of IAA biosynthesis (Bangerth *et al.*, 2000; Roitsch and Ehne, 2000). This increase in CK's is under the control of the basipolar IAA transport. Thus, whereas apically produced auxins down regulate CK's in the roots, root produced CK's up regulate auxins in lateral and terminal buds. This suggests an intimate mutual interrelationship between these hormones possibly by maintained negative/positive feedback regulation (Bangerth *et al.*, 2000).

CK's are known for stimulating cell division and thereby enhancing metabolic activity. In addition if CK's are applied to resting lateral buds, they can be released from dominance and even be transformed into dominant shoots (Steffens and Stutte, 1989). Along with this effect, the application of CK's lead to a great increase in IAA exports out of the treated buds. Auto transport autoinhibition (ATA) functions in both directions, accordingly the higher IAA export from the new dominant bud will reduce IAA export from the shoot apex (Bangerth *et al.*, 2000). It can be said in conclusion that, dominance imposed on lateral buds or fruits/seeds is seldom absolute. More frequently it is only partially expressed. Under these conditions a mutual homeostatic equilibrium of auxins, originating in the apex, and CK's presumably from the roots may regulate the growth rate of dominated organs via ATA at junctions and CK regulated cell division in the buds or apex of lateral

shoots (Bangerth et al., 2000). The following assumptions can be made from above information:

- The possible role of girdling during flower initiation is that developing buds receive a higher amount of root derived CK's, because of the disruption of the basipetal transport of IAA, which will enhance metabolic activity. Furthermore the bud will export more IAA and its sink strength will improve. The end result will be a better quality reproductive bud, which will be better differentiated because of the higher amount of CK and metabolic activity.
- A second explanation for the effect of girdling is that girdling disrupts the basipetal IAA hormone signal thereby removing apical dominance (Noël, 1970; Wertheim, 1990). Accordingly stimulating the development of basal buds and enhancing the sink strength of these usually dominated organs. This will help a developing reproductive bud to be initiated earlier and will lead to higher quality flowers, furthermore will more meristems to react to inductive signals.

5.2. Effect of fruit thinning on flower induction

Fruit thinning is commonly practiced in many fruit bearing woody perennials to improve fruit quality and to prevent biennial bearing. Biennial bearing has its origin in the negative effect of the presence of fruits on reproductive bud development units (return bloom) (Tromp, 2000).

In view of the negative effect of fruit on reproductive bud development, probably the positive effect of thinning is due to the removal of fruits. However, this may be an over simplification by ignoring the fact that early removal of fruit stimulates shoot growth which may reduce return bloom (Palmer *et al.*, 1991).

In general, the effect of thinning on return bloom decreases with time and is most pronounced when carried out at bloom or shortly thereafter (Tromp, 2000). If thinning is completed before 40 days after full bloom it should positively affect return bloom. This is partly due to the removal of future sources of GA's as a low GA to CK relationship favours flower initiation as discussed previously.

Conclusion

Due to new developments in the production of horticultural crops there will always be the tendency to improve the profitability of a crop. This can be obtained by ensuring a regular and sustainable yield of fruit of superior quality.

Reproductive bud development is one of the most important aspects in ensuring a sustainable yield and high quality fruit. It plays a role at two development phases increasing the yield. Firstly it can increase the total number of reproductive buds by increasing the number of meristems reacting to favourable inductive conditions. Secondly it can enhance the quality of the reproductive buds by improving flower differentiation, which will result in more reproductive buds setting fruit. Therefore it is necessary to understand the factors affecting reproductive bud development. To understand reproductive bud development is difficult, because there are a large number of factors which are closely related and integrated with each other. Hormonal factors are the closest related to reproductive bud development. GA has a positive effect on crop load by reducing abscission of the present crop. High GA levels have a negative effect on reproductive bud induction and therefore the following season's crop. The main sources of GA are the seeds and growing shoots. Therefore the growth rate of shoots the month prior to shoot growth cessation (start of flower initiation) is inversely related to the number of reproductive buds per shoot.

CKon the other hand is the hormone which is essential for reproductive bud development by enhancing the sink strength of a developing meristem and by the removal of apical dominance. Furthermore a shift to a low GA:CK ratio will promote generative development during the time of flower induction.

Auxin has a negative effect on reproductive bud development by intensifying the negative effects of GA's and by the inhibiting effect of apical dominance on developing meristems. When the auxin export decreases from a dominant organ (the inhibition on the bud decreases), the developing meristem's priority as a sink rises and bud initiation can commence. By advancing initiation a better differentiated bud will form.

The question is how to manipulate these factors to achieve the ideal conditions for reproductive bud development. Usually the aim of such manipulations is to improve flower number and flower quality by manipulating flower initiation and flower differentiation respectively.

It is well known that girdling shifts the balance from vegetative development to reproductive development. How this is achieved is not yet fully understood. By girdling pear trees in the beginning of December (time of flower initiation), basipetal IAA transport to the roots will be disrupted leading to an increase in transport of root-derived CK to developing meristems. This implies that the metabolic activity of the meristem will be enhanced thereby increasing the sink strength of the meristem. Ultimately this will lead to better differentiated flowers and therefore flowers of high quality.

Fruit thinning removes a source of GA's, thereby improving the GA:CK ratio for flower induction. Furthermore the sink demand of the total number of fruit decreases, which will lead to more carbohydrate exported to the developing meristems.

Therefore it is essential to improve our knowledge on reproductive bud development, which will extend our understanding of tree manipulations. This will help in decision making of which manipulation to use and when being the optimal time.

Literature cited

- Bangerth, F. and Ho, L.C. 1984. Fruit position and fruit set sequence in a truss as factors determining final size of tomato fruits. *Ann. Bot.* 53: 315-319.
- Bangerth, F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiol. Plant.* **76:** 608-614.
- Bangerth, F. 2000. Abscission and thinning of young fruits and their regulation by plant hormones and bioregulators. *Pl. Gr. Regul.* **31:** 43-59.
- Bangerth, F., Li, C. and Gruber, J. 2000. Mutual interaction of auxin and cytokinins in regulating correlative dominance. *Pl. Gr. Regul.* **32:** 205-217.
- Bijhouwer, J. 1924. Die periodisiteit van de knopontwikkeling bij den appel. *Meded. Landb. Hoogesch. Wageningen* 27: 1-64.
- Browning, G., Kuden, A. and Blake, P. 1992. Site of (2RS, 3RS)-paclobutrazol promotion of auxillary flower initiation in pear cv. Doyenne du Comice. *J. of Hort. Sci.* **67:** 121-128.

- Bubán, T. and Faust, M. 1982. Flower bud induction in apple trees: Internal control and differentiation. *Hort. Rev.* 4: 174-203.
- Bubán, T. 1996. Flower development and formation of sexual organs. In Nyeki J. and Soltesz M (eds.). pp 3-54. Floral biology of temperate zone fruit trees and small fruits. Akademiai Kiado. Budapest.
- Bubán, T. 2000. The use of benzyladenine in orchard fruit growing: a mini review. *Pl. Gr. Regul.* **32:** 381-390.
- Bubán, T. and Lakatos, T. 2000. Contributions to the efficacy of benzyladenine as fruit thinning agent for apple cultivars. *Acta. Hort.* **514:** 59-68.
- Callejas, R. and Bangerth, F. 1997. Is auxin export of apple fruit an alternative signal for inhibition of flower bud induction. *Acta. Hort.* **463**: 271-277.
- Carbonell, J. and Garcia-Martinez, J. L. 1980. Fruit set of un-pollinated ovaries of *Pisum sativum* L. Influence of vegetative parts. *Planta*. **147**: 444-450.
- Carrera, M. 1982. Flower initiation in pear varieties. Acta. Hort. 124: 157-163.
- Chan, B.G. and Cain, J.C. 1967. The effect of seed formation on sequent flowering in apple. *Proc. Amer. Soc. Hort. Sci.* 91: 63-68.
- Crabbé, J. J. 1984. Vegetative vigor control over location and fate of flower buds in fruit trees. *Acta Hort*. **149**: 55-63.
- Dann, I.R., Wildes, A.R., and Chalmers, D.J. 1984. Effects of limb girdling on growth and development of competing fruit and vegetative tissues of peach trees. *Aust. J. Plant Physiol.* **11:** 49-58.
- Du Plessis, P., Theron, K.I. and Griesel, H.M. 1998. Effect of autumn application of Chloromequat on reproductive bud development, fruit set and production of the pear cv. Doyenne du Comice. *Acta Hort.* 475: 251-264.
- Du Plooy, P., Jacobs, G. and Cook, N.C. 2002. Quantification of bearing habit on the basis of lateral bud growth of seven pear cultivars grown under conditions of inadequate winter chilling in South Africa. *Sci. Hort.* **95:** 185-192.
- Faust, M. 1989. Physiology of Temperate Zone Fruit Trees. John Wiley and Sons Inc., New York: pp 169-229.

- Ferree, D.C. and Palmer, J.W. 1982. Effect of spur defoliation and ringing during bloom on fruiting. Fruit mineral level, and net photosynthesis of 'Golden Delicious' apple. *J. Amer. Soc. Hort. Sci.* **107(6):**1182-1186.
- Ferree, D.C., Bishop, B.L., Schupp, J.R., Tustin, D.S. and Cashmore, W.M. 2001. Influence of flower type, position in the cluster and spur characteristics on fruit set and growth of apple cultivars. *J. of Hort. Sci. and Biotech.* **76(1):** 1-8.
- Fukui, H., Imakawa, S. and Tamura, T. 1985. Relation between early drop of apple fruit, CK and gibberellin. J. Jap. Soc. Hort. Sci. 54: 287-292.
- Fulford, R.M. 1966. The morphogenesis of apple buds. III. The inception of flowers. *Ann. Bot.* **30**: 207-219.
- Goldsmith, M.H.M. 1977. The polar transport of auxin. *Ann. Rev. Plant. Physiol.* 28: 439-478.
- Gil, G.F., Martin, G.C., and Griggs, W.H. 1973. Fruit-set and development in the Pear: Diffusable growth substances from seeded and seedless fruits. *J. Amer. Soc. Hort. Sci.* **98(1):** 51-54.
- Gruber, J.D. and Bangerth, F. 1990. Diffusiable IAA and dominance phenomena in fruits of apple and tomato. *Physiol. Plant.* **79:** 354-358.
- Jonkers, H. 1979. Biennial bearing in apple and pear: a Literature review. *Sci. Hort.* **11:** 303-317.
- Lauri, P.E. and Térouanne, E. 1999. Effect of inflorescence removal on the fruit set of the remaining inflorescences and development of the laterals on one year old apple (Malus domestica Borkh.) branches. *J. of Hort. Sci. and Biotec.* **74(1):** 110-117.
- Li, C.J., Guevara, E., Herrera, J. and Bangerth, F. 1995. Effect of the apex excision and replacement by 1-naphtylacetic acid on CK concentration and apical dominance in pea plants. *Physiol. Plant.* **94:** 465-469.
- Li, C.J. and Bangerth, F. 1999. Autoinhibition of indoleacetic acid transport in the shoots of two branched pea (*Pisum sativum*) plants and its relationship to correlative dominance. *Physiol. Plant.* **106:** 415-420.

- Luckwill, L.C. 1970. The control of growth and fruitfulness of apple trees. In: Luckwill LC and Cutting CV (eds) pp 237-254. Physiology of tree crops. London. New York: Academic Press.
- Luyten, I.D.A. and De Vries, L.I. 1924. Die periodiciteit van de knopontwikkeling bij den peer. *Meded. Landb. Hoogesch. Wageningen.* **15:** 1-61
- McLaughlin, J.M. and Greene, D.W. 1984. Effects of BA, GA₄₊₇ and diaminozide on fruit set, fruit quality, vegetative growth, flower initiation and flower quality of 'Golden Delicious' Apple. *J. Amer. Soc. Hort. Sci.* **109(1):** 34-39.
- Miller, S.S. 1988. Plant bioregulators in apple and pear culture. *Hort. Rev.* **10:** 309-401.
- Noël, A.R.A. 1970. The girdled tree. Bot. Rev. 36: 162-195.
- Palmer, J.W., Cai, Y.L. and Endjamo, Y. 1991. Effect of part-tree flower thinning on fruiting, vegetative growth and leaf photosynthesis in 'Cox's Orange Pippin' apple. *J. Hort. Sci.* **66:** 319-325.
- Pratt, C. 1988. Apple flower and fruit: Morphology and anatomy. *Hort. Rev.* **10:** 273-308.
- Proctor, J.T.A. and Palmer, J.W. 1991. The role of spur and bourse leaves of three apple cultivars on fruit set and growth and calcium content. *J. Hort. Sci.* 66: 275-282.
- Quinlan, J. D. and Preston, A. P. 1971. The influence of shoot competition on fruit retention and cropping of apple trees. *J. Hort. Sci.* **46:** 525-534.
- Retamalus, J. B. and Bukovac, M. J. 1986. Studies on abscission of pthalamide induced parthenocarpic sour cherry fruits. *J. Amer. Soc. Hort. Sci.* 111: 703-707.
- Roitsch, T. and Ehne, R. 2000. Regulation of source/sink relations by cytokinins. *Pl. Gr. Regul.* **32:** 359-367.
- Steffens, G.L. and Stutte, G.W. 1989. Thidiazuron substitution for chilling requirement in three apple cultivars. *J. Pl. Gr. Regul.* 8: 301-308.
- Stephan, M., Bangerth, F. and Schneider, G. 2001. Transport and metabolism of exogenously applied gibberellins to *Malus domestica Borkh*. cv. Jonagold. *Pl. Gr. Regul.* 33: 77-85.

- Taiz, L. and Zeiger, E. 1998. Plant physiology. 2nd ed. Sunderland, Mass. : Sinauer.
- Tromp, J. 1976. Flower-bud formation and shoot growth in apple as effected by temperature. *Sci. Hort.* **5:** 331-338.
- Tromp, J. 1982. Flower-bud formation in apple as influenced by various gibberelins. *J. Hort. Sci.* **57:** 277-282.
- Tromp, J. 1984. Flower-bud formation in apple as affected by air and root temperature, air humidity, light intensity, and day light. *Acta Hort.* **149:** 39-47.
- Tromp, J. 2000. Flower-bud formation in pome fruit as affected by fruit thinning. *Pl. Gr. Regul.* **31:** 274-282.
- Van Zyl, H.J. 1979. Vrugsetstudies met betrekking tot *Pyrus communis, L.*, cv. Packham Triumph. *PhD. Thesis* University of Stellenbosch: Stellenbosch.
- Verheij, F.A. 1996. Morphological and physiological aspects of the early fase of flower bud formation. *PhD. Thesis* Agricultural University Wageningen: Wageningen.
- Walters, J.H. 1968. Die differensiaise verloop van reproduktiewe knoppe van *Pyrus Communis* cv. Bon Chretien en *Pyrus Communis* X *Pyrus pyrifolia* cv. Kiefer. *MSc. Thesis* University of Stellenbosch: Stellenbosch.
- Wertheim, S.J. 1990. De Peer. Proefstation voor de Fruitteetlt, Wilheminadorp: pp 88-94.
- Westwood, M.N. and Bjornstad, H.O. 1974. Fruit-set as relted to girdling, early cluster thinning and prunning of 'Anjou' and 'Comice' pear. *Hort. Sci.* **9(4)**: 342-344.
- Westwood, M.N. 1978. Temperate zone pomolgy: Physiology and culture, third edition, Portland, Oregon: Timber Press.
- Williams, R.R. 1965. The effect of summer nitrogen application on the quality of apple blossom. *J. Hort. Sci.* **40**: 31-41.

PAPER 1: REPRODUCTIVE BUD DEVELOPMENT OF PEARS (PYRUS COMMUNIS L.) WITH EMPHASIS ON THE BOURSE SHOOT

Abstract

For consistent yields in pear fruit production, knowledge of the development of the reproductive bud is required. The aim of this study was to gain more insight in the development of the primordial bourse shoot. The bourse shoot is important because of the ability of a bourse shoot to become reproductive, which can lead to bourse-over-bourse bearing. The progression of reproductive bud development in 'Forelle' and 'Rosemarie' was studied from primordial bourse shoot initiation until dormancy the following season. The primordial bourse shoot development in the reproductive bud before full bloom is poorly documented. The primordial bourse shoot was initiated in February The primordial bourse shoot progressed during dormancy with a plastochron length of 60 to 80 days in June. The rate of preformed leaf formation increased rapidly until August, when the plastochron was 5 days. 'Rosemarie's' primordial bourse shoot development was more advanced at full bloom. This is one of the possible reasons for the higher bourse-over-bourse bearing habit of the cultivar. The number of leaves of the bourse shootof 'Rosemarie' was significantly greater than with 'Forelle', which has a low tendency for bourse-over-bourse bearing. Flower initiation of the terminal bud of the bourse shoot was 56 and 77 days after full bloom for 'Forelle' and 'Rosemarie', respectively. Initiation was well correlated with the cessation of bourse shoot growth. An increase in mitotic activity occurred during flower differentiation of the terminal bourse bud, with a peak of floral appendage formation during December and January. From February until dormancy enlargement of the floral parts took place.

Introduction

Regular and substantial yields of superior quality fruit are the most important parameters for successful fruit growing. With a broader knowledge of the development of the reproductive buds these parameters should be easier to achieve.

In the past, numerous scientists studied the development of the reproductive bud, but little emphasis was place on the primordial bourse shoot. Luyten and De Vries (1924) disected the mixed bud of 'Beurre Hardy' in December (Northern Hemisphere) and found in the axils of the first two foliage leaves vegetation points bearing 2 to 5 leaf primordia. These vegetation points can develop into a bourse shoot. Walters (1968) also found primordial shoots or flowers in the leaf axils. He found that the primordial shoot could also form in the axils of the transitional leaves. The bourse is important for achieving regular yields because it is a potential bearing site.

The aim of this study was to determine when the bourse meristem and the primordial shoot develop and to follow its procession over time. The two cultivars, which were used, were 'Forelle' and 'Rosemarie'. They differ in their bearing habits. Whereas both cultivars bear mainly on spurs on two-year-old wood, 'Rosemarie' has the ability to bear fruit on one-year-old shoots, which can lead to bourse-over-bourse bearing (Du Plooy *et al.*, 2002). By comparing the two cultivars it should be possible to get a better understanding of the bourse shoot development and the possible factors that increase bourse-over-bourse bearing.

Materials and methods

Plant material

Reproductive buds or bourse shoots were collected from the Welgevallen Experimental Farm, situated in the Stellenbosch area of the Western Cape, South Africa (34°55'S; 19°02'E). The area is characterised by a Mediterranean climate: cold, wet winters and warm, dry summers (500 Richardson chill units). 'Rosemarie' and 'Forelle' trees were used. 'Forelle' trees on quince rootstock with a 'Beure Hardy' interstock were planted in 1998 at a spacing of 3.8m x 1.25m in a North-South row orientation. 'Kieffer' trees were the cross pollinator at a density of 10%. 'Rosemarie' trees on BP1 rootstock were planted in 1992 at a spacing of 4.5m x 2.0m with the same row orientation as the 'Forelle'. 'Packham's Triumph' and 'Early Bon Chretien' were the cross pollinators at a density of 6.6 % and 3.3 %, respectively. Trees are trained to a three-wire-trellis central leader system.

Data recorded

At two-week-intervals, from April 2002 to May 2003, five reproductive units per cultivar were sampled at random. Reproductive units were

disected and the following variables were recorded using a macroscope (Wild photo marcoscope M 400, with a 64 x enlargement): (1) the number of preformed leaves of the primordial bourse shoot or neoformed leaves of the bourse shoot, (2) the length of the longest bourse shoot leaf and (3) the length of the bourse shoot. During spring and summer bud (4) development of the bourse shoot and the time of flower initiation was monitored, (5) the rate of appendage formation in the bourse shoot terminal bud was calculated, (6) the bud scales, transitional leaves, true leaves and flowers were measured and (7) the size of the inflorescence was measured before dormancy.

Fifteen one-year-old reproductive units were tagged at random on 20 trees of each cultivar. These units varied from units bearing 1 to 3 fruit to units where all fruit had aborted. Some units had a well-developed bourse shoot, while others formed a bourse bud. The following data were recorded from these tagged units: (1) the number of fruit harvested in 2002 and 2003, and the sizes and seed content of these fruit, (2) the vegetative growth (bourse shoot) was measured and number of leaves counted and (3) the percentage of bourse shoots becoming reproductive terminally was determined.

Results and Discussion

In the 2002 season the primordial bourse shoot was detected in May 2002. It consisted of three leaves and the average length of the longest leaf was 3 mm (Fig. 1a). In 2003 the primordial bourse shoot was detected in January 2003. It consisted of two leaves and the average length of the longest leaf was 1mm (Fig. 1b). During dormancy (May until end of August) the development was generally slow, and the average number of leaves initiated in June was 0.5 and 0.38 for 'Rosemarie' and 'Forelle', respectively, resulting in a plastochron of 60 days for 'Rosemarie' and 80 days for 'Forelle'. With 'Rosemarie' there was increase in leaf primordia initiation with a plastochron of 13 days, resulting in 2.38 leaves added. In the case of 'Forelle' the increase was only 0.66 with a plastochron of 47 days. This difference can possibly be attributed to a difference in chilling requirements between the two cultivars as 'Rosemarie' has a lower chilling requirement than 'Forelle'. In August the plastochron increased again for both cultivars to 5.31 and 6.86 for 'Rosemarie' and 'Forelle', respectively, resulting in an addition of 3.9 and 2.65 leaf primordia. Further development of the primordial bourse shoot was now mainly in terms of leaf

enlargement and the leaf number remained more or less constant for the rest of the season. By 20 August the 'Rosemarie' and 'Forelle' had initiated 7.27 and 6.79 preformed leaves, respectively (Fig. 2). It seems that the cultivar with the higher tendency for bourse-over-bourse, bearing viz. 'Rosemarie', (Fig. 3) formed more preformed leaves than 'Forelle'.

The leaves developed extensively during the dormancy period. . The outer foliage leaves develop stipules (Luyten and De Vries, 1924) and these were first seen by the end of July at the base of the outer foliage leaves, while leaf hairs became more distinctive on the apical side of the leaf (Fig. 4a). The number of leaf hairs increased and before full bloom the leaves were completely covered with hairs (Fig. 4b). From two weeks before full bloom until two weeks after full bloom the rate at which the leaves enlarged increased exponentially (Fig. 5). Two weeks after full bloom the outer leaves had reached their final size and had probably become carbohydrate exporters (Faust, 1989). These carbohydrates are important for cell division and fruit enlargement. Cell division of pears continues until 9-weeks after full bloom (Westwood, 1978) and during this period the leaves of the bourse and the bourse shoot are responsible for supplying assimilates to the young fruits (Webster, 2000). 'Forelle' initiated an average number of 2.2 new-formed leaves after full bloom and 'Rosemarie' 3.4 (Fig. 2). The difference can be attributed to the tendency for the 'Rosemarie' to form a bourse shoot whereas 'Forelle' normally only produces a bourse bud. This is also the main reason why bourse shoot growth cessation was three weeks earlier in 'Forelle' (Fig. 6).

Flower development

Floral initiation is defined as the first visible change in the meristem. The first morphological change that occurs in pears is the broadening of the apex, which also becomes convex, followed by its lengthening into a cylindrical shape and topped by a hollowing formed by the sepal primordia of the king flower (Carrera, 1982).

The terminal buds of 'Forelle' bourse shoots initiated the reproductive bud 56 days after full bloom whereas in 'Rosemarie' this happened 77 days after full bloom (Fig. 6). The time of initiation is correlated with bourse shoot growth cessation. Hence, because of the longer duration of bourse shoot growth in 'Rosemarie' initiation was later than in 'Forelle'. Westwood (1978) and Van Zyl

(1979) made similar observation with flower initiation on spur shoots of pears. They proposed that initiation is about sixty days after full bloom at the time of shoot growth cessation. Verheij (1996) observed in apples that the appearance of the dome-shaped meristem does not occur in all floral buds at once, but is spread over weeks. A similar observation was made in 'Rosemarie' and 'Forelle', namely that initiation of the bourse shoot terminal buds was spread over a period of 5 weeks. Preceeding to the reproductive initiation, foliage leaves and transitional leaves developed. Verheij (1996) also observed a rapid increase in floral appendage formation in apples.

Floral Differentiation

For both cultivars there was a rapid increase in appendage formation from initiation (Fig. 7) until the end of January (Fig. 8). The average flower number counted before dormancy was 7 and 7.6 for the 'Rosemarie' and 'Forelle', respectively. Walters (1968) had observed a lower number of flowers for 'Bon Chretien' and 'Kieffer', and observed four flowers by the end of April (Southern Hemisphere). The lower number can be attributed to the differences in cultivars, different accumulation of chill units between the seasons or due to different cultural practices. The bourse shoot flower buds were largely completed at the start of dormancy. Tromp (2000) found similar results for the spur buds of pears. Verheij (1996) stated that the number of flowers per cluster varied only slightly with different environmental conditions, suggesting that this number is mainly genetically determined.

Floral differentiation refers to the morphological transformation of the apex leading to the formation of an inflorescence and it follows directly after initiation (Verheij, 1996). Differentiation is characterised by an increase in mitotic activity and in cell division. In addition, the rate of primordia production by the apex increases and bracts (leaf-forms in which the lamina and stipules are entirely suppressed) are formed (Bubán and Faust, 1982).

For the period from February to May the inflorescence, excluding the bract leaves, increased by 70-80% in both cultivars (Fig. 9). This enlargement is mainly due to an enlargement in flower size, because the number of appendages remained approximately constant.

Fruit set

Of the two cultivars 'Rosemarie' has the ability to bear bourse-over-bourse (Du Plooy *et al.*, 2002). In 'Rosemarie' the percentage tagged units bearing bourse-over-bourse and flowered bourse-over-bourse but without setting fruit, was higher than in 'Forelle' (Fig. 3).

Conclusion

The bourse shoot was initiated after all the flowers were formed at the end of January. This implies that in the reproductive bud hierarchy the bourse shoot followed after flower formation. Before and during dormancy the progression of the bourse shoot was slow, with the progression mainly in the formation of preformed leaves. After dormancy the preformed leaves enlarged rapidly and some new-formed leaves were formed. The 'Rosemarie', with the higher tendency for bourse-overbourse bearing, (Fig. 3) formed more preformed leaves than 'Forelle' did (Fig. 2). Furthermore, 'Forelle' developed a small number of new-formed leaves, which is in agreement with the cultivar's tendency to form bourse buds. On the other hand the 'Rosemarie' developed a bourse shoot, which lead to more new-formed leaves than in the case of 'Forelle'. Huet and Lemoine (1972) stated that the minimum number of leaves required for fruit to set is six, and from Fig. 2 we can see that the average number of leaves for 'Forelle', eight leaves, was just above this critical number. In addition, Lauri and Térouanne (1999) found a positive relationship between leaf number and flowers in a flower cluster (flower quality) and also between leaf number and fruit set. Leaves are important for the developing flower because they act as a source of assimilates and hormones. Active leaves ensure that promotive substances produced elsewhere in the plant reach the developing bud.

'Forelle' bourse shoot growth cessation was two weeks before that of 'Rosemarie'. This lead to earlier flower initiation, that was well correlated with bourse shoot growth cessation. Differentiation follows after initiation and all the flowers were formed by the end of January. From January until full bloom organ enlargement took place and the new bourse shoot was initiated.

Literature cited

- Bubán, T. and Faust, M. 1982. Flower bud induction in apple trees: Internal control and differentiation. *Hort. Rev.* **4:** 174-203.
- Carrera, M. 1982. Flower initiation in pear varieties. Acta. Hort. 124: 157-163.
- Du Plooy, P., Jacobs, G. and Cook, N.C. 2002. Quantification of bearing habit on the basis of lateral bud growth of seven pear cultivars grown under conditions of inadequate winter chilling in South Africa. *Sci. Hort.* **95:** 185-192.
- Huet, J. and Lemoine J. 1972. Etude des effects feuilles et des fruits sur l'induction florale des brachyblastes du poirier. *Physiol. Végétale.* **10:** 529-545.
- Faust, M. 1989. Physiology of Temperate Zone Fruit Trees. John Wiley and Sons Inc., New York: pp 169-229.
- Lauri, P.E. and Terouanne, E. 1999. Effect of inflorescence removal on the fruit set of the remaining inflorescences and development of the laterals on one year old apple (Mallus domestica Borkh.) branches. *J. Hort. Sci. Biotech.* **74(1):** 110-117.
- Luyten, I.D.A. and De Vries, L.I. 1924. Die periodiciteit van de knopontwikkeling bij den peer. *Meded. Landb. Hoogesch. Wageningen.* **15:** 1-61.
- Richardson, E.A., Schuyler, D.S. and Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *Hort. Sci.* **9(4):** 331-332.
- Tromp, J. 2000. Flower-bud formation in pome fruit as affected by fruit thinning. *Pl. Gr. Regul.* 31: 27-34.
- Van Zyl, H.J. 1979. Vrugsetstudies met betrekking tot *Pyrus Communis*, L., cultivar Packham's Triumph. PhD. Thesis, University of Stellenbosch, Stellenbosch.
- Verheij, F.A. 1996. Morphological and physiological aspects of the early phase of flower bud formation. PhD. Thesis, Agricultural University Wageningen, Wageningen.
- Walters, J.H. 1968. Die differensiaiseverloop van reproduktiewe knoppe van *Pyrus communis* cv. Bon Chretien en *Pyrus communis* X *Pyrus pyrifolia* cv. Kiefer. MSc. Thesis, University of Stellenbosch, Stellenbosch.

Webster, A.J. 2002. Factors influencing the flower, fruit set and fruit growth of European pears. *Acta Hort.* **596(2):** 699-709.

Westwood, M.N. 1978. Temperate zone pomolgy: Physiology and culture, third edition, Portland, Oregon: Timber Press.

Figures

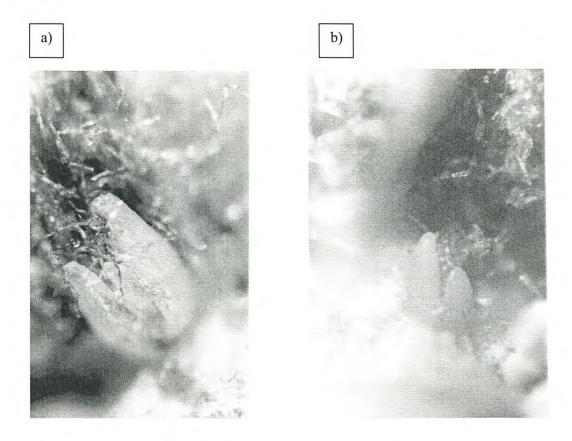


Fig. 1: (a) ('Rosemarie'; 32 X enlarged): First detection of the primordial bourse shoots at the end of May 2002. At this stage the primordial bourse shoot consists of three leaves with an average length of 3 mm for the outer leaf. (b) ('Rosemarie'; 64 X enlarged): First detection of the primordial bourse shoots at the end of January in 2003. The primordial bourse shoot consists of two leaves with an average length of 1mm for the outer leaf.

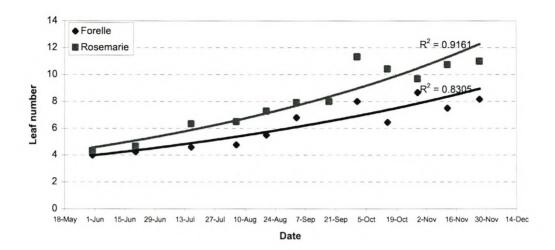


Fig. 2: Average number of bourse shoots leaves (preformed as well as new-formed) from time of primordial bourse shoot initiation until bourse shoot growth cessation. Full bloom was the 13 and 20 September for 'Rosemarie' and 'Forelle', respectively.

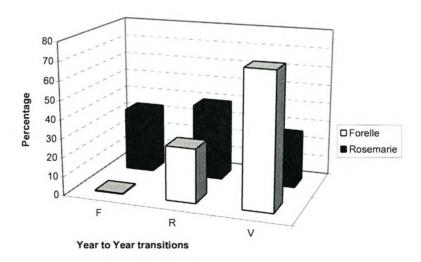


Fig.3: The percentage tagged units bearing bourse-over-bourse (F), flower bud without setting fruit (R) and alternate between the years (V).

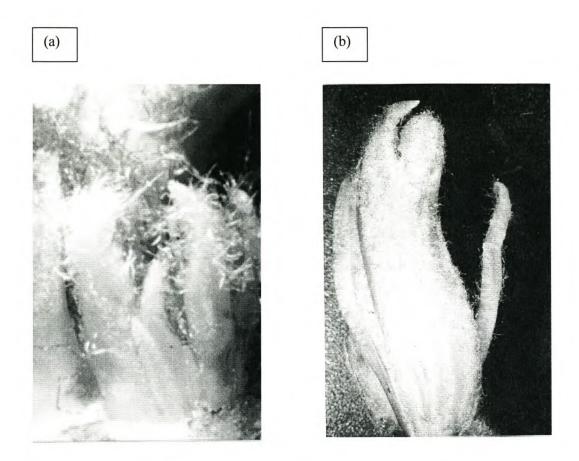


Fig. 4 (a): Leaf stipules are distinctable at the base of the outer foliage leaves and leaf hairs become more distinctive at the apical side of the outer leaves. ('Rosemarie', 16 July 2002, 20X enlarged). (b) Two weeks prior to full bloom. Outer leaves are covered with leave hairs ('Forelle', 3 September 2002, 8X enlarged).

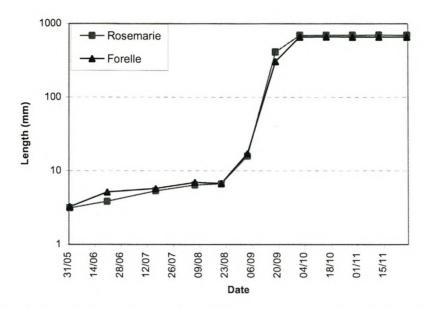


Fig. 5: Average bourse shoot outer leaf length enlargement over time. Full bloom was the 13 and 20 September for 'Rosemarie' and 'Forelle', respectively.

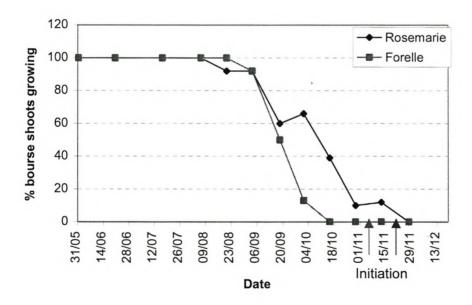


Fig. 6: Percentage active growing bourse shoot apices over time. Flower initiation was the 3 and 16 November for 'Forelle' and 'Rosemarie' respectively.



Fig. 7: The start of flower initiation in the terminal bud of the bourse shoot. The meristem changes from flat shape to dome shape ('Forelle', 3 November 2002, 64X enlarged)

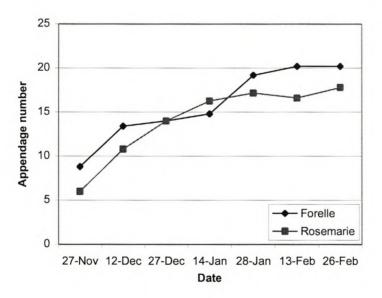


Fig. 8: The average number of floral appendages of 'Forelle' and 'Rosemarie' formed during flower differentiation.

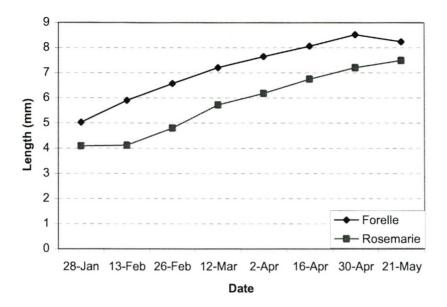


Fig. 9: The length of the average flower cluster with the bract leaves and transition leaves removed for the bourse shoot's terminal reproductive bud.

PAPER 2: VARIATION IN PRUNING SEVERITY AND BRANCH QUALITY ON PRIMARY AND SECONDARY GROWTH OF 'PACKHAM'S TRIUMPH' PEARS (PYRUS COMMUNIS L.)

Abstract

The influence on sink strength of severe dormant pruning and the quality of 2-year-old wood was investigated during the 2002/03 season. Pear trees, *Pyrus communis* L. 'Packham's Triumph' was used in the study conducted in the Western Cape, South Africa. The sink strength of primary growth increased by 40 % for short bearing units (SBU's) and 140 % for thick bearing units (BU's) as compared to long bearing units (LBU's) and thin BU's respectively. The increase in primary growth was due to better fruit set and larger fruit in the SBU's and the thick BU's. Since the increase in primary growth is less for SBU's compared to thick BU's the conclusion, which can be made, is that branch diameter influenced sink strength more than branch length. With increase in branch diameter the size of the xylem transport system increases more than that of the phloem. The increase in xylem transported metabolites, in particular root derived cytokinin seems to predominantly influence the magnitude of the sink strength.

Introduction

The profitable commercial production of pears in South Africa has become increasingly difficult over the last decade. This is explained by the costs of production increasing at a much faster rate than compensatory increases in yield or market returns to the grower. To justify investments in pears it is essential to increase market returns by improving the fruit size and quality.

Fruit size of pears is dependent on the sink strength of the fruit. Sink strength influences the amount of assimilates utilised by the fruit. Sink strength can be conceptualised as the product of two components, sink activity, which is a measure of the potential flux of assimilate accumulation, and sink size which is a measure of a potential volume for biomass gain (Patrick, 1988). Both of these

characteristics are subject to hormonal regulation. In addition to their effect on sink growth, plant growth regulators also exert a mobilising influence (Patrick, 1988).

Assimilates are allocated in a different order between plant organs. Wardlaw (1990), prioritises sink strength in the following order: seeds > fleshy fruit parts = shoot apices and leaves > cambium > roots > storage. The aim of the first experiment was to alter the sink size of secondary growth by two different severities of pruning cuts. Leaving the severe pruning cut with only half of the length of two-year-old-wood as a sink for secondary growth compared with the less severe pruning cut. By reducing the sink of secondary growth in the more severe pruning cut, the idea was that the fruits and the bourse shoots will utilise this extra available assimilates due to the reduction of the sink size for secondary growth. Furthermore the more severe pruning cut will cause an increase in plant growth regulators (Grocshowska *et al.*, 1984). As mentioned earlier plant growth regulators play an important role in sink strength.

The aim of the second experiment was to see how the diameter of the two-year-old-wood influenced the sink strength of the 2-year-old-unit. This will help to decide during dormant pruning if certain units are capable to size fruit sufficiently to meet the required market standards.

Materials and methods

Plant material: 'Packham's Triumph' trees on the farm Kromfontein were used. The farm is situated in the Koue Bokkeveld area (1794 Richardson chill units) of the Western Cape, South Africa. The area is characterised by a Mediterranean climate, with cold wet winters (1794 Richardson chill units) and warm dry summers. The 'Packham's Triumph' trees on BP2 rootstock, were planted in 1983 at a spacing of 4.5m x 1.75m in a North-South row orientation and are trained to a central leader system.

Treatments

Two-year-old spurred units were randomly selected in the winter of 2002. Units were headed back, during the last week of June, by pruning into the two-year-old wood.

Severity of pruning (Experiment 1)

The lengths of the units after pruning varied. Short bearing units (SBU's) and long bearing units (LBU's) were 28 cm and 56 cm long, respectively.

Diameter of two- year-old bearing units (Experiment 2)

The basal diameter of the bearing units was varied. The basal diameter of thin bearing units (thin BU's) and thick bearing units (thick BU's) were less than 8 mm and more than 14 mm, respectively. Both thin and thick BU's were headed back by pruning to a final length of 28 cm.

On all BU's three distally situated spurs with large developed terminal buds were left. All other spurs were removed by thinning cuts. At anthesis, 3 October 2002, two flowers per inflorescence were pollinated by hand using a glass stave. Viable pollen of the compatible pear cultivar Rosemarie was used. The rest of the flowers in the spur cluster were removed.

The BU's were randomly selected, with 20 repetitions for each treatment.

Data collected

The difference in spur quality between the BU's was measured by recording the weight difference for the sum of the three spurs between the BU's. Differences in flower quality were determined by counting the number of appendages (bract leaves, leaves and flowers) formed in the reproductive buds.

At harvest, 10 February 2003, the whole BU with it fruits were removed by pruning and brought to our laboratories. The following data were recorded. Fruit set per BU; fruit length and diameter; number of aborted and mature seeds per fruit; fresh and dry weight of bourse plus bourse shoot per BU; fresh and dry weight of fruit individually and fresh and dry weight of seeds per fruit. Dry weight was determined by drying the fresh material at 120 °C in a convection oven until there was no change in the mass (5 days).

Statistical analyses

Data were analysed by performing analyses of variance using the GLM (General Linear Models) Procedure in the SAS (Statistical Analysis System) program (SAS, 1990).

Results

For 'Packham's Triumph' primary growth on SBU's and thick BU's increased compared to LBU's and thin BU's (Table 1). In both cases the increase was due to an increase in fruit dry weight, the result of better fruit set and larger fruits (Table 1). The contribution of the bourse and bourse shoot to the dry weight accumulation of the primary growth is less than 12 % for the different types of bearing units. However, the 16.16 gm allocated to the bourse and bourse shoot on thick BU's is significantly more than the 2.76 g for thin BU's (Table 1).

The number of mature and aborted seed per fruit did not differ for SBU's and LBU's. Fruit on thick BU's contained 5.2 mature seeds, which is significantly fewer than the 7.8 for thick BU's (Table 2). Fresh weight of spurs was significantly more on thick BU's as well on LBU's compared to thin BU's and SBU's, but this difference was not reflected in the composition of the reproductive buds borne terminally on the spurs (Table 3).

Discussion

Fruit set

Increased fruit set on both SBU's and thick BU's as compared to LBU's and thin BU's, respectively, cannot be explained by differences in flower quality. The greater fresh weight of spurs on LBU's and thick BU's is not reflected in the number of appendages (flowers, leaves and bracts) in the mixed reproductive buds of 'Packham's Triumph' pears. The advantage of a better spur quality on LBU's does not compensate for the apparent positional advantage of spurs borne on SBU's in terms of fruit set. Since the increase in fruit set of SBU's over LBU's is only 20 % compared to the 70 % increase of thick BU's over thin BU's it appears that, spur quality is positively correlated with fruit set when positional effects are eliminated. Since number and dry weight of seed per fruit did not differ between SBU's and LBU's reasons other than those related to pollination and fertilisation should be considered for the increased fruit set on SBU's. Like wise the higher fruit set on thick

BU's despite a lower seed content implies that factors other than pollination and fertilisation were responsible for the increased set.

Pruning 'Packham's Triumph' at the interculation between one and two-year-old wood increases fruit set (Saunders *et al.*, 1991). They concluded that set was affected more negatively by basipetal transport of auxin produced by new developing shoots distal to the young fruitlets,- a concept first proposed by Bangerth (1989), than shoot:fruit competition for limited metabolites. Since the currant BU's were prepared by heading back into two-year-old wood, shoot growth distal to the fruitlets as a factor affecting set was thus eliminated.

Increase of 20 % in both fruit number and mean dry weight per fruit for SBU's compared to LBU's contribute in equal proportions to the increase in fruit dry weight for SBU's. However, when thick- and thin BU's was compared, increased fruit numbers on thick BU's were responsible for ca. 70 % of the increased fruit dry weight per BU. We conclude therefore that fruit set of 'Packham's Triumph' is affected more by BU diameter than BU length. With an increase in BU diameter the size of the xylem transport system increases more than that of the phloem. It may also be justified to conclude that fruit set is more dependent on xylem transported metabolites, in particular root produced hormones, than metabolites supplied by the phloem. This conclusion is supported by previous work. At bud swelling in spring cytokinin and gibberellin content of apple xylem sap was 4 and 3 times higher in pruned than non-pruned trees, respectively (Growchowska et al., 1984). Gibberellic acid sprayed on pear trees improves fruit set (Deckers and Schoofs, 2002). The cytokinin activity in seeds of fruits likely to drop is only 1/40 to 1/15 of that in fruit that persist (Fukui et al., 1985, cited by Bubán, 2000). We do not imply that carbohydrates are unimportant with respect to fruit set, it is however our view that the fruit set responses induced by the pruning treatments is hormone related.

Fruit size

Fruit sink strength = sink activity (dry mass increase/unit time) x sink size (fruit numbers) (Patrick, 1988). With increasing fruit numbers per tree (sink size) sink activity of individual fruit decreases with smaller fruit as a result. This is the basis for fruit thinning whereby fruit numbers per tree is reduced to gain in fruit size. The reduction in fruit size with increase in fruit numbers has in most cases been attributed to source limitation (Lakso, 1994; Wünsche and Lakso, 2000).

However, in a resent study by Marini (2003) it was shown that by reducing the number of fruiting shoots on peach trees, but keeping fruit numbers per tree constant it increased fruit size. We argue that the supply of root produced hormones to fruiting shoots is improved by reducing their numbers. This in turn improves sink activity of fruits and in spite of more fruit per fruiting shoot, fruits are larger.

The increase in fruit size on SBU's and thick BU's in spite of 20 % and 70 % more fruit per bearing unit as compared to LBU's and thin BU's respectively could be due to an improved supply of root produced hormones to the BU's. Sink activity of fruit is improved resulting in larger fruit. The source was not affected by the pruning treatments therefore improved sink: source relationship cannot explain the larger fruit. Palmer et al. (1997) found that leaf assimilation is stimulated by crop productivity (increase in sink size) and that leaf assimilation rate was curvilinear with crop load for 'Braeburn' apples, up to a maximum crop of 12 fruit m⁻² leaf area. Non-cropping trees leaf assimilation rate was at times 64 % lower rate than that of heavy cropping trees. With partial defoliation the photosynthetic rate of the remaining leaves was enhanced by 37 % compared to the control (Zhou and Quebedeaux, 2003). Currently the main argument for better fruit size due to fruit thinning is an improved photosynthetic supply after thinning. There was no alteration in the source-sink relationship by pruning, but the fruit size was improved. We argue that the partitioning of root-produced hormones to fewer sites, due to fruit thinning; must be strongly considered as the reason for the improved fruit size following thinning.

Literature cited

- Bangerth, F. 1989. Dominance among fruits/sinks and the search for a correlative signal. *Physiol. Plant.* **76:** 608-614.
- Bubán, T. 2000. The use of benzyladenine in orchard fruit growing: a mini review. *Pl. Gr. Regul.* **32:** 381-390.
- Deckers, T. and Schoofs, H. 2002. Improvement of fruit set on young pear trees cultivar 'Conference' with gibberellins. *Acta Hort*. **596(2)**: 735-744.
- Fukui, H., Imakawa, S. and Tamura, T. 1985. Relation between early drop of apple fruit, cytokinin and gibberellin. *J. Jap. Soc. Hort. Sci.* **54:** 287-292.

- Grochowska, M.J., Karaszewska, A., Jankowska, B., Maksymiuk, J. and Williams, M.W. 1984. Dormant pruning influence on auxin, gibberellin, and cytokinin levels in apple trees. *J. Amer. Soc. Hort. Sci.* **109(3):** 312-318.
- Lakso, A.N., 1994. Apple, pp 3-43 In: B. Schaffer and P.C. Andersen (eds.). CRC Handbook of environmental physiology of fruit crops. vol. 1. Temperate Crops. CRC press, USA.
- Marini, R.P. 2003. Peach fruit weight, yield, and crop value are affected by number of fruiting shoots per tree. *Hort. Sci.* **38(4):** 512-514.
- Palmer, J.W., Giuliani, R. and Adams, H.M. 1997. Effect of crop load on fruiting and leaf photosynthesis of 'Braeburn'/M.26 apple trees. *Tree Phys.* 17: 742-746.
- Patrick, J.W. 1988. Assimilate partitioning in relation to crop productivity. *Hort. Sci.* **23(1):** 33-40.
- Richardson, E.A., Schuyler, D.S. and Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. **9(4)**: 331-332.
- SAS Institute Inc., 1990. SAS/STAT User's guide, version 6. 4th ed. Vol.1 and 2, Cary, NC, USA.
- Saunders, R.C., Jacobs, G. and Strydom, D.K. 1991. Effect of fruit set and shoot growth of 'Packham's Triumph' pear trees. *Sci. Hort.* 47: 239-245.
- Wardlaw, I. F. 1990. The control of carbon partitioning in plants. *New Phytol.* 116: 341-381.
- Wünsche, J.N. and Lakso, A.N. 2000. The relationship between leaf area and light interception by spur and extension shoot leaves and apple orchard productivity. *Hort. Sci.* **35(7):** 1200-1206.
- Zhou, R. and Quebedeaux, B. 2003. Changes in photosynthesis and carbohydrate metabolism in mature apple leaves in response to whole plant source-sink manipulation. *J. Amer. Soc. Hort. Sci.* **128(1):** 113-119.

Tables

Table 1: Differences in dry mass allocated for primary growth, fruit set, average fruit dry weight and secondary growth for the different severity in pruning cuts and different basal diameter BU's for 'Packham's Triumph'.

	SBU's	LBU's	Pr>F	Thick BU's	Thin BU's	Pr>F
Primary growth (dm in g)						
Total (dm in g)	131.65 ^a	93.18 ^b	0.0194	140.1 ^b	58.12 a	< 0.0001
Fruit (dm in g)	124.30 a	85.20 ^b	0.0109	123.9 b	55.36 a	< 0.0001
Bourse and bourse shoots (dm in g)	7.35 a	7.98 ^a	0.7215	16.16 ^b	2.76 a	< 0.0001
Number of fruits	4.88 a	4.10 ^b	0.0454	4.53 b	2.65 a	0.0016
Average fruit dry weight (g)	25.7 a	20.32^{b}	0.0197	26.90 b	20.34 a	0.0091
Secondary growth (dm in g)	1.223 a	4.449 ^b	0.0236	5.041 ^b	1.992 ^a	0.0062

Table 2: The seed content of the set fruits of 'Packham's Triumph' with the different pruning severities and different basal diameter BU's

	SBU's	LBU's	Pr>F	Thin BU's	Thick BU's	Pr>F
Aborted seeds	3.417 a	3.066 a	0.4932	2.046 a	3.888 b	0.0020
Seeds	6.396 a	6.594 a	0.7514	7.821 ^a	5.249 ^b	0.0030

Table 3: Differences in fresh spur weight and flower quality in the dormant phase between the different pruning severities and different basal diameter BU's for 'Packham's Triumph'.

	SBU's	LBU's	Pr>F	Thin BU's	Thick BU's	Pr>F
Sum of 3 spurs in June (fm in g)	0.5044 a	0.6565 b	0.0210	0.4375 a	0.8272 b	0.0003
Flower quality						
Bract leaves	7.2 ^a	7.0 ^a	0.6938	7.4 ^a	7.8 a	0.2415
Flowers	7.6 ^a	7.4 ^a	0.7655	7.0 a	7.0 a	1.0000
True leaves and transition leaves	2.6 a	1.8 a	0.4468	1.4 a	1.6 a	0.8608

PAPER 3. THE EFFECT OF SCORING AND 6-BENZYLADENINE APPLICATION DURING FLOWER INDUCTION OR INITIATION PHASE ON RETURN BLOOM IN *PYRUS COMMUNIS* L.

Abstract

The influence of scoring and 6-benzyladenine application, during the flower induction phase was investigated. Pear trees, *Pyrus communis* L. 'Doyenne du Comice', 'Forelle' and 'Rosemarie' were used in the study conducted in the Western Cape, South Africa. The yield of 'Doyenne du Comice' increased with 38 % in scored trees compared to the control. The increase in yield was due to 50 % more fruits on the scored trees in comparison to the control trees. The increase in fruit number per tree was due to a higher percentage reproductive buds per tree and improved quality of these buds. For 'Rosemarie' scoring at the correct time resulted in a 40 % increase in reproductive buds. Scoring disrupts basipetal transport in the phloem, which results in the removal of apical dominance and an increase in root derived cytokinins. More meristems can respond to inductive conditions and the higher concentration of cytokinins during inductive conditions leads to improved flower quality. In 'Doyenne du Comice' trees, the combination of BA application and scoring, lead to bigger inflorescences, with more flowers.

Introduction

A prerequisite for a large crop is the presence of a sufficient number of reproductive buds at the start of the season, but the quality of the flower cluster is equally important.

Flower quality is measured in terms of their ability to set, retain and size fruit until harvest (Webster, 2002). To improve flower quality you need to increase the inflorescence size. Ferree *et al.* (2001) found a positive relationship between flower dry weight and fruit set and harvest fruit weight. Furthermore there is a positive relationship between number of leaves and flowers in the inflorescence and fruit set (Lauri and Terouanne, 1999). Early bud development of apple is characterised by an increase in the number of appendages i.e. bud scales,

transition leaves and true leaves in the bud (Bijhouwer, 1924). Flower quality can be improved by earlier initiation, which will lead to a longer period of differentiation, or by increasing the rate of differentiation. Flower initiation is the first visible change of flower formation in the meristem, which in pear is seen as the broadening of the apex. Directly after flower initiation, flower differentiation follows resulting in the formation of the different floral parts.

The aim of this study was to improve the inductive conditions for initiation and thereby increasing the number of reproductive buds initiated and also enhancing the process of initiation, which will result in better quality of buds.

Two strategies were evaluated, viz. scoring and applying exogenous cytokinin (6-benzyladenine, BA). The thought being that by scoring the tree at the start of flower initiation, the basipolar transport of auxin will be disrupted, which will lead to an increase in root-derived cytokinin (Li *et al.*, 1995). It is well known that foliar thinning sprays of BA cause return bloom to increase the following season in apple cultivars (Mclaughlin and Greene, 1984). BA sprayed trees have more flowers within an inflorescence compared to the unsprayed trees (Bubán, 2000).

This root-derived cytokinin, as well as that applied exogenously should stimulate cell division in the developing reproductive bud and thereby raising the metabolic activity of the bud. Furthermore the cytokinin can release meristems from apical dominance and therefore allow them to react to inductive conditions and becoming reproductive (Bangerth *et al.*, 2000).

Materials and methods

Experiment 1:

Plant material

Three pear cultivars, i.e. Rosemarie, Forelle and Doyenne du Comice were used in this trial. 'Forelle' and 'Rosemarie' pear trees were from Welgevallen Experimental farm situated in the Stellenbosch area (500 Richardson chill units) of the Western Cape, South Africa (34°55'S; 19°02'E). While the 'Doyenne du Comice' pear trees were from a commercial orchard at Langrivier in the Koue Bokkeveld region (1794 Richardson chill units) of the Western Cape. The Western Cape is characterised by a Mediterranean climate with cold, wet winters and warm, dry summers. The Koue Bokkeveld region is a cooler region than the

Stellenbosch region. 'Forelle' trees planted on a Quince rootstock with a 'Beurré Hardy' interstock were planted in 1998 at a spacing of 3.8m x 1.25m in a North-South row orientation. 'Kieffer' trees is the cross pollinator at a density of 10 %. 'Rosemarie' trees were planted in 1992 at a spacing of 4.5m x 2.0m with the same row orientation as the 'Forelle'. Both of these cultivars are trained to a 3-wire-trellis central leader system. 'Packham's Triumph' and 'Early Bon Chretien' are the cross pollinators at a density of 6.6 % and 3.3 %, respectively. 'Doyenne du Comice' on BP3 rootstock was planted in 1990, at a spacing of 4m x 1.5m with East-West row orientation. 'Packham's Triumph' trees are used as cross pollinator at a density of one branch per tree.

Methodology:

The trees were scored \pm 20 cm above the graft union by making use of a pair of citrus scoring pliers (Cape Agricultural Product Pty. Ltd.). The three wheels of the scoring pliers produce a narrow cut through the phloem and decrease the risk of cutting too deep in the cambium layer. The scoring is effective in inhibiting phloem transport for about two weeks. The trail was a randomised design with two treatments, (a) control and (b) scored treatment. A single tree was used as a replicate with 10 replications. The different cultivars were scored on the following dates:

- 'Rosemarie' scored 29 November 2001 (79 days after full bloom, d.a.f.b.)
- 'Doyenne du Comice' scored 30 November 2001 (56 d.a.f.b.) and 18 November 2002 (57 d.a.f.b.) the same trees were scored again 10 cm above the position used in the previous season.
- 'Forelle' scored 12 December 2001 (88 d.a.f.b.)

Experiment 2:

Plant material:

'Doyenne du Comice' trees were used at Kromfontein and Nooitgedacht two commercial farms situated in the Koue Bokkeveld area of the Western Cape, South Africa (33°12'S; 19°19'E). A Mediterranean climate with cold, wet winters and warm, dry summers characterise the area. 'Doyenne du Comice' trees on BP3 rootstock were planted at Kromfontein, in 1992 at a spacing of 4.0m x

1.5m with a North-South row orientation. 'Doyenne du Comice' trees at Nooitgedacht, were planted on BP1 rootstock in 1995 at a spacing of 4m x 1.25m with a North-South row orientation. On both of the sites the trees were trained to a three-wire-trellis central leader system.

Methodology and experimental design:

6-Benzyladenine (BA) (VBC 30001; Valent BioSciences Corporation) was applied at 150 ml⁻¹per 100 L, at a rate of 1.5 L per tree by means of a hand-held, air blast, high-pressure spray. The product contains a surfactant. The temperature in the orchard was determined at the start and the end of the BA application. No spraying was done if the orchard temperature was above 27°C. A scoring treatment (as described in Exp. 1), with or without BA application was also included and treatments are summarised in Table 1. The treatments were arranged in a randomised complete block design, with ten treatments, and ten single tree replicates with two buffer trees between sprayed treatments.

Experiment 3:

The same 'Rosemarie' or chard as in experiment 1 was used to evaluate the effect of time of scoring. A randomised block design was used with five treatments (Table 1) and ten single tree replicates. The scoring was done using the same method as described in experiment 1.

Data collected

Experiment 1:

The total yield per tree was recorded at harvest in 2003. On a sample of 25 fruit per tree the following was determined on each fruit; (1) fruit length, (2) fruit diameter, (3) fruit mass and (4) the seed content.

Fifteen, one-year-old reproductive units (spurs) were tagged at random in spring 2001, on every replicate of each cultivar. These spurs differed with some bearing fruit, varying in number from one to three or those where no fruit had set. On some units one or two well-developed bourse shoots formed, while others formed only bourse buds. The following data were recorded from these tagged units to determine differences in bourse-over-bourse bearing tendency between the treatments: (1) The number of fruit harvested in 2002 and 2003, and the sizes and

seed content of these fruit, (2) the vegetative growth (bourse shoot) was measured and number of leaves counted and (3) the number of reproductive buds initiated terminally on the bourse shoots was counted. The number of reproductive buds per potential bearing site (reproductive and vegetative buds) on three scaffold branches was recorded for the 'Doyenne du Comice' in bloom 2003 (return bloom).

Experiment 2:

Two terminal buds per tree, were collected weekly at random, from 5 November 2002 to 2 December 2002. These buds were dissected to monitor the bud development stage. A sample of 25 fruit was collected; at harvest in 2003, on each replicate and each of the fruit was analysed for: (1) abnormal shapes, (2) mass and (3) the incidence and intensity of fruit russeting, which was determined by the South African fruit industries pear colour charts, no. P 8 and P 9. Where score one represent a small incidence of russeting and eight severe russeting. The number of reproductive buds per potential bearing site (reproductive and vegetative buds) on three scaffold branches was recorded in bloom 2003 (return bloom).

Experiment 3:

Random samples of two terminal spur buds were collected weekly per tree, on the different scoring dates, and these buds were dissected to monitor the bud development stage. The number of reproductive buds per potential bearing site (reproductive and vegetative buds) on three scaffold branches was recorded in bloom 2003 (return bloom).

Statistical analysis:

The data were analysed by the PROC GLM procedure in the SAS program (SAS, 1990).

Results

Experiment 1:

The scoring, 57 d.a.f.b., during the estimated flower initiation phase, resulted in a significant increase in the yield and the yield-efficiency (yield in kg per cm stem circumference) of 'Doyenne du Comice' (Table 2). In the case of 'Rosemarie' the increase in yield and yield-efficiency was not significant, but the

same tendency as for 'Doyenne du Comice' was observed (Table 3). For the 'Forelle' there were no significant differences or tendency for an improvement in yield between the two treatments (Table 4).

For 'Doyenne du Comice' and 'Rosemarie', the higher yield following the scoring treatment was, due to a larger number of fruit harvested and not an increase in fruit size (Table 2 and 3).

In the 'Doyenne du Comice' trees of Langrivier, percentage reproductive buds (return bloom in spring 2003) was increased significantly by the scoring treatment, even though the yield of the scored trees was 40% higher during the previous season (harvest 2003) (Table 2).

In all three cultivars the number of reproductive units (spurs) that resulted in bourse-over-bourse bearing was increased by scoring, but not significantly (Tables 5 to 7). This was true for situations where a bearing bourse shoot was developed from a bearing unit, as well as a situation where the bearing unit gave a bourse shoot which had a terminal reproductive bud which flowered, but did not set (bourse-over bourse flowering).

Experiment 2:

The two sites responded differently towards the treatments. At Nooitgedacht there was a significant difference in percentage reproductive buds between treatments, with the earlier scored and combination of sprayed and scored treatments resulting in the largest number of reproductive buds. All three treatments; spraying BA, scoring and the combination of scoring and spraying BA, resulted in a significant larger inflorescence (number of flowers per inflorescence) than the control. The combination of the two treatments resulted in the largest inflorescence (Table 8). Of the three application dates, the last date gave the largest inflorescence (Table 8). At Kromfontein, the treatments had no effect on the percentage reproductive buds formed or the inflorescence size. There was more variation in percentage reproductive buds between the trees at Kromfontein compared to Nooitgedacht, which can be seen in the larger least significance differences for Kromfontein compared to Nooitgedacht (Table 8).

The BA application did not cause the fruit to be malformed or russeted (Table 9).

Experiment 3:

The scoring treatments done on 'Rosemarie' formed 30 % more reproductive buds than the control (Table 10). There was a linear decrease in the percentage reproductive buds from the earlier to the later scoring treatments (Table 10). The decrease in the percentage reproductive buds over time resulted in the scoring treatment on the 4th December 2002 not differing significantly from the control (Table 10).

Discussion

In experiment 1 the scored 'Doyenne du Comice' and 'Rosemarie' trees, produce a higher yield than the control due to more fruit (Table 2 and 3). The higher number of fruit can be attributed to two factors. Firstly there could have been a higher percentage of reproductive buds (more flowers clusters). In experiment 2 and 3 and in the return bloom of the 'Doyenne du Comice' in experiment 1 is it clear that scoring can increase the percentage reproductive buds (Table 8, 9 and 2). It is also clear that the right timing to score the tree is critical. Experiment 3 showed that the earlier scoring treatments for the 'Rosemarie' resulted in the highest percentage reproductive buds with a decline in percentage reproductive buds when the scoring was done later (Table 10). A possible reason is that with earlier removal of apical dominance, more meristems can react to favourable conditions for initiation. Thus the scored 'Doyenne du Comice' trees of experiment 1 formed 34 % more reproductive buds than the control. What makes this increase in reproductive buds more extraordinary is that the scored trees, yielded 40 % more fruit the previous season compared to the control (Table 2). The reason for the higher percentage of reproductive buds could be by disrupting the basipetal auxin signal by scoring, apical dominance was removed (Noël, 1970). Thus more meristems were released from apical dominance and could respond to inductive conditions and become reproductive.

Secondly there could have been an improvement in the flower quality, which will lead to flowers that had a better potential to set and retain it fruits. Flower quality is generally defined in terms of fertility, i.e. the capacity of flowers to respond to fruit setting stimuli. Good quality flowers are those in which the stigmas remain receptive and the embryo sac stays viable for a long period of time, thereby increasing the chance for successful pollination (Williams, 1965). A good quality

cluster has many flowers with short stalks, and a high tendency to set fruit. Flower pedicle length and dry weight as well as flower dry weight are positively related to harvest fruit weight and fruit set (Ferree *et al.*, 2001). Lauri and Térouanne (1999) found a positive relation between the number of flowers and fruit set. Flower quality is associated with the time in the season that the flower formed, strong blossoms are old, i.e. they were formed early in the previous season, while weak blossoms are young, i.e. formed late in the season. In experiment 2 the tendency was there that scoring could improve flower number in an inflorescence (Table 8). Again timing seems to play a critical role in obtaining the necessary results, as the response at the Kromfontein site was not as good as at Nooitgedacht, where the bud development was not as advanced at the time of scoring (Table 8).

Due to the scoring during flower initiation, the developing bud may receive a higher concentration of cytokinin. Cytokinins are known to stimulate cell division and thereby enhancing metabolic activity. This implies that the sink strength of the developing bud will be enhanced, which will lead to an increase in auxin export and will ensure good vascular connection. The overall effect will be that flower differentiation will occur earlier and that the rate of flower differentiation will be enhanced. Thus, ultimately leading to more advanced reproductive buds. The synthetic cytokinin applied in experiment 2 did not support this argument, but the results of both the sites for experiment 2 compared to Langrivier (exp.1) was disappointing, because the scoring on it's own did not lead to an increase in percentage reproductive buds.

In experiment 1 the tagged units of the scored trees flowered more bourse-over-bourse (bearing bourse over bourse + flower bourse over bourse) than the control in all three cultivars, but not significantly so. The number of these bourse shoot flowers actually setting fruit was also higher for the scored treatment in 'Doyenne du Comice' and 'Forelle' compared to the control. These results support the argument that scoring causes flowers of superior quality. It seems that spraying synthetic cytokinin on it own did not significantly increase the number of flowers in an inflorescence, but in combination with the scoring treatment it enhanced inflorescence quality, because on both sites in experiment 2 we found that the combination of spraying and scoring on 2 December 2002 resulted in the highest number of flowers in the inflorescence.

In experiment 1 the effect of the scoring treatment was not as significant in the 'Rosemarie' and 'Forelle' as in the 'Doyenne du Comice'. One possible explanation for this is that flower initiation was earlier in the warmer climate of Stellenbosch than Koue Bokkeveld and therefore the timing of scoring the tree was to late in 2001. The warmer climate in Stellenbosch leads to earlier shoot growth cessation and shoot growth cessation is correlated with flower initiation (Paper I; Tromp, 2000). Thus flower initiation would be earlier in Stellenbosch than in Koue Bokkeveld. The scoring was done the 29 and the 28 of November 2001 for the 'Rosemarie' and the 'Doyenne du Comice', respectively.

For the 'Forelle' in Experiment 1 there was no difference between the two treatments. Reasons for this could be that the timing of the scoring was too late. The 'Forelle' trees were scored 12 December 2001, which was two weeks later than the 'Rosemarie' (30 November 2001), while it was clear from Paper I that 'Forelle's' flower initiation was two weeks earlier than in 'Rosemarie'. Furthermore the total yield of this orchard was very low, indicating other possible reasons for the low number of fruits.

To conclude it is clear that scoring pear trees during the induction phase or at the start of flower initiation is highly beneficial for the crop of the tree, but the timing of the scoring treatment is extremely important. It is highly likely that cytokinins play a role in the effect of the scoring, although spraying a synthetic cytokinin did not have the same positive effect as scoring.

Literature cited

- Bangerth, F., Li, C. and Gruber, J. 2000. Mutual interaction of auxin and cytokinins in regulating correlative dominance. *Pl. Gr. Regul.* **32:** 205-217.
- Bijhouwer, J. 1924. Die periodisiteit van de knopontwikkeling bij den appel. *Meded. Landb. Hoogesch. Wageningen.* 27: 1-64.
- Bubán, T. 2000. The use of benzyladenine in orchard fruit growing: a mini review. *Pl. Gr. Regul.* 32: 381-390.
- Ferree, D.C., Bishop, B.L., Schupp, J.R., Tustin, D.S. and Cashmore, W.M. 2001. Influence of flower type, position in the cluster and spur characteristics on fruit set and growth of apple cultivars. *J. Hort. Sci. Biotech* **76(1):** 1-8.

- Lauri, P.E. and Terouanne, E 1999. Effect of inflorescence removal on the fruit set of the remaining inflorescences and development of the laterals on one year old apple (*Malus domestica* Borkh.) branches. *J. Hort. Sci. Biotech.* **74(1):** 110-117.
- Li, C.J., Guevara, E., Herrera, J. and Bangerth, F. 1995. Effect of the apex excision and replacement by 1-naphtylacetic acid on cytokinin concentration and apical dominance in pea plants. *Physiol. Plant.* **94:** 465-469.
- Mclaughlin, J.M. and Greene, D.W. 1984. Effects of benzyladenine and daminozide on fruit set, fruit quality, vegetative growth, flower initiation, and flower quality of 'Golden Delicuos' apple. *J. Amer. Soc. Hort. Sci.* **109(1):** 34-39.
- Noël, A.R.A. 1970. The girdled tree. Bot. Rev. 36: 162-195.
- SAS Institute Inc., 1990. SAS/STAT User's Guide, Version 6. 4th ed. Vol. 1 and 2, Cary, NC, USA.
- Richardson, E.A., Schuyler, D.S. and Walker, D.R. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. **9(4):** 331-332.
- Tromp, J. 2000. Flower-bud formation in pome fruit as affected by fruit thinning. *Pl. Gr. Regul.* **31:** 274-282.
- Webster, A.J. 2002. Factors influencing the flower, fruit set and fruit growth of European pears. *Acta Hort.* **596(2)**: 699-709.
- Williams, R.R. 1965. The effect of summer nitrogen application on the quality of apple blossom. *J. Hort. Sci.* **40:** 31-41.

Tables

Table 1: The different treatments used in Experiment 2 and 3. Scoring was done \pm 20 cm above the graft union by making use of a pair of citrus scoring pliers . Benzyladenine (BA) was applied at 150 ml⁻¹per 100L water.

Experiment 2 ('Doyenne du Comice')	Experiment 3 ('Rosemarie')
Trea	utments
1. Control	1. Control
2. Scored tree on 11 Nov. (48 d.a.f.b.)	2. Scored tree on 13 Nov. (63 d.a.f.b.)
3. Scored and BA applied on 11 Nov.	3. Scored tree on 20 Nov. (70 d.a.f.b.)
4. Scored tree on 18 Nov. (55 d.a.f.b.)	4. Scored tree on 27 Nov. (77 d.a.f.b.)
5. BA applied on 18 Nov.	5. Scored tree on 4 Dec. (84 d.a.f.b.)
6. Scored and BA applied on 18 Nov.	
7. Scored tree on 2 Dec. (69 d.a.f.b.)	
8. BA applied on 2 Dec.	
9. Scored and BA applied on 2 Dec.	

Table 2: The effect of scoring, 57 d.a.f.b. in December 2001, on yield, yield-efficiency, average fruit weight and average fruit number for the harvest of 2003. The return bloom was determined at bloom 2003, (% reproductive buds per potential bearing sites) after scoring 58 d.a.f.b. in 2002. The same 'Doyenne du Comice' trees of Langrivier, Koue Bokkeveld were used over two seasons.

	Control	Scored	Pr>F
Yield (kg fruit per tree)	26.57 a	36.71 b	0.0384
Efficiency (kg fruit per cm stem circumference)	0.554 a	0.765 b	0.0259
Average fruit weight (g)	184.80 a	169.81 a	0.1663
Estimated average fruit number	147.10 a	220.06 ^b	0.0131
Return bloom	35.19 a	47.27 b	0.0009

Table 3: The effect of scoring 79 d.a.f.b. in November 2001 on yield, yield-efficiency, average fruit weight and average fruit number for the harvest of 2003 on 'Rosemarie', Welgevallen, Stellenbosch.

	Control	Scored	Pr>F
Yield (kg per tree)	32.78 a	35.80 a	0.5284
Efficiency (kg per cm stem circumference)	0.8017 a	0.9063 a	0.3442
Average fruit weight	103.35 a	98.39 a	0.4548
Estimated average fruit number	322.87 a	371.10 a	0.3718

Table 4: The effect of scoring 88 d.a.f.b. in December 2001 on yield, yield-efficiency, average fruit weight and average fruit number for the harvest of 2003 on 'Forelle', Welgevallen, Stellenbosch.

	Control	Scored	Pr>F
Yield (kg per tree)	6.64 ^a	6.15 a	0.8064
Efficiency (kg per cm stem circumference)	0.269 a	0.241 a	0.7119
Average fruit weight	171.50 a	175.65 a	0.5440
Estimated average fruit number	40.13 a	35.11 a	0.6756

Table 5: Proportion (%) of the difference in year-to-year, from spring 2001 to harvest 2003, transitions between treatments, for 15 tagged units per 'Doyenne du Comice' tree, Langrivier, Koue Bokkeveld.

	Control	Scored	Pr>F
Bourse-over-bourse bearing	2.10 a	7.0 a	0.2340
Bourse-over-bourse flowering	11.70 a	9.10 a	0.5514
Alternating (between veg. and rep.)	51.90 a	54.50 a	0.3500
Latent (remain dormant)	34.20 a	29.30 a	0.4298

Table 6: Proportion (%) of the difference in year-to-year, from spring 2001 to harvest 2003, transitions between treatments, for 15 tagged units on each 'Forelle', Welgevallen, Stellenbosch.

	Control	Scored	Pr > F
Bourse-over-bourse bearing	0 a	0.7 ^a	0.3574
Bourse-over-bourse flower	26.88 a	30.30 a	0.6888
Alternating (between veg. and rep.)	73.11 ^a	69.9 a	0.6866

Table 7: Proportion (%) of the difference in year-to-year, from spring 2001 to harvest 2003, transitions between treatments, for 15 tagged units on each 'Rosemarie', Welgevallen, Stellenbosch

	Control	Scored	Pr>F
Bourse-over-bourse bearing	35.95 a	31.40 a	0.5467
Bourse-over-bourse flower	35.60 a	43.30 a	0.2182
Alternating (between veg. and rep.)	28.65 a	25.10 a	0.6948

Table 8: Percentage reproductive buds of potential bearing sites and flower number per infloresence for 'Doyenne du Comice' at Kromfontein and Nooitgedacht.

Volume in brackets are the percentage of dissected buds that were reproductive. Footnote 1 representing Kromfontein and 2 Nooitgedacht.

Experiment 2	df	Kror	nfontein	Nooitgedacht		
Treatments		% Rep.	Avg.	% Rep.	Avg.	
			number of		number of	
			flowers		flowers	
Control		38.87 ^a	9.37 ab	43.58 ab	8.20 ^d	
Scored: 11 Nov (15 % ₁ , 0 % ₂)		38.91 ^a	9.47 ab	47.41 ab	8.64 cd	
BA applied & scored: 11 Nov		43.80 ^a	9.01 ^b	53.41 ^a	8.97 abc	
Scored: 18 Nov (35 % ₁ , 15% ₂)		39.20 ^a	9.33 ab	44.29 ab	9.12 ab	
BA applied: 18 Nov		41.40 ^a	8.84 ^b	37.81 bc	8.58 cd	
BA applied & scored: 18 Nov		42.23 ^a	9.45 ab	45.34 ab	9.25 ^a	
Scored: 2 Dec (80% ₁ , 40% ₂)		48.58 ^a	9.40 ab	32.97 ^c	8.67 bcd	
BA applied: 2 Dec		44.35 a	9.43 ab	38.94 bc	8.51 cd	
BA applied & scored: 2 Dec		43.68 ^a	10.08 ^a	44.10 ab	9.34 ^a	
Pr>F		0.6345	0.5148	0.013	< 0.0001	
LSD		10.639	0.9605	10.142	0.478	
Sig. Level		Washington .				
Contrasts						
Control vs. trt.	1	0.4286	0.9536	0.8483	0.0003	
Control vs. scored	1	0.4053	0.9644	0.439	0.0034	
Control vs. BA applied	1	0.6076	0.5661	0.3771	0.0987	
Control vs. BA applied & scored	1	0.4581	0.6162	0.3503	< 0.0001	
Scored vs. BA applied & scored	1	0.9032	0.5206	0.0538	0.0061	

Table 9: The results of analysed sample of 2003 'Doyenne du Comice' harvest, for the two sites, Kromfontein and Nooitgedacht.

Experiment 2	admonday.	Kromfon	tein	N	Nooitgedag	ght
Treatments	Avg.	Russet	malformed	Avg.	Russet	malformed
	mass.			mass.		
Control	270.0 a	2.75 a	0.0 a	199.5 ^d	2.20 ^a	0.025 ab
Scored: 11 Nov.	266.4 a	2.55 a	0.11 a	243.8 a	2.41 a	0.021^{ab}
BA applied & scored: 11 Nov.	269.8 a	2.73 ^a	0.0^{a}	227.0 abc	2.38 a	0.052^{ab}
Scored: 18 Nov.	247.2 ^a	2.55 a	0.016 ^a	231.0 abc	2.27 ^a	0.08 b
BA applied: 18 Nov.	244.5 ^a	2.46 ^a	0.0^{a}	220.7 abcd	2.29 a	$0.026\ ^{ab}$
BA applied & scored: 18 Nov.	246.0 a	2.63 ^a	0.0 a	231.4 abc	2.43 ^a	0.087^{ab}
Scored: 2 Dec.	266.4 ^a	2.54 ^a	0.136 a	239.8 ab	2.21 ^a	0.012 ^b
BA applied: 2 Dec.	245.1 ^a	2.81 ^a	0.0 a	209.3 ^{cd}	2.28 a	0.022 ab
BA applied & scored: 2 Dec.	266.5 ^a	2.56 a	0.0^{a}	214.1 ^{cd}	2.15 ^a	0.12 a
Pr>F	0.5811	0.6078	0.5763	0.0283	0.681	0.4309
LSD	34.734	0.399	0.1634	9.782	0.4513	0.1075

Table 10: Percentage reproductive buds of total potential bearing sites in bloom 2003 for the different scoring treatments done in 2002

Treatments % Reproductive buds	df	Control 39.19 °	Scored 13 Nov 52.98 ab	Scored 20 Nov 55.89 ^a	Scored 27 Nov 50.50 ab	Scored 4 Dec 46.06 bc	Pr>F								
								Sig. Level							
								Control vs trt.	1						0.0004
Treat * Linear	1						0.0422								
Treat * Quadratic	1						0.1945								

General discussion

Reproductive bud development is a major factor determining yield. For improvement in yield, the number of reproductive buds can be increased by manipulating the flower induction or by improving flower quality by creating favourable conditions during flower initiation and differentiation. Therefore, a good knowledge of reproductive bud development is essential.

The bourse shoot was initiated after all the flowers were formed at the end of January. This implies that in the reproductive bud hierarchy, the bourse shoot followed after flower formation. Before and during dormancy the progression of the bourse shoot was slow with the progression mainly in the formation of preformed leaves. After dormancy the preformed leaves enlarged rapidly and some new-formed leaves were formed. Cultivars with a high tendency to bear bourse-over-bourse, formed more preformed as well as new-formed leaves compared to cultivars with low tendency for bourse-over-bourse bearing. Leaves are important for the developing flower as they act as a source of assimilates and hormones. Active leaves ensure that promotive substances produced elsewhere in the plant reach the developing bud.

Increased bearing unit (BU) diameter as well as a decrease in BU length for 'Packhan's Triumph' lead to higher fruit set compared to long BU's and thin BU's. The increase in fruit set cannot be explained by differences in flower quality. The advantage of a better spur quality on long bearing units (LBU's) does not compensate for the apparent positional advantage of spurs borne on short bearing units (SBU's) in terms of fruit set. Since the increase in fruit set of SBU's over LBU's is only 20 % compared to the 70 % increase of thick BU's over thin BU's it appears that, spur quality is positively correlated with fruit set when positional effects are eliminated. Since number and dry weight of seed per fruit did not differ between SBU's and LBU's reasons other than those related to pollination and fertilisation should be considered for the increased fruit set on SBU's. Like wise the higher fruit set on thick BU's despite a lower seed content implies that factors other than pollination and fertilisation were responsible for the increased set.

Increase of 20 % in both fruit number and mean dry weight per fruit for SBU's compared to LBU's contributed in equal proportions to the increase in fruit dry weight for SBU's. However, when thick and thin BU's were compared, increased fruit numbers on thick BU's were responsible for ca. 70 % of the

increased fruit dry weight per BU. It is therefore concluded that fruit set of 'Packham's Triumph' is affected more by BU diameter than BU length. With an increase in BU diameter the size of the xylem transport system increases more than that of the phloem. It may also be justified to conclude that fruit set is more dependent on xylem transported metabolites, in particular root produced hormones, than metabolites supplied by the phloem.

The increase in fruit size on SBU's and thick BU's in spite of 20 % and 70 % more fruit per bearing unit as compared to LBU's and thin BU's respectively could be due to an improved supply of root produced hormones to the BU's. Sink activity of fruit is improved resulting in larger fruit. The source was not affected by the pruning treatments therefore improved sink:source relationship cannot explain the larger fruit. Currently the main argument for better fruit size due to fruit thinning is an improved photosynthetic supply after thinning. There was no alteration in the source sink relationship by pruning, but the fruit size was improved. We argue that the partitioning of root-produced hormones to fewer sites, due to fruit thinning; must be strongly considered as the reason for the improved fruit size following thinning. This theory should be evaluated further by repeating these pruning trials on other cultivars and also by manipulating source size by defoliation.

Scoring 'Doyenne du Comice' trees during the flower induction phase resulted in a higher yield due to higher fruit numbers compared to control. The higher number of fruit can be attributed to two factors. Firstly there were more active sites on the scored trees, which lead to a higher percentage of reproductive buds. This was also seen in an increase in return bloom in scored 'Rosemarie' trees, but the timing of scoring is critical. Earlier scoring treatments for the 'Rosemarie' resulted in the highest percentage reproductive buds with a decline in percentage reproductive buds when the scoring was postponed. The reason for the higher percentage of reproductive buds could be by disrupting the basipetal auxin signal by scoring, apical dominance was removed. Thus more meristems could respond to inductive conditions and become reproductive. When apical dominance was removed earlier, more meristems reacted to favourable conditions for initiation.

Secondly there could have been an improvement in the flower quality, which will lead to flowers that are able to set and retain it fruits. Flower quality is generally defined in terms of fertility, i.e. the capacity of flowers to respond to fruit setting stimuli. A good quality cluster has many flowers with short stalks, and

a high tendency to set fruit. Flower quality is associated with the time in the season that the flower formed, strong blossoms forming early, while weak blossoms are young, i.e. formed late. The tendency was there that scoring improved the flower number per inflorescence. Due to scoring the tree, during flower initiation, the developing bud received a higher concentration of cytokinin. Cytokinin enhances the sink strength of the developing bud. The overall effect was that flower differentiation occurred earlier and that the rate of flower differentiation was enhanced. This resulted in high quality reproductive buds.

It is clear that scoring pear trees during the induction phase or at the start of flower initiation is highly beneficial for the crop of the tree, but the timing of the scoring treatment is extremely important. It is highly likely that cytokinins play a role in the effect of the scoring, although spraying a synthetic cytokinin did not have the same positive effect as scoring.