Studies of apple bud dormancy and branching under conditions of inadequate winter chilling

By

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Declaration

I, the undersigned, herby declare that the work contained in this thesis is my own original work and has not been previously, in its entirety or part, been submitted at any university for a degree.

Summary

In order to study the dormancy of apple buds in conditions of inadequate chilling a number of trails were done during 2000 and 2001.

Year-old, unbranched shoots of 'Royal Gala', 'Braeburn', 'Cripps' Pink' and 'Granny Smith' apple were harvested randomly from bearing commercial orchards in the Koue Bokkeveld [33°S, 945m, ca.1300 Utah model chill units (CU)] and Elgin (34°S, 305m, ca.750CU) regions of the Western Cape, South Africa, respectively. Shoots were chilled at 5-7°C. Two replicate bundles were removed from the cold room, prepared and forced at 25°C with continuous illumination until budburst had occurred on at least 25% of the shoots per bundle. The change in the rate of budburst over time was calculated for each orchard and to this response; either a linear or a quadratic function was fitted. Poorly correlated variables were selected that best describe these functions. Using these variables, the orchards were separated into cluster groupings that represented a dormancy pattern. The first split separated the lower chilling requirement cultivars from the higher cultivars. The second and third split separated the orchards according to area differences. The clusters representing the warmer area orchards initially entered deeper into dormancy before exiting. The clusters for the colder area immediately had an increased budburst rate. This data confirm that the chilling requirement includes a period of dormancy induction. An important genotype and environment interaction, other than cold unit accumulation, was observed that could be responsible for terminating bud dormancy.

Terminal apple buds from 'Royal Gala' Braeburn', 'Cripps' Pink' and 'Granny Smith' apples were cut from orchards in the Koue Bokkeveld and Elgin regions of the Western Cape, South Africa. Buds were harvested every two weeks during the dormant period. The buds were cut in half and leaf scales removed before the water potential were measured. Fresh and dry weights of the buds were also determined. The data presented confirms the changes in availability of free water in dormant buds and that it could be measured in this way. A definite influence of temperature was illustrated. The water potential from buds in a cold production area (Koue Bokkeveld) behaved more "normally" – water is in a bound form during most of the winter and change to an available form later in winter - whereas buds from a warmer production area did not change much in water potential or content.

In the trial, two-year-old proleptic-branched shoots, ca. 500mm long, were selected from a 'Royal Gala' orchard in the Koue Bokkeveld region in the Western Cape, South Africa. During the dormancy period of 2000, shoots received two cold

treatments; chilling in a cold room at 5-7°C and the natural chilling received in the field. In 2001, the trail was repeated, but only with the field chilling. The shoots received five dormant pruning treatments: control (not pruned), pruning back to the fourth lateral (heading) before or after chilling; and removal of the 2nd and 3rd laterals (thinning) before or after chilling. After pruning and chilling treatments, the shoots were removed from the orchard or cold room every two weeks and forced in a growth chamber. The rate of bud burst (1/days to 50% bud burst) was calculated for the terminal buds of the lateral shoots. Laterals were categorisation according to position: the terminal extension shoot, the 4th lateral, and all other laterals were pooled. Removing distal tissue by pruning (heading more than thinning) promoted bud burst on laterals. Pruning before chilling was more effective than after chilling. The correlative phenomena that inhibit bud burst on proximal shoots within two-year-old branches were manipulated by pruning.

The branching response of one-year-old unbranched shoots, 0.5m long, from 'Royal Gala' and 'Cripps' Pink' apple and 'Rosemary' pear were studied after physical manipulation treatments. Shoots for treatment a to d were re-orientated from either a horizontal or vertical position or left in the original position as control, treatment e to h involved the same re-orientation of shoots and were headed. The amount of growth (in mm) from each node was recorded as well as the position from the terminal bud. The 'Cripps' Pink' had a definite shift in the acrotonic branching pattern (for headed and unheaded), towards a more basitonic response. The reduced effect on 'Royal Gala' and 'Rosemary' suggest a difference in genotype response to the treatments as well as time of treatment.

Opsoming

Ter wille van die navorsing oor die invloed van gebrekige koue op dormansie van apple knoppe en die gepaardgaande probleme is 'n reeks proewe gedoen gedurende 2000 en 2001.

Jaar oue onvertakte lote van 'Royal Gala', 'Braeburn', 'Cripps' Pink' en 'Granny Smith' appels is ewekansig geoes vanaf komersieële boorde in die Koue Bokkeveld [33°S, 945m, ca.1300 Utah koue eenhede (CU)] en Elgin (34°S, 305m, ca.750CU) omgewings van die Wes Kaap , Suid Afrika. Die lote is daarna verkoel gehou by 5-7°C. Lote is elke twee weke vanuit die koue kamer geneem en geforseer met 25°C en deurlopend belig. Die aantal knoppe wat groenpunt bereik het is genoteer totdat 25% van die lote begin bot. Die verandering oor tyd vir elke boord is bereken en 'n liniëre of kwadratiese funksie is daarop gepas. Swak gekorreleerde waardes is gekies wat die funksies die beste beskryf. D.m.v hierdie die waardes is die boorde in groepe ingedeel wat 'n dormansie patroon verteenwoordig. Na die eerste vedeeling is die hoë en lae koue behoefte kultivars geskei. In opvolgende verdelings is die boorde verder in die twee areas geskei met elk 'n spesifieke dormansie patroon. Die groepe wat die warmer area se boorde bevat het aanvanklik dieper in dormansie in beweeg voor dit 'n styging in groei potensiaal getoon het. Die groepe vanaf die kouer produksie area het onmiddelik 'n verhooging in bot tempo getoon. Die data bevestig dat 'n koue behoefte 'n periode van dormansie induksie insluit. 'n Belangrike kultivar–omgewing-interaksie, ten spyte van koue eenhede akkumulasie, is waargeneem wat verantwoordlik kan wees vir beëindiging van dormansie.

Om die verandering van water status in dormante appel knoppe te bestudeer, was die volgende proef uitgevoer. Terminale apple knoppe van dieselfde vier kultivars en vanaf die selfde twee areas in die Wes Kaap as bogenoemde, is elke tweede week gedurende die winter 2001 gesny vanaf komersieële boorde. Daarna is die knoppe middel deur gesny en die skudblare verwyder voor die vars massa gemeet en daarna die waterpotensiaal bepaal is. Die data het bevestig dat daar veranderings in beskikbaarheid van vry water in dormante knoppe gedurende dormansie plaasvind. 'n Definitiewe invloed van temperatuur op waterpotensiaal is geïllustreer. Die waterpotensiaal van knoppe in die kouer produksie area toon 'n meer normale respons (gedurende die winter is die water in 'n gebonde vorm, wat later in die winter na vry water verander). Daar teenoor is daar in die knoppe van die warm produksie area nie veel verandering in waterpotensiaal of water massa getoon nie.

Gedurende die winter van 2000 is twee jaar oue proleptiese vertakte 'Royal Gala' lote, ongeveer 500mm lank, gekies vanaf 'n boord in die Koue Bokkeveld. Die lote is verdeel en het twee koue behandelings ontvang. Koue kamer by 5-7°C en natuurlike koue in die boord. In 2001 is net die natuurlike koue behandeling herhaal. Daar is vyf dormante snoei behandeling op die lote gedoen; kontrole (geen), snoei terug tot die vierde lateraal voor en na die koue; verwydering van die 2de en 3de laterale voor en na koue. Na koue en snoei is die lote verwyder en in die groeikamer geforseer by 25°C en met konstante illuminasie. Die tempo waarteen die laterale gebot het is bereken (1\dae to 50% groen punt) waarna die laterale in klasse gedeel is; terminale knop, die vierde lateraal en die res van die laterale saam. Verwydering van distale weefsel d.m.v. snoei verhoog die tempo waarteen laterale knoppe groenpunt bereik. Snoei voor die koue behandeling was meer effektief as daarna. Die korrelatiewe fenomeen wat bot inhibeer van proksimale lote kan gemanipuleer word in die twee jaar apple loot.

Die vertakkings gedrag van een jaar oue onvertakte 'Royal Gala', 'Cripps' Pink' apple en 'Rosemary' peer lote, 0.5m lank, is ondersoek na fisiese manipulasies gedoen is gedurende mid winter 2000. Vir die eerste vier behandelings (a,b,c,d) is die lote in 'n horisontale of vertikale possisie gelos as kontrole, of horisontale of vertikale gebuig en daar gehou d.m.v. binddraad. Behandelings e tot h het dieselfde behels maar die lote is ook nog in die helfte deur gesny (getop). Die hoeveelheid groei in mm vir elke node is aangeteken asook die posisie vanaf die terminale knop. Die 'Cripps' Pink' het 'n definitiewe veskuiwing vanaf 'n akrotoniese na 'n basitoniese vertakkingspatroon getoon. Die reaksies op die manipulasies of die gebrek daaraan ('Royal Gala' en 'Rosemary') kan 'n aanduiding wees dat genotipes verskillend reageer op die behandelings asook op die tyd wat dit gedoen was.

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CONTENTS

Declaration

Summary

Opsomming

Dedication

Acknowledgements

1. LITRATURE REVIEW: Dormancy and branching of deciduous fruit trees.

1.1 Introduction **1**

1.2 Dormancy **1**

1.2.1 Temperature effect on dormancy **2**

1.2.1.1 Optimum temperature **2**

1.2.1.2 Negation of chilling **4**

1.2.1.3 Influence of inadequate chilling on dormancy **4**

1.2.1.4 Chilling requirements **5**

1.2.2 Cellular changes in dormant buds **6**

1.2.2.1 Changes in membrane status **6**

1.2.2.2 Cellular membrane changes **7**

1.2.3 Hormones and dormancy **8**

1.2.3.1 Gibberellins **8**

1.2.3.2 Cytokines **8**

1.2.3.3 Auxin **8**

1.2.3.4 Abscisic acid (ABA) **9**

1.2.4 Water in dormant buds **9**

1.3 Apical dominance **11**

1.3.1 Definition 11

1.3.2 Growth factors involved in axillary bud growth 11

1.3.3 Effect of hormones in apical dominance 12

1.4 Branching 13

1.4.1 Sylleptic and proleptic branching 14

1.4.2 Factors determining branching type 14

1.5 Apical dominance vs. Apical control 15

1.6 Apical control of branch growth 16

1.6.1 Hormonal involvements 16

1.6.2 Transport of water and mineral nutrients 17

1.6.3 Photosynthesis 17

1.6.4 Assimilate allocation 17

1.6.5 Gravimorphism 17

1.6.6 Apical control of branch angel 18

1.6.7 Summary of apical control 18

1.7 Acrotony vs. Basitony 19

1.7.1 Influence of endo- and paradormancy on branching 19

1.7.2 Paradormancy as a correlative factor in branching 20

1.7.3 Development of acrotony 20

1.8 Correlative dominance signals 21

1.8.1 Primigenic dominance 21

1.8.2 Positional advantage 22

1.9 References 22

2. PAPER 1: THE PROGRESSION OF APPLE BUD DORMANCY DURING ARTIFICIAL CHILLING OF FOUR CULTIVARS FROM CLIMATOLOGICALLY DIFFERENT SITES **32**

3. PAPER 2: CHANGES IN WATER POTENTIAL OF APPLE BUDS DURING DORMANCY **40**

4. PAPER 3: PRUNING EFFECTS ON THE DEVELOPMENT OF CORRELATIVE PHENOMENA IN 2-YEAR OLD 'ROYAL GALA' APPLE BRANCHES **51**

5. PAPER 4: INFLUENCE OF BENDING AND HEADING ON THE ACROTONIC BRANCHING HABIT OF APPLE AND PEAR SHOOTS **63**

6. GENERAL DISCUSSION **76**

7. CONCLUSION **80**

1. LITRATURE REVIEW

Dormancy and branching in deciduous trees

1.1 Introduction

The apple production regions in the Western Cape have inadequate winter chilling to satisfy the dormancy-breaking requirement. This will not change in the near future and could even become more evident. Inadequate chilling leads to a situation where dormancy symptoms could persist. "Delayed foliation" is a major symptom observed when deciduous fruit trees grown in mild winter conditions (Rauh, 1939; Jacobs *et al.,* 1981). Chilling models used in deciduous fruit production were found to be inadequate in warm winter conditions (Linsley-Noakes & Allen, 1990; Erez, Linsley-Noakes & Allen, 1994).

A better understanding of the physiological changes in the dormant bud as it reacts to the different environmental cues is necessary before such models could be successfully used. The growth response is not only a bud dormancy problem but also about the correlative influences in the shoot between the terminal and lateral disbudded shoot pieces. An understanding of these plant growth mechanisms in order to manipulate them is necessary for quality fruit production.

1.2 Dormancy

Deciduous fruits and nuts stop growing in late summer or fall, drop their leaves and are dormant during winter, then resume growth in the spring. This synchrony between plant and environment is important to the survival of the plant. Growing plants are non-hardy and dormancy during winter is necessary to survival. Temperate species have developed adaptive physiology processes for cessation of growth and acclimatization against cold. Winters in temperate zones may have fluctuations between cold and mild temperatures, thus species have evolved with long chilling requirements that they will not begin to grow in mid winter even though it may warm up to growing temperatures for a few days.

The problem with the mechanism arises when species bred in a specific climate is moved to an area with different prevailing climate (Westwood, 1993). This "new" climate could have a negative influence on the dormancy pattern of this specific plant. More often than not, an altering of the time of budburst follows. Frost damage to the flowers may happen if dormancy was released to soon. On the other hand, if there were a lack of chilling an uneven and erratic flowering would be the result. Cleary these scenarios, which are detrimental to economic fruit

production, make it vital to have a better understanding of dormancy and its related influence in the plant.

Three classes of dormancy have been identified (Lang, 1987).

a) Ecodormancy: buds are dormant because of external conditions unfavorable to growth.
b) Paradormancy: buds are dormant from the inhibitory influence of another plant part, as the dormancy of lateral buds due to the dominance of the shoot terminal.
c) Endodormancy: buds are dormant because of internal physiological blocks within an organ that prevent growth even under ideal external conditions for growth. Chilling temperatures above freezing temperatures terminate endodormancy.

The onset of endodormancy is the transition in autumn from ecodormancy or paradormancy to endodormancy (Lang, 1987). The prevailing fact in dormancy is that it is a reaction on an environmental signal. The effect of shortened day length has a dormancy induction effect in some species, although in *Malus* sp., temperature is the important factor.

1.2.1 Temperature effect on dormancy

Although the influence of temperature on dormancy has been extensively studied, its role is not well understood. The desire of fruit producers to grow apples in warmer climates where the cold requirements cannot be met by the local prevailing climate necessitates the understanding of temperature on the apple bud. Only then can manipulations of the dormant period be done to increase bud burst and obtain even flowering at the desired time.

1.2.1.1 Optimum temperature

The critical element in the development of dormancy is low temperatures. In autumn low temperature let buds to enter into the first stadium of dormancy, as can be seen when buds become slow to react on favorable temperature and only grow slow at high temperatures. Release of dormancy requires a period of chilling during winter, followed by a rise in temperature in spring (Fuchigami *et al.*, 1982; Richardson *et al.*, 1974). Several studies indicate the same low temperature can intensify dormancy in the fall, and break dormancy later in winter (Denis, 1994).

The most effective chilling temperatures for apple buds were found to be between –0.6°C and 16.5°C, with an optimum at 7.2°C (Shaltout & Unrath, 1983). This was the same as in a number of species. For example, Gilreath and Buchanan (1981) found temperatures in the range of 0 to

7°C to be the most effective at breaking dormancy in rabbit eye blueberry, Erez and Lavee (1971) established 3 to 8°C to be most effective in peach, and Mahmood *et al.*, (2000b) concluded that temperatures near 3°C break dormancy in cherry more effectively than higher or lower temperatures. Following adequate chilling buds are able to grow normally at cold or warm temperatures in the spring. Temperature provides both information as well as an essential condition for growth (Cannell, 1989).

Dormancy must be seen as a continuous process with chilling accumulation that will continuously shorten the time for budbreak and increase growth rates, as seen in many temperate fruit species, i.e., *Pyrus* spp. (Couvillon & Erez 1985b; Scalabrelli and Couvillon, 1985), *Prunus persica* (Couvillon & Erez 1985a), and *Malus* spp. (Shaltout & Unrath 1983).

Although cold is a prerequisite for dormancy release, and used in models estimating dormancy release it has been established that the chilling efficiency of low temperature was increased by cycling with moderate temperatures (15°C) (Richardson *et al.*, 1974; Erez *et a*l., 1988; Kobayashi *et al.*, 1982; 1983; Erez & Couvillon, 1987). Moderate temperatures promote the chilling effect, mostly in the latter stages of dormancy. They concluded from their study that the level of high (day) temperature in diurnal cycles is of critical importance for adequate bud burst under marginal growing conditions with warm winters.

If dormancy is seen as a sequence of events from dormancy onset to budbreak without boundaries, a bud will have the ability to respond to warm temperature at any time during dormancy with morphological development or a change in physiological activity (Vegis, 1973). This ability can be expressed as a temperature-growth response curve. Chilling simply changes the buds response to temperature by increasing it's potential rate of development (Campbell, 1978). Cannell (1989) showed that as dormant buds are progressively chilled, the thermal time required for them to reach full bloom (or bud burst) should progressively decrease. Results of Scalabrelli and Couvillon (1986) support this statement by indicating the reduction of growth degree hours when peach buds have prolonged chilling. When buds are partially chilled, they grow rapidly only at high temperature (>20°C) whereas fully chilled buds grow rapidly at cooler temperatures (10°C). Vegis (1973) interpreted it as an increase in temperature range over which the buds can grow as their dormancy is released, and Citadin *et al.* (2001) found full bloom will depends on the time chill units as well as the growing degree hours were start to be recorded.

1.2.1.2 Negation of chilling

In earlier work of Couvillon and Erez (1985) temperatures of 19°C or greater (for periods of longer than 6 hours) in a diurnal cycle with chilling were found to negate chilling in dormant peach buds. Long periods of exposure to 23°C negate chilling only if applied during the early stages of chilling accumulation. These periods must be longer than 7 days .The degree of chilling negation induced by these exposure periods does not seem to be as severe as that of similar temperature given in short cycles.

1.2.1.3 Influence of inadequate chilling on dormancy

In the absence of adequate winter chilling, dormancy is prolonged, the blossoming period is protracted, flower buds abscise and fruit set is poor (Black, 1952). However, time of flowering in spring depends not only on an adequate exposure to cold but also on the subsequent accumulation of heat units (Overcash, 1963; Lang *et al.*, 1985; Citadin *et al.*, 2001).

Unfavourable spring temperature conditions (limited hours above 18°C) and limited chilling during winter have been associated with reductions in growth rate, development of the buds and a resulting low yield in deciduous fruits. The effect of inadequate chilling have been observed in different species i.e., peach (Erez & Lavee, 1971), pear (Spiegel-Roy & Alston, 1979), apple (Jackson *et al.*, 1983), and cherry (Mahmood *et al.*, 2000a).

Delayed foliation in apple trees is a symptom of a modification in the normal bud bursting pattern due to insufficient chilling during dormancy (Jacobs *et al.*, 1981). A resulting change in the growth habit of the tree will also be evident. The delayed and erratic bud bursting on shoots changes the normal acrotonic bursting pattern and growth habit towards the more problematic basitonic form. Proximal branches develop unchecked by the apical control of the leader shoot of the apple tree (Cook *et al.*, 1998). The implications are a reduction in fruiting wood in exchange for more aggressively growing autonomous vegetative shoots. An increase in the rate of vegetative growth, flower size and fruit set in cherry trees after sufficient chilling, was documented by (Mahmood *et al.*, 2000a). These results could indicate that more and better fruiting wood was produced that resulted in the higher fruit set. Hauagge and Cummins (1991b) said that the effects of inadequate chilling could be observed in every aspect of the growth cycle of the plant; the intensity of the symptom is related to the amount of chilling that is lacking. This lack is the main limiting climatic factor governing the distribution of temperate zone species.

The application of chemicals has been necessary to achieve adequate bud burst and cropping in production areas with sub–optimal chilling. The commercial resistance towards chemical use for fruit production, make knowledge of the inheritance pattern of the amount of chilling required to break dormancy important for the development of effective breeding strategies (Hauagge & Cummins, 1991e). They also stated that any gene that would effect branching pattern, onset of dormancy, temperature efficiency for breaking dormancy, or chilling negation would probably modify the length of the dormancy period or the action of the genes that could be directly involved in dormancy.

1.2.1.4 Chilling requirements

The chilling duration needed to release dormancy varies not only among species but also between cultivars within a species. Cold requirement is a characteristic generally used to compare genotypes in relation to the termination of the dormant period. It is a valid criterion but takes into consideration only one point in the dormancy dissipation curve (Hauagge & Cummins, 1991c). Hauagge & Cummins (1991a) indicate that apple genotypes differ not only as to when changes in dormancy intensity take place, but also in the patterns and rates at which these proceed. These genotypic differences have implications for adaptation of a particular genotype to diverse environmental condition, as well the loss of precision by generalized modelling.

Optimum temperatures for cultivars are not constant and the studies of Gilreath and Buchanan (1981) indicated that there are cultivar differences in the effectiveness of different chilling temperatures and accumulated chill-unit requirement.

Erez and Couvillon (1987) said that variations in peach cultivars responses could be due to quantitative requirements or from a difference in response to low or high temperature in peach buds. Citadin *et al.* (2001) concluded their study on peach buds by stating that endodormancy is not a discrete but gradual and quantitative process represented by a continuous increase in the speed of blooming and leafing as heat accumulation increases. This behaviour varies with both genotype and environment. They also found that chilling above the requirement of a cultivar reduces heat requirement for budbreak, and tends to make the heat requirement of different cultivars uniform.

Scalabrelli and Couvillon (1986) found that not only are there cultivar chilling differences but also bud type differences. Terminal vegetative peach buds have the shortest chilling requirement compared to lateral vegetative and flower buds, which have the similar chilling requirements.

Results of Citadin *et al.* (2001) concur this with the differences they observed in time of blooming and leafing, which they attributed to differences in heat requirement between flower and vegetative buds.

1.2.2 Cellular changes in dormant buds

During dormancy, the entire tissue of the apical meristem loses its development vector, and settles into an aspatially heterogeneous state (Kauffman, 1993). This process involves a change in the properties of a cell in the apical meristem. These changes are a result of environmental signals for species sensitive for climate changes such as temperature e.g. *Malus sp.*

1.2.2.1 Changes in cellular status

All the cells in the apical meristem are connected by plasmodesmata, forming a symplast. These plasmodesmata play an important role in plant growth. Plasmodesmata are tubular structures that extend through the adjacent cell walls and the middle lamella of nearly all-living cells. They not only play a part in nutrient transport but also are also vital for transporting plant signals in the form of hormones.

There is evidence by Shepherd and Goodwin (1992) in *Chara spp* that these intercellular communication channels are associated with plant growth and dormancy development. They found in a period of dormancy a restricted cell-to-cell communication, inactive branch dactyls and restricted growth, whereas in spring active growing branch dactyls of *Chara* spp were characterized by extensive intercellular communication. The results of Jian *et al.* (1997) concur with Shepard and Goodwin and show that in short day-induced dormancy of popular, the frequency of plasmodesmata decreased and the diameter of the plasmodesmata pores reduced, influencing intercellular communication. Recent work of Jian *et al.* (2000) suggest that intercellular communication channels and the levels of intracellular calcium are also involved in the development of dormancy in poplar (*Populus deltoides*).

Intracellular changes that take place as a result of dormancy induction have been proposed to be a way of studying and measuring the dormant state of a bud. Bonhomme, Rageau and Gendraud (2000) reported that ATP/ADP ratio did not prove to be the marker of endodormancy that they were looking for. However, it reveals the state of primordial submitted to endodormancy

and/or short or long distance paradormancy inhibitions. It seems to be a good marker of the primordia's ability to respond at favourable temperatures and start strong growth *in situ*.

This finding corresponds with observations of Aue, Leconte and Pétel (1998) that a higher H^+ATPase activity was observed in the buds at the end of endodormancy, than in the underlying tissue. This might indicate that nutrients could be supplied to the buds because of the higher H^+ATPase activity in the membrane. A similar revision was noted by Marquat *et al.* (1996) on non-dormant trees where the buds had higher total and active sucrose absorption than the underlying tissue.

By the increase of the H^+ATPase, Aue *et al.* (1998) postulated that dormancy release in peach buds could be related to the modification of plasma membrane ATPase quality in buds and the underlying tissue. This increase in ATPase activity in the cell membranes as well as proton pumping gives rise to a pH increase (Pétel *et al.,* 1992). Their results also show the internal pH of a dormant bud is lower than that of the underlying tissue and stem. By revising the competing power of the different tissues, the bud may overcome this block to its development.

1.2.2.2 Cellular membrane changes

A change in the properties of cell membranes during dormancy of vegetative apple buds was associated with an increase in specific fatty acid contents of the phospholipids (Wang and Faust, 1990). Erez *et al.* (1997) showed that this increase was correlated with efficient chilling in peach vegetative and floral buds. The major changes found was an increase of linoleic acid, which is produced by oleate desaturase (Lyons, 1973), a membrane bound enzyme presumably activated by low temperatures. During dormancy, Wang and Faust (1990) noted an increase of linoleate from 20% to 40% of total fatty acid content and an increase of linolenate during bud break of 5%.

These changes and other major increases in the total level of phospholipids in the cell membrane between late autumn and winter, accentuate the fact that dormancy development is a local phenomenon, to be overcome by each bud. There is little communication between buds during this trying time (Erez, 2000).

1.2.3 Hormones and dormancy

The French school considers the influence of hormones in dormancy with scepticism; they think they play a secondary role, but are not the key factor. Their argument follows from the fact that dormancy is too complicate a process to be controlled by one or two factors. They see it is the last stage of a cascade of correlative inhibitions (Champagnat, 1983) that begins with apical dominance (distal inhibition by shoot tissues) and ending in an endogenous inhibition of the meristem (Dennis 1994).

1.2.3.1 Gibberellins

The increase of Gibberellins (GA) observed in buds after chilling is thought to have a closely related link to dormancy release. In addition, when GA was applied in winter, its effect on dormancy release was positive in most cases (Vegis 1964). The increase in terminal bud break from applied GA resulted in increased apical dominance (Erez et *al.*, 1979), which don't occur if buds received adequate chilling. Saure (1985) thinks it is unlikely that GA really can substitute for chilling during deep dormancy.

1.2.3.2 Cytokinins

Cytokinins are known to counteract the inhibition of lateral bud growth resulting from apical control (Li & Bangerth, 1992; Cook *et al.*, 1998). Saure (1985) suggested that cytokines probably has some supplementary function in dormancy release, but is not the cause. There is an increase of cytokinins, which start shortly before budburst and increase rapidly with bud swelling, and peaks around budburst. This cytokinin peak in spring is believed to originate from the shoot and not the roots (Tromp & Ovaa, 1990; Cutting *et al.*, 1991; Faust *et al.*, 1997). Cytokinins apparently hasten the development of buds that have been at least partially released from dormancy (Saure, 1985). Bangerth (1994) found that the cytokinin concentration in the xylem exudates is under the control of the polar auxin-transport system.

1.2.3.3 Auxin

Saure (1985) reported that auxin, besides being involved in the inhibition of lateral bud development, participate also in the induction of dormancy. Results of Cline (1996) support this earlier evidence that auxin is synthesized in the terminal bud transported basipetally and then, in some manner, has an inhibition effect on axillary bud growth.

The IAA found by Golcal *et al.* (1991) in *Phaseolus* axillary buds indicates that growing buds contain more IAA than dormant buds. Therefore, Strafstrom (2000) found it more probable that auxin inhibits axillary bud growth by an indirect mechanism, either by promoting the synthesis of a secondary inhibitor or by inhibiting the synthesis of a growth promoter.

Faust *et al.* (1997) concluded from earlier work that there is no question that auxin has an effect in promoting correlative inhibition, not only during paradormancy but also during endodormancy.

1.2.3.4 Abscisic acid (ABA)

The high levels of abscisic acid (ABA) associated with seed dormancy (Koorneef *et al.* 1989) and with plant responses to environmental stresses, such as temperature, water or wounding, are well know. This resulted in the study of the possible relationship between ABA and bud dormancy. The work of Tamas *et al.* (1981) that found ABA is not transported from inhibiting organs let Strafstrom (2000) to think that there is a ABA synthesis within the bud or in the vicinity of the bud, perhaps in respond to IAA within the stem. ABA also appears to be important in inhibiting the growth of paradormant buds. It was found that the concentrations are elevated in dormant *Phaseolus* and *Elytrigia* buds (Gocal *et al.*, 1991; Pearce *et* al., 1995). Piola *et al.* (1998) recently show a close correlation between ABA accumulation in the cedar needles and the buds exit from dormancy.

There are several opinions of the effect of ABA listed in the review by Saure (1985) that argued for a more indirect effect on budbreak. However, Faust *et al.* (1997) think that the effect of defoliation indicates that ABA or other chemical inhibitors cannot be completely discounted. Even though ABA may not be linearly correlated with dormancy, it seems to have an effect on its development. McAnish (1991) thinks evidence for this statement could be found in the results of Jacobson & Shaw (1989) and Mundy & Chua (1988), who found that autumn levels of ABA could be involved in the induction of dehydrins and in changes in the permeability of membranes.

Ethylene does not appear to play a role in inhibiting bud growth (Romano *et al.* 1993).

1.2.4 Water in dormant buds

Water, being the main solvent for cellular components that are responsible for physiological development, makes it logical to expect that any changes of its mobility in the bud tissue, will

accompany the physiological changes associated with dormancy (Sugiura *et al.*, 1995). The water content of a dormant apple buds is 49% of the total weight and increases to 59% after exposure to cold temperatures between 4 and 9°C, before they are able to resume growth (Faust *et al.*, 1991). This change of water in the bud is not only a weight increase, but also of the state of the water in association with macromolecules as well as a change in the distribution in the cellular structures.

Faust *et al.* (1991) correlated the ability of buds to resume growth with satisfaction of their chilling requirement and conversion of water from a "bound" to "free" form. The water bound to or perturbed by macromolecules (called structured water), can be distinguished from the free water by magnetic resonance imaging (MRI). In 1991, Faust *et al.* determined that the conversion of water from a bound to a free form is an incremental process and proceeds in proportion to chilling. They also found that they cannot distinguish between ecodormant and paradormant buds, but could separate endodormant buds from the others. Buds do not enlarge appreciably during dormancy when water is bound. Buban and Faust (1995) determined that bud enlargement commenced in early February (Northern Hemisphere) and occurred only after at least 30% of total water was converted to free water.

The involvement of hormones in the chance in the state of water in bud cells has been found. If the water in paradormant buds is relatively bound, TDZ (a cytokinin analog) can free the water; in contrast, the application of IAA can keeps the water bound, even after TDZ treatment (Lui *et al.*, 1993; Wang *et al.*, 1994).

Water in endodormant buds is found primarily in the cell wall matrix, while water in the ecodormant or paradormant buds is mainly intercellular (Faust *et al.*, 1991). This movement of water is related to hardiness and acclimatisation of plant tissue. The biophysical question of precisely how cold acclimatisation and dormancy are related still remains.

From data of Vertucci and Stushnoff (1992) it appears that acclimatisation of vegetative apple buds involve at lease two processes, firstly an increase in tolerance to dehydration and secondly, an increase in the level of non-freezable water. This process may involve changes in the concentration of protective solutes or in the behaviour of water at macromolecular interface. Arora, Wisniewski & Davis, (1992) found dehydrin-proteins in endodormant buds (and other tissues). Dehydrins are hydrophilic proteins that are induced during cold stress and/or

dehydration. Dehydrins, due to their high hydrophilicity, are possible candidates to bind water and prevent freeze injury.

The interlinking nature of dormancy and cold hardiness suggests that through the study of the different mechanisms of the physiological state of the bud, a better understanding will be possible. Knowledge of phenomena like supercooling, anatomical features of freezing avoidance (Quamme, Su & Veto, 1995), photoperiodic influences on cold acclimatisation (Fennell & Hoover, 1991), and production of cold induced substrate like dehydrins (Arora *et al.*, 1993) and anthocyanins (Leng *et al.*, 2000), may contribute to comprehend this plant growth regulation system.

1.3 Apical dominance

1.3.1 Definitions

The annual growth cycle of temperate perennials includes at least three distinct types or phases of bud dormancy: paradormancy, endodormancy and ecodormancy (Borchert, 1991). In general, one phase of the cycle must be completed before the next can begin (Fuchigami & Nee, 1987). Paradormancy, also know as summer dormancy, is the temporary dormancy which precedes winter or endodormancy in temperate woody plants (Crabbé & Barnola, 1996; Dennis, 1994). Apical dominance, the control exerted by the terminal bud over the outgrowth of the lateral buds, is thought to play a primary role in this paradormancy of these current lateral buds which normally do not grow out until the following spring after over wintering (Cline & Deppong, 1999).

The critical test for apical dominance control of a species is the effect of shoot apex decapitation and defoliation on release of the lateral buds. Cline and Deppong (1999) concluded from their decapitation and defoliation study that apical dominance does play a role in certain species, e.g., the hybrid red/silver maple and the *Malus* sp. which Wang, Faust and Line (1994) reported on. Although they found that in other species, decapitation/defoliation do not significantly release lateral bud outgrowth. These results support findings of Jankiwicz and Stecki (1979) that there are several mechanisms acting together to inhibit axillary buds and not only apical dominance.

1.3.2 Growth factors involved in axillary bud growth

In several studies into apical dominance and the inhibition of axillary bud growth found evidence that leaves (young and mature) are a sources of inhibitors. They could also be a dominating competitor for water and nutrients (Borchert, 1991; Crabbé, 1970; Crabbé & Barnola, 1996).

Another factor most commonly attributed with the lack of lateral bud growth is insufficient shoot vigor (or growth rate). This is obviously dependent on light and nutrients and is difficult to quantify (Cline & Deppong, 1999). Increasing age of buds with possible abscisic acid accumulation at lower node positions is also thought to contribute to the inhibition of *Malus* buds (Theron *et al.*, 1987)

Suzuki (1990) reported a positional effect in mulberry shoots, were lower lateral buds were more inhibited. He suggested that inhibition arises from actively growing neighboring shoots. Girdling, defoliation and bud removal trails let him to conclude that the inhibiting effect seems indicative of both auxin induced inhibition and a nutrient or water competition effect. These results demonstrate that acropetal influence is important in bud dominance relationships.

1.3.3 Effect of hormones in apical dominance

The role of hormones in apical dominance is clear. The fact that alterations in auxin and cytokinin content in shoots can significantly affect lateral bud outgrowth together with the fact that these hormones are naturally present in plant tissue suggest that apical dominance may be strongly influence by the interaction between these two growth substances (Cline *et al.*, 1997).

Bangerth *et al.* (2000) established that the effect of the dominant organ can be mimicked by application of auxin, which prevents the fairly rapid adjustment of the IAA export from the remaining, dominated organ, after a dominant organ was removed. They think this could suggest that auxin transport is the decisive event and not the allocation of assimilates.
Wang *et al.* (1994) investigated this possible role of Indole-3-actic acid (IAA) on apical dominance of apple. Their results suggested the IAA, presumably produced by the terminal buds, restrict water movement to lateral buds and inhibit their growth. The change in water movement could alter membrane lipid composition and thus induce lateral bud growth. Results of Cline *et al.* (1997) show evidence of auxin in subtending mature leaves as well as in the shoot apex and adjacent small leaves that could contribute to the apical dominance of a shoot.

Cytokinins, which may originate from roots or shoots, are powerful initiators of lateral bud outgrowth in many species (Pillay & Railton, 1983). There effect however, appears to be secondary in most cases to the inhibitory effect of some signal originating from the upper shoot (Cline, 1991) because of the cytokinin peak in the bud only after growth starts. Although cytokinins alone are seldom regarded as being sufficient to release inhibition, continuous

treatment with synthetic cytokinins not only overcome inhibition of lateral buds, but can even turn them into dominant organs (Cline, 1994; Li & Bangerth, 1992). To re-start growth of a dominated organ, a short pulse of cytokinin may be necessary (Li *et al.*, 1995), particularly for new cell division, which is one of the first events observed in lateral buds after being released from dominance (Strafstrom, 1993).

Cytokinin and auxin interact in a complex manner to control metabolism and content in the shoot. In the correlative signals required for an apical dominance effect, from a dominant to a dominated organ, auxin and cytokinins are obviously important components. Bangerth (1994) presented evidence that cytokinin concentrations in the xylem exudates is under the control of the polar auxin transport system, however this is not a simple one-sided regulation. In a recent publication, Bangerth *et al.* (2000) formulated a theory concerning IAA transport and the resulting effect on apical control. By using exogenous auxin and cytokinins on apple, pea and tomato plants, they formulated a hypothesis concerning IAA export and transport. They suggested that differences in IAA export from, and transport capacities of, dominant and dominated shots may be explained by a mechanism called auxin transport auto-inhibition (ATA). This mechanism describes that where the two streams of IAA met in the transport pathway, the first stream of auxin (from the dominant organ, i.e., terminal meristem) inhibit the export stream of IAA from the other organ. This organ then becomes a dominated organ, which will result in an inability to export the auxin produced in the organ, thus keeping the meristem inhibited. These authors found ATA to be sufficient to impose dominance without the need for other regulators.

However, to release organs from dominance, a cessation of the ATA may not be sufficient for growth to resume. The powerful auxin antagonistic abilities of cytokinins let Bangerth, Li and Gruber (2000) into a conclusion that there must be a dynamic and strong mutual interaction between auxin produced in the shoot and the cytokinins produced in the roots. This interrelationship between these hormones is possibly maintained via a negative/positive feedback regulation (Bangerth, 1994). This may be important in regulating the balance between root and shoot growth.

1.4 Branching

Branching in deciduous trees occur manly according to one of two alternative developmental processes. Hallé, Oldeman and Tomlinson (1978) describe these two processes as sylleptic and proleptic branch development.

1.4.1 Sylleptic and proleptic branching

Syllepsis is the continuous development of a lateral shoot from apical meristem to establish a branch, without an evident intervening period of rest of the lateral meristems. Branches so developed are referred to as sylleptic branches. Prolepsis, on the other hand, is the discontinuous development of a lateral shoot from a apical meristem to establish a branch, with some intervening period of dormancy of the lateral bud.

The developmental distinction between these two kinds of branching can be stated by saying that a sylleptic branch is synchronous in its development with its parent axis, but a proleptic branch is not. Although the initiation of the branch meristem, in both instances, is an event developmentally continuous in time with the activity of the parent meristem.

In most temperate trees there is an age difference of one year between a branch and the axis on which it is inserted, because superficially visible lateral meristems usually over winter as dormant lateral buds. Okubo (2000) defined the induction of dormancy as the change of the primordia that cease growing for a while and don't produce shoots. This one-year time lag in branching development then gives rise to the predominately proleptic branching of *Malus* species.

1.4.2 Factors determining branching type

Dormancy as a control mechanism lets one growth cycle occur in a year and limits the continuity of the growth cycle genetically and environmentally (Okubo, 2000). Bringing in to consideration that temperate plants, which have a dormancy mechanism and branches more proleptic, evolved from tropical plants (mostly sylleptic), may lead to the deduction that proleptically branching species still posses the ability of sylleptic branching under ideal growing conditions.

Hallé *et al.* (1978) named several cases were treatments induced premature budbreak and consequently produced the morphological futures of a sylleptic branch in a shoot which otherwise would have been proleptic. Hallé *et al.* (1978) deducted from earlier studies (Gill, 1971; Gill & Tomlinson, 1971; Brown McAlpine & Kormanik, 1967) that sylleptic branching is correlated with rate of shoot growth. This lead to a hypothesis by Tomlinson and Gill (1973) which suggested that the switch from "lower" state, which determined syllepsis, is conditioned by a "threshold" which in turn is determined by growth "vigour" of the parent shoot. Once this vigor

exceeded, the balance is tipped from the lower to the higher state (Hallé *et al.*, 1978). A possible explanation for this phenomena could be found in work by Sachs and Thimann (1967) who showed the increased vigour of the elongating shoot lowers the sensitivity of the lateral buds to inhibition more so than it increase the inhibitory power of the main apex. This provides an alternative to explanations of branching solely in terms of "apical dominance" i.e., the production of a growth inhibiting substance by the terminal meristem.

This complex mechanism of branching led Brown *et al.* (1967) to propose the term "apical control" to describe the inhibition of growth of proleptic branches. This concept is in contrast to the term "apical dominance" describing bud outgrowth through the inhibition of growth of sylleptic branches. Brown *et al.* (1967) used "apical control" to describe the physiological condition that give rise to the overall shape and form of the tree crown via various branching pattern.

1.5 Apical dominance vs. Apical control

In temperate plants when a lateral meristem is formed in the first year, apical dominance determines whether the meristem initially forms a sylleptic branch or forms a bud. In the second year, apical control regulates the amount of elongation, orientation and diameter growth of proleptic branches from previously dormant buds (Wilson, 2000).

Cline (1997) defines apical dominance as "the control exerted by the shoot apex over the outgrowth of the lateral buds". He proposed that the term apical control applies to the control exerted on lateral shoots after the bud has start elongating, even if the meristem has not passed through a period of dormancy. Wilson (2000) said the difference in the literature concerning terminology, e.g., acrotony, apical control and apical dominance, must not obscure the probability that as a branch is formed from a latent bud on to a lateral branch, the mechanisms controlling growth would also change.

The difference in age of a tree and its branches (with one and more year old shoots attached) contributes to the complex nature of tree architecture. Cline (1997) considers apical dominance as the control of lateral bud outgrowth by the apex in an individual branch during the current seasons growth. He referred to apical dominance as the control over branch elongation, orientation and is concerned with "the influence of the main growing point on all branches of a perennial plant" (Martin, 1987), or as Bollmark *et al.* (1995) describe it, "the influence of the top of the tree on the branches lower down".

The first separation of these concepts was when Brown *et al.* (1967) summarized their findings by stating apical dominance should only be used to describe the pattern of bud inhibition on currently elongating shoots. Apical control seems better to describe the physiological conditions governing the excurrent (hierarchic) and decurrent (polyarchic) growth forms.

Wilson (2000) found both apical control and dominance have one key problem to consider. What triggers the start of growth of lateral buds? The problem with apical control is what inhibits further growth of lower, proximal lateral shoots. He stressed that apical control inhibits not only shoot elongation, as in apical dominance, but also cambial activity and thickening of existing branches.

1.6 Apical control of branch growth

Branch growth can be viewed as the production through growth processes of new branch biomass from assimilates produced by the tree. Apical control could influence branch growth either by affecting hormone action or distribution of water and even sufficient assimilate allocation.

In turn, environmental effects could reduce overall growth rates of the tree or branch, thereby affecting apical control. It has been shown that apical control can be reduced, e.g., by shading conifer trees (O'Connell & Kelty, 1994), as well as in higher order, slower growing branches (Remphrey & Davidson, 1992), in slow growing trees (Moorby & Wareing, 1963), or in trees with nutritional deficiencies (Brown *et al.*, 1967).

1.6.1 Hormonal involvement

The polar nature of apical control parallels the polar transport of auxin. Generally, the uppermost, distal shoot inhibits the lower, proximal shoots. The original proposed mechanism for apical dominance by Thimann and Skoog (1933) was that auxin from the parent terminal directly inhibited lateral bud growth. In later years, strong support was found for other hormones, particularly cytokinins, playing a role in the dominance breaking mechanisms.

The combination of cytokinin with auxin was found to regulate the amount of lateral shoot growth. Chen, Bollmark and Eliasson, (1996) found a positive relationship between cytokinin content and lateral bud size of Norway spruce during the critical period of bud formation that

determines shoot length. This corresponds with results of Little (1970) on *Pinus strobes*. He found a positive relationship between the endodormant bud size and size of new shoots.

1.6.2 Transport of water and mineral nutrients

The Borchert and Honda (1984) hypothesis states that transport of water and nutrients to the lateral branches is restricted relative to transport to the terminal shoots and for that reason branch growth is reduced relative to the terminal. Wilson (2000) found studies supporting this hypothesis, but several observations suggest that difference in transport is the result, not the cause of apical control.

1.6.3 Photosynthesis

The effect of apical control on photosynthesis is not well studied, however observations of well-lit branches appear to escape some apical control, and they have a higher rate of photosynthesis. Presumably, the increased photosynthesis permits growth, and increased growth may in turn, increase hormone production. This could then results in a more autonomous position in the branch system.

1.6.4 Assimilate allocation

Wilson (2000) reported that branch growth seems to be determined by the relative competitive abilities of the branch and the parent axis. An allocation hypothesis would suggest that retention of branch assimilate occurs when the branch sink strength exceeds the terminal sink strength.

1.6.5 Gravimorphism

The effect of re-orientation of shoots from an orthotropic to a plagiotropic position on shoot growth is called gravimorphism and is expressed as a shift from an acrotonic towards a basitonic branching habit. Basitony is seldom expressed on apple shoots, except under specific conditions (including gravimorphism) which Cook *et al.*, (2000) listed as growth after girdling or notching, following conditions of sub-optimum winter chilling, or by the localized application of cytokinins in spring and/or autumn. All these examples have an influence on the auxin and cytokinin balance.

Wareing and Nasr (1961) found vertical shoots grow faster than a shoot hold to an angle from the vertical. They also show that shoot angle can modify the effect of apical control within and between shoots. Branches bent horizontal loose the capacity to control the growth of distal branches and results in a more proximal shoots becoming dominant.

1.6.6 Apical control of branch angle

In branches, the equilibrium position is that position where the branch does not produce wood with differential growth stresses. Branches of most angiosperm species released from apical control may trigger the formation of tension wood along with increased radial growth of the branch. (Wilson & Archer, 1983).

If the equilibrium position of a shoot is vertical, it is termed orthotropic and horizontal is termed plagiotropic. Some branches are irreversibly plagiotropic and will never bend upward after removal of apical control as can be seen in *Araucaria* (Timell, 1986). The equilibrium position of other plagiotropic branches can change orientation if released from apical control. This could be seen in *Pinus strobes* branches that are initially plagiotropic after decapitation of the terminal but they eventually bend upwards to a vertical position to become orthotropic (Wilson, 1973). This new vertical equilibrium position could be due to the differentiation of new wood cells. Wilson (2000) reported that the different findings on apical control of branch orientation are confusing. He asks the question of how, or even whether apical control regulates the equilibrium position of a branch, and thus regulates the formation of reaction wood and growth stresses.

1.6.7 Summary of apical control

In his paper, Wilson (2000) put forward two possible mechanisms for apical control.
The first mechanism involves the prolonged hormone production by the branch at promotive levels after the removal of apical control. The branch will then be improved as a sink, which will result in the higher rate of assimilate allocation and growth. The question arising from this is how does the controlling distal shoot regulate the hormone production in the proximal branches. The alternative mechanism is that reduce assimilates, due to export to the stem, inhibits growth even with adequate hormones in the branch. In this case, removing apical control would reduced the sink strength of the parent shoot/stem, permitting assimilate retention in the branch and allowing continued growth and production of hormones by the branch.

Wilson (2000) argued that most of the factors regulating branch growth may be eliminated as primary cause of apical control, e.g., water transport, direct hormone action, gravimorphism and photosynthesis. These factors react too slow and are more a result of apical control than a cause of it. In contrast to apical dominance, where lateral buds either grow or do not, there is a

wide range of levels of apical control under different conditions both between and within individual plants.

1.7 Acrotony vs. Basitony.

The influence of winter cold in the proleptic branching habit is very important in apple tree architecture. After endodormancy, budburst is proleptic, with the bursting of the terminal and many lateral buds along the axis. Not all of these buds become long extension shoots and many remains as short shoots or spurs. The most distal or apical buds, however, appear dominant and are most commonly the buds that burst and form extension shoots. This distal extension shoot-forming tendency is referred to as acrotony (Rauh, 1939). This is opposed to basitony, where long shoots originate from lateral buds of more proximal origin (Cook *et al.,* 1998). Trunk formation in apple tree is the result of acrotony and is therefore a desired process (Champagnat, 1984).

1.7.1 Influence of endo- and paradormancy on branching

With the predominantly proleptic branching habit of apple, over wintering involves the entrance into and exit from endodormancy, a process that appears to be promoted by low temperature. The resulting bud bursting after winter dormancy is proleptic, with bursting of terminal and lateral buds on the axis (Dennis, 1994; Crabbé, 1994). Seasonal differences exist in the depth of dormancy between terminal and lateral buds. During dormancy, lateral buds appear less endodormant than terminal buds (Crabbé, 1987; Hauagge & Cummins, 1991). This tendency however is not static.

It appears that, on entrance into endodormancy, an basitonic tendency prevail that becomes more acrotonic to the end of dormancy (Barnola & Crabbé, 1991). In intact shoots, this increased growth potential of the basal buds is seldom expressed in terms of shoot growth. Nevertheless, under specific conditions, e.g., gravimorphism (Wareing & Nasr, 1961) and insufficient winter chilling a basitonic tendency can be seen. In apple shoots, the bursting of basal buds is most inhibited, possibly by the correlative inhibition by distal shoot tissues (Champagnat, 1983).

The influence of temperatures on entrance and exit of dormancy is well known, but according to Cook *et al.* (1998), dormancy could be the sum of inhibitors and not only one factor. This agrees with the "French school" which implies dormancy can be seen as the sum of the endodormant

component plus the paradormant component (factors outside the bud) of hormonal substrate inaccessibility and distal shoot inhibition (Dennis, 1994; Crabbé, 1994).

1.7.2 Paradormancy as a correlative factor in branching

Paradormancy is expressed when part of a plant has an inhibitory influence on another plant part, such as the dormancy of lateral buds due to the dominance of the terminal meristem. The paradormant component of bud break largely includes inhibition by distal shoot tissue (Champagnat, 1983; Cook *et al.*, 1998; Faust *et al.,* 1995). Under superfluous chilling the terminal bud exerts primigenic dominance (Bangerth, 1989) via an increased growth rate over the lateral buds. Dominance is then further accentuated by inhibition by the distal shoot tissue (paradormancy). Because of the positional advantage, the terminal bud, in the absence of paradormant inhibition is capable of establishing dominance over more basally positioned buds.

It has been suggested in temperate species that apical dominance plays a primary role in paradormancy and hence the repression of current lateral bud outgrowth early in the growing season before the establishment of dormancy (Champagnat, 1986; Crabbé & Barnola, 1996; Faust *et al.*, 1997).

1.7.3 Development of acrotony

During the dormant period as chilling accumulates; there is a proximal shift of bud bursting. This was found by Barnola and Crabbé (1991) and it appears that an acrotonic tendency shift to a basitonic branching tendency early in the winter and at the end of winter again become acrotonic as sufficient chilling is accumulated. Results of Cook *et al.* (1998) also found a basitonic tendency exhibited in early winter, but it was poorly defined and was associated with a generally low growth potential compared to the acrotony that developed before spring.

Insufficient chilling impedes the development of acrotony in apple. Cook *et al.* (1999) concluded that this appears to be due, in part, to an inherent low growth rate of the buds and less synchronization among buds at the time of spring budburst resulting in both delayed and a more erratic budburst. These authors argue that under sub-optimal chilling conditions, paradormancy accounts for most of the inhibition of the upper lateral buds.

The development of acrotony is necessary in order for the development of a dominant central axis (leader). Insufficient chilling results in an increased tendency towards basal dominance (Cook & Strydom, 1998), which result in autonomy of individual, proximally situated branches. These autonomous branches develop without the control of the central axis, over time, the hierarchy of the tree is disrupted, and the formation of a dominant trunk is impeded. This shift from acrotony toward basal dominance is detrimental from a tree training perspective (Lespinasse & Lauri, 1996).

1.8 Correlative dominance signals.

The problems associated with a hormonal signal transferring the dominance effect give rise to a hypothesis by Bangerth (1989). The correlative dominance signals can frequently account for the observed dominance effects, in which both dominance and competition mechanisms may occur together. He stated that the sequence of sink development might establish the dominance effect.

1.8.1 Primigenic dominance

Primigenic dominance is suggested by Bangerth (1989) to describe the inhibition in which the earlier developed sink inhibits the later developed organs. This could be illustrated by the acrotonic bud burst after adequate chilling (Cook *et al.,* 1998), which results in the distal buds exerting primigenic dominance via an increased growth rate.

A new hypothesis concerning the IAA transport in the correlative signal is suggested by Bangerth *et al.*, (2000). They stated a difference in IAA export from, and transport capacities of, dominant (distal) and dominated shoots (proximal), may be explained by a mechanism of auxin transport auto-inhibition (ATA). The earliest and stronger export of IAA from the dominant shoot inhibits auxin export from the dominated shoot at the point where the auxin streams converge. The auxin in the dominated shoot then inhibits the shoot to develop.

Erratic budbursting and delayed foliation due to sub optimal chilling could result in the increase in inhibition capacity of the distal shoot. Champagnat (1983) eliminated this inhibition by notching and girdling, this practices impede the transport of auxin and is used commercially and could be seen as a support of the new hypothesis. The basitonic branching habit that results from sub-optimal chilling could result in a less clearly defined hierarchy between distal and proximal shoots, indicative of weaker acrotony (Cook *et al.,* 1998). The basal shoots could

establish primigenic dominance over shoots that are more distal and become an active exporter of auxin which result in a shoot that become autonomous. This is the result of the distal shoots inability to exert apical control over the basal buds and shoots.

1.8.2 Positional advantage

In order for an organ to dominate other, it must have a positional as well as a time (primigenic) advantage over the dominated organs. In sylleptic branching, the proximal shoots become more dominating because they are initiated before the more distal shoots formed later from the terminal meristem. This can lead to a basal dominant shoot that becomes autonomous.

In proleptic branching, the terminal bud can establish primigenic dominance because of a positional advantage (Cook *et al.* 1998). This then leads to a well-defined acrotonic branching habit, which is necessary for adequate tree training practices.

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2. Paper 1: The progression of apple bud dormancy during artificial chilling of four cultivars harvested from climatologically different sites

Abstract.

During May 2000, 1-year-old, unbranched shoots of four apple (*Malus* x *domestica* Borkh.) cultivars; Royal Gala, Braeburn, Cripps' Pink and Granny Smith were harvested randomly from bearing commercial orchards in the Ceres (Koue Bokkeveld) [33°S, 945m, ca.1300 Utah model chill units (CU)] and Elgin (34°S, 305m, ca.750CU) regions of the Western Cape, South Africa, respectively. Shoots were prepared and chilled at 5-7°C. Two replicate bundles were removed from the cold room, prepared and forced at 25°C with continuous illumination until budburst had occurred on at least 25% of the shoots per bundle. The change in the rate of budburst over time was calculated for each orchard over time and to this response, either a linear or a quadratic function was fitted. Non-correlated arbitrarily chosen variables were selected from the functions. Using these variables, the orchards were separated into cluster groupings that represented a dormancy pattern. The first split separated the lower chilling requirement cultivars from the higher cultivars. The second and third split separated the orchards according to area differences. The clusters representing the warmer area (Elgin) orchards after initially receiving artificial chilling entered deeper into dormancy before exiting. The clusters for the colder areas (Ceres) immediately after receiving artificial chilling had an increased budburst rate. These data confirm that the chilling requirement includes a period of dormancy induction. An important genotype and environment interaction, other than cold unit accumulation, was observed that could be responsible for terminating bud dormancy.

Keywords: apple, dormancy, cultivar, inadequate chilling

Introduction

Growth cessation, terminal bud formation, leaf senescence and defoliation make up the morphological sequence of endodormancy development in most woody plants, including *Malus* spp. (Hauagge and Cummins, 1991c). Dormancy in woody species is generally induced naturally in autumn when day length and temperatures decrease, and the dormant state is broken or released during the winter by exposure to chilling temperatures (Cannell, 1989)

After completion of dormancy, apple budburst occurs promptly and uniformly in genotypes that are adapted to the environment. However, dormancy symptoms may persist if winter is neither long enough nor cold enough to adequately break dormancy. "Delayed foliation" is a major

symptom observed when deciduous fruit trees are grown in mild winter conditions (Ruck, 1939; Jacobs *et al.*, 1981)

Chilling models used in deciduous fruit production were found to be inadequate in warm winter conditions (Linsley-Noakes & Allan, 1994; Erez, Linsley-Noakes & Allan, 1990). Cook and Jacobs (2000) concluded that in mild winter production areas, temperatures that should normally promote chilling requirement satisfaction, enhanced dormancy. Their results showed that the bud dormancy progression not only differ between cultivars, but also between the same cultivars in deferent areas. Different endodormancy patterns observed by Cook and Jacobs (2000) between Granny Smith and Golden Delicious apples supports the findings of Hauagge and Cummins (1991a; 1991c) that cultivars not only differ in terms of changes of dormancy intensity but also in terms of patterns and rates of change. These patterns are cultivar specific and are influenced by local chilling regimes. It is therefore difficult to develop a universal model for accurately predicting the termination of bud dormancy for various genotypes growing under different environments (Hauagge and Cummins, 1991c).

The chilling requirement is a cultivar specific characteristic used to compare genotypes in relation to the termination of dormancy. This, however, only takes into consideration one point in the dormancy-developmental curve. Different genotypes vary not only in their rate of dormancy dissipation, also in the time of induction and the effect of chilling during the dormant period (Halgryn, Theron & Cook, 2001). The study of the pattern of dormancy development and dissipation of cultivars under controlled environmental conditions would assist in grouping cultivars for practical uses, e.g., cultivar and cross-pollinator combinations and timing and dosage of dormancy breaking chemicals. The aim of this trail was to characterize the progression of bud dormancy at a constant temperature of four apple cultivars from two areas, and to form cultivar groups showing a similar dormancy response.

Materials and Methods

One-year-old, unbranched shoots of four cultivars; 'Royal Gala', 'Braeburn', 'Cripps' Pink' and 'Granny Smith' were harvested randomly from bearing commercial orchards in the Ceres (Koue Bokkeveld) [33°S, 945m, ca.1300 Utah model chill units (CU)] and Elgin (34°S, 305m, ca.750CU) regions of the Western Cape, South Africa, respectively. The shoots were taken on 24 May (Ceres) and 30 May (Elgin) from two orchards per cultivar per site (on a North and South facing slope, respectively). In Ceres ca. 450 Utah CU were received before harvest on 24 May

and only ca. 100 Utah CU before 30 May in Elgin. From each orchard, 12 bundles of ten shoots were harvested, defoliated where necessary, and, to avoid desiccation, wrapped in moist paper before cold storage in plastic bags in an upright position at 5-7°C. Two replicate bundles were randomly selected and removed from the cold room every 14 days. The bundles were placed in 5L white plastic buckets with 1ℓ of water containing 5ml. ℓ/1 household bleach (5% sodium hypochlorite), and then transferred to growth chamber that maintained at a constant 25°C and illumination of 215 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation, to force budburst. The water in the buckets was replaced three times a week and the basal 0.5cm of each shoot was cut weekly to avoid any restrictions of water uptake.

The number of shoots with budburst (green tip of a terminal or lateral bud) in each bundle was recorded every two-three days until budburst had occurred on at least 25% of the shoots per bundle.

The rate of budburst was calculated as [1/(days to 25% budburst)] (Cannell, 1989). The data were statistically analysed, using SAS, release 6.12 (SAS Institute, 1996), by Principal Component Analysis (PROC FACTOR), then Cluster Analysis (PROC CLUSTER), and finally by Canonical Discriminate Analysis (PROC CANDISC).

Results and discussion

The change in the rate of budburst (1/days to 25% budburst) over time was calculated for each orchard. By the first forcing date (late May), some orchards exhibited the lowest rate of budburst (maximum dormancy) whereas in many orchards the growth rate decreased before increasing with subsequent chilling. To this response, either a linear or a quadratic function was fitted. The function with the highest fit was always selected (the mean R^2 was 0.92±0.05). Subsequently numerous variables from these functions were calculated (x- and y-intercepts and turning point, growth rates at 100, 250, 5000, 1000, 1500, 2000 chilling hours at 4-7°C and amount of chilling needed for a growth rate of 0.1, 0.15, 0.2 and 0.3). From these variables the following poorly correlated variables were then selected by Principal Component Analysis; the chilling hours at 7°C required to reach the respective budburst rates of 0.1, 0.15 and 0.3; the rate of budburst at 500 or 3000 h of chilling at 7°C; and the minimum rate of budburst (this was assumed to be turning point for quadratic functions and the rate at the first observation date for linear functions). Using these variables, the orchards were separated, using Cluster Analysis, respectively into three, four, and five cluster groupings that represented a progression in rate of budburst or the dormancy pattern (Figure 1).

The first split (three cluster groups) separated the lower chilling requirement cultivars 'Cripps Pink' and 'Granny Smith' from the higher chilling 'Royal Gala' and 'Braeburn' (Figure 1). The only orchards deviating from this were 'Cripps' Pink' North from Ceres and 'Royal Gala' South from Ceres. This 'Cripps' Pink' variation might be due to the microclimate of the northern slope, which could receive less chilling than southern slopes. The 'Royal Gala', southern slope orchard from Ceres behaved different to all other orchards, exhibiting a very slow budburst rate, and was grouped into its own cluster. No apparent explanation is presented for this obvious exception.

The second and third split into four and then five cluster groupings separated orchards according to area differences (Figure 1). After the third split Cluster 1 contains the low chilling cultivars from Elgin and Cluster 2 those from Ceres. The effect of area on dormancy pattern was also expressed in the second split where 'Braeburn' orchards from Ceres were separated from those from Elgin.

Separation of the five cluster groupings (resulting from the third split) was confirmed using Canonical Discriminant Analysis, and the mean value of each of the abovementioned variables determined for each cluster. These variable means were then used to plot the cluster dormancy patterns (Figure 2). The dormancy response to chilling time was quadratic for Cluster 1 through 4, whereas Cluster 5 ('Royal Gala' South from Ceres) was linear. As mentioned the poor growth and chilling response of this 'Royal Gala' orchard was the exception and will not be discussed further.

Cluster 1, all 'Cripp's Pink' and Granny Smith' orchards from Elgin initially entered deeper into dormancy before exiting (increased budburst rate) with more chilling. Cluster 2, 'Granny Smith' from Ceres and 'Cripp's Pink' North from Ceres, was already dormant and chilling immediately broke dormancy. In Ceres ca. 350 Utah CU more than in Elgin were received before harvest on 24 May. As a result of these different turning points (maximum endodormancy), Cluster 2 never reached the same rate of budburst as Cluster 1. Cluster 4, 'Braeburn' from Elgin, entered dormancy during cold storage but less than the other clusters (minimum rate of budburst >0.1) to exit from dormancy slower than 'Braeburn' from Ceres (Cluster 3). Cluster 3 orchards were in a deeper dormancy at harvest and then exited dormancy slower than Cluster 1 and 2 but slightly faster than Cluster 4.

Studies done in the same areas (Ceres and Elgin), under field conditions by Cook and Jacobs (2000), found a difference in the progression of bud dormancy between the areas. In Ceres, a maximum dormancy was reached earlier in winter without considerable chilling (<100 CU), whereas in Elgin, 600 CU accumulated before a maximum was obtained. They argue that temperatures other than those used to calculate chilling units induced dormancy in Ceres, possibly freezing temperatures or frost.

These data confirm that the rate of budburst consistently corresponds to chill accumulation increasing with chilling period (Saure, 1985; Cannell, 1989; Haugge & Cummins, 1991b). 'Granny Smith', 'Cripp's Pink' and 'Braeburn' shoots collected from the warmer Elgin still required a period of chilling to enter dormancy. This confirms the previous findings of Cook and Jacobs (2000) that the chilling requirement includes a period of dormancy induction as seen when chilling temperatures in late autumn cause apple bud to react progressively slower towards favourable growing temperatures. A positive chilling response (increased rate of budburst) is only effective after a maximal dormancy has been reached (Saure, 1985; Cannell, 1989; Haugge & Cummins, 1991b).
These results, furthermore, support the view of Haugge and Cummins (1991a) of important genotype and environment interactions (e.g., early autumn frost) other than cold unit accumulation, that are responsible for terminating bud dormancy. Only two factors differ between buds used in this trail, climatic conditions before artificial chilling and the genotype. While artificial chilling can increase the rate and uniformity of budburst (Citadin *et al.*, 2001) it could not replace the growth potential lost as a result of inadequate climatic stimulus formation during dormancy induction.

In conclusion, marked differences in the expression of apple bud dormancy of cultivars from areas with different climate, highlight the difficulty in quantification of chilling requirements. Differences in dormancy patterns under field conditions could be related to specific cultivar response in relation to the stimulation and negation effects of temperatures on dormancy induction in addition to dormancy breaking. Grouping cultivars into higher or lower chilling requirement groups was accomplished, but the interaction with climatic effects must also be taken into account.

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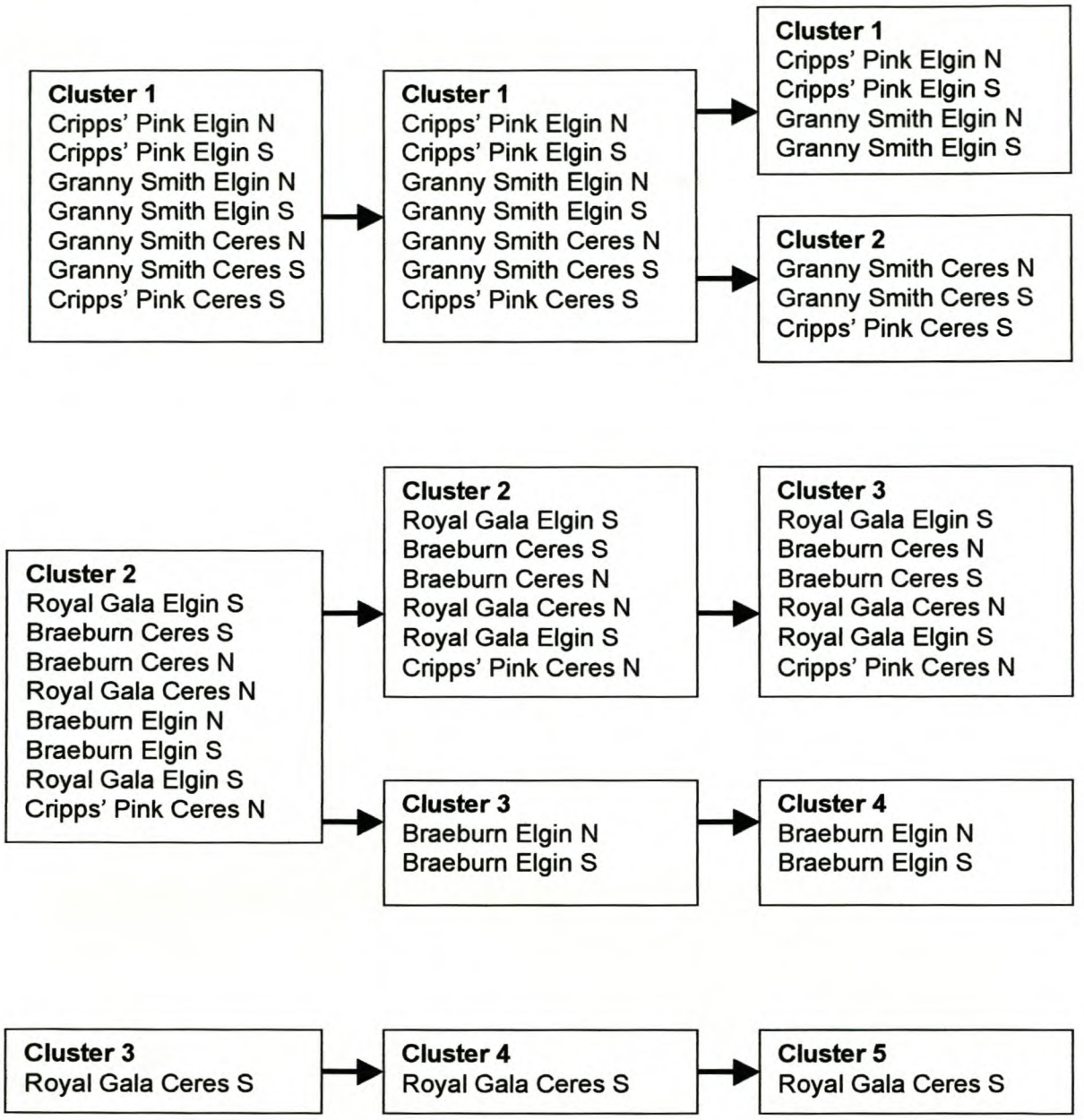

Figure 1 Organization chart of four cultivars from Elgin and Ceres (Koue Bokkeveld) grouped into clusters separated based on dormancy patterns.

[X] N and S indicate for each orchard respectively, a northern or southern slope.

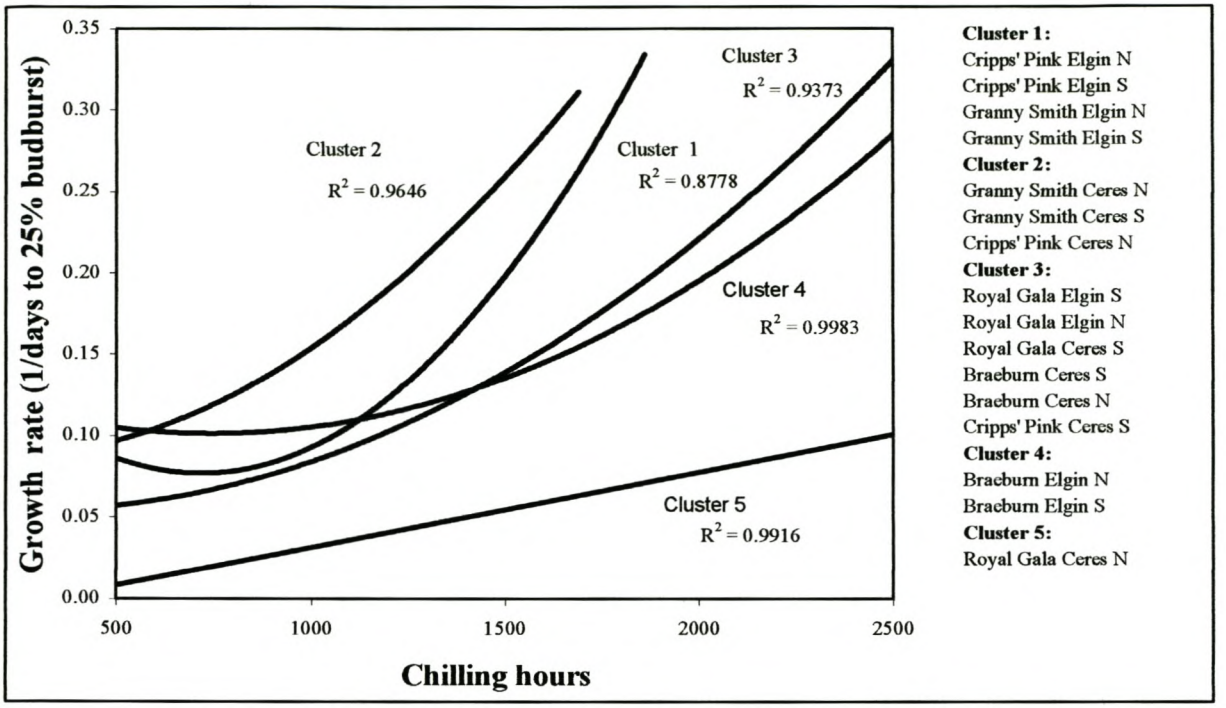

Figure 2 The progression in apple bud dormancy between cultivar groupings depicting a different chilling response.

3. Paper 2: Changes in the water potential of apple buds during dormancy

Abstract

Terminal apple buds from four cultivars Royal Gala, Braeburn, Cripps' Pink, and Granny Smith were cut from orchards in the Ceres (Koue Bokkeveld) (33°S, 945m, ca 13000CU) and Elgin (34°S, 305m, ca 750CU) regions of the Western Cape, South Africa. Buds were harvested every two weeks during the dormant period. The buds were cut in half and scale leaves removed before the water potential was measured. Fresh and dry weights of the buds were determined. The data confirm changes in availability of free water in dormant buds and that water availability can be easily measured in this way. A definite chilling influence was observed; water potential from buds in a cold production area (Koue Bokkeveld) increased with chilling whereas buds from the warmer Elgin showed little change in water potential or content.

Keywords: Apple, dormancy, terminal bud water potential, chilling.

Introduction

Temperate zone fruit, including apple, need chilling before they resume normal budburst after dormancy in winter. Chilling models are used to predict the chilling regime and the satisfaction thereof, however, little is known about the physiological/bio-chemical events that mark the end of the chilling period (Faust, 1989). Progress in the development of a dormant bud cannot be clearly determined by its appearance. However, some cellular components change during dormancy progression that can be measured to indicate the physiological state of the bud. For example abscisic acid (ABA) levels have been found to be highest during endodormancy and decreasing during ecodormancy (Seeley & Powell, 1981). An accumulation of starch in sour cherry flower buds (Felker *et al.*, 1983), and an increase in desaturated membrane lipids of apple buds (Wang and Faust, 1990) have been documented. However, water being the main solvent for cellular components that are responsible for physiological development, it is logical to expect that any changes in water mobility in the bud tissue, will accompany the physiological changes associated with dormancy (Sugiura *et al.,* 1995).

Water status of biological samples have been measured using different techniques; MRI (Faust *et al.,* 1991; Lui *et al.,* 1993), NMR and DSC (Differential Scanning Calorimetry) (Sugiura *et al.,* 1995), in order to describe the little know physiological and biochemical events that mark the end of chilling. Conversion of bound to free water occurs equally in low- and high-chilling cultivars, and it appears that processes involved in chilling also convert water in buds from

bound to a free form (Faust *et al.,* 1991). In this research, we observed the water status of terminal apple buds by determining the water potential during endodormancy.

Materials and Methods

Terminal buds of four apple cultivars; Royal Gala, Braeburn, Cripps' Pink and Granny Smith were selected randomly from bearing commercial orchards in the Ceres (Koue Bokkeveld) (33°S, 945m, ca.1300CU) and Elgin (34°S, 305m, ca.750CU) regions of the Western Cape, South Africa, respectively. Terminal vegetative buds on ca. 20cm long shoots were harvested every two weeks from the two climatologically different areas from 20 May 2001 onwards. Collecting stopped before dormancy-breaking chemicals were applied in the orchards (mid to late August). In each of the areas, two replicate orchards (on north and south facing slopes) were selected for each of the cultivars. Each replication constituted a pooled sample of ca. 30 terminal buds.

In the laboratory, the buds were cut from the subtending shoot, halved and the bud scales (dry leaf like structures enclosing the bud) removed before their water potential was determined using a Dewpiont Potentiameter (Wp4, Decagon Devices, Inc., Pullman, WA, USA). The fresh and dry weights of the buds were also determined. TinytagPlus data loggers (Gemini Data Loggers (UK) Ltd. Chichester, West Sussex, England) were placed in Stevenson screens in the orchard. The hourly mean temperature was logged for the duration of the trail. Data were analysed using the GLM and LSMEANS procedures of SAS, release 6.12 (SAS Institute, 1996).

Results and discussion

A definite trend of a low water potential at the start of the season that increased towards the end of winter was observed (Figures 1,2, and 3). Chilling probably plays a role in this increase in water availability (Figure 3). The water potential of the four cultivars differed with cultivar and area. In the Ceres (Figure 2 and Table 2), the water potential of 'Cripps' Pink' was the lowest of the four cultivars until early June, but at the end of winter (August) increased to levels significantly higher than the rest. No significant difference in water potential between 'Royal Gala', 'Braeburn' and 'Granny Smith' was observed.

The cultivars behaved somewhat differently in Elgin compared to Ceres (Figures 1 and 2). In Elgin the water potential started higher but ended lower. The 'Cripps' Pink' buds from Elgin did not show the low water potential of those from Ceres at the start of the season but was the only

cultivar that had the same water potential at the end of the trail (Tables 1 and 2). The mean bud water potential of the combined cultivar measurements is shown in Figure 3. During the trail, the water potential measurements from Elgin were at the start higher (more available water) than Ceres measurements, but changed less during dormancy.

The bud moisture content followed the same trend as the water potential (Figure 4). The water content values (% water) from Ceres increased from 48% to 56% (middle August). Whereas in Elgin started the water content remained constant, ca. 53%. The values from the Ceres correspond with findings of (Faust *et al.,* 1991) who reported 41% water content before and 59% after chilling. These data, although not statistically analysed, could be interpreted that in endodormant buds water is bound or structured and that these properties change with chilling.

Clearly chilling facilitates the process of changing water properties during dormancy, if the Elgin and Ceres values are compared (Figure 3,4). During dormancy temperatures are ca. 5°C lower in Ceres than in Elgin. Chilling in Elgin was inadequate to change the water content and properties.

The data presented in this paper confirms the changes in availability of free water in dormant buds. By using the water potential measurements, these changes could be seen. The influence of different temperature regimes was also illustrated. The water potential from a bud in a cold area (Ceres) behaved more "normally" (decreased of free water during available water at the start of winter and the resulting increased availability at end of winter). Whereas buds from Elgin did not change much in water potential or content. The changes of water properties in the bud during dormancy are primarily a mechanism to avoid chilling injury to the bud. These injuries are related to cellular structural damage due to freezing water. The changes in water properties in Ceres could be interpret as an acclimation process as a result of the lower temperatures and their potential damaging effect on cell integrity.

Water in endodormant buds is found primarily in the cell wall matrix, while water in the eco- and paradormant bud is mainly intercellular (Faust *et al.*, 1991). This movement of water is related to hardiness and acclimation of plant tissue. It appears that acclimation of vegetative apple tree buds involved at leased two processes, firstly an increase in tolerance to dehydration and secondly, an increase in the level of non-freezable waters (Vertucci & Stushnoff, 1992). This process may involve changes in the concentration of protective solutes (dehydrins-proteins) or in the behaviour of water at macromolecular interface (Aurora, Wisniewski & Davis, 1992).

The interlinking nature of dormancy and cold hardiness suggests that thorough the study of the different mechanisms of the physiological state of the bud, a better understanding will be possible. Knowledge of phenomena like supercooling, anatomical features of freezing avoidance (Quamme, Su & Veto, 1995) and production of cold induced substrates like dehydrins (Aurora, Wisniewski & Davis, 1992) could contribute alongside measurements of water properties to comprehend this fascinating aspect of plant growth regulation.

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Figure 1 Change during endodormancy in the mean water potential values of terminal buds on extension shoots of four apple cultivars grown in Elgin (buds were harvested from orchards on a Northern and Southern slope for each of the cultivars).

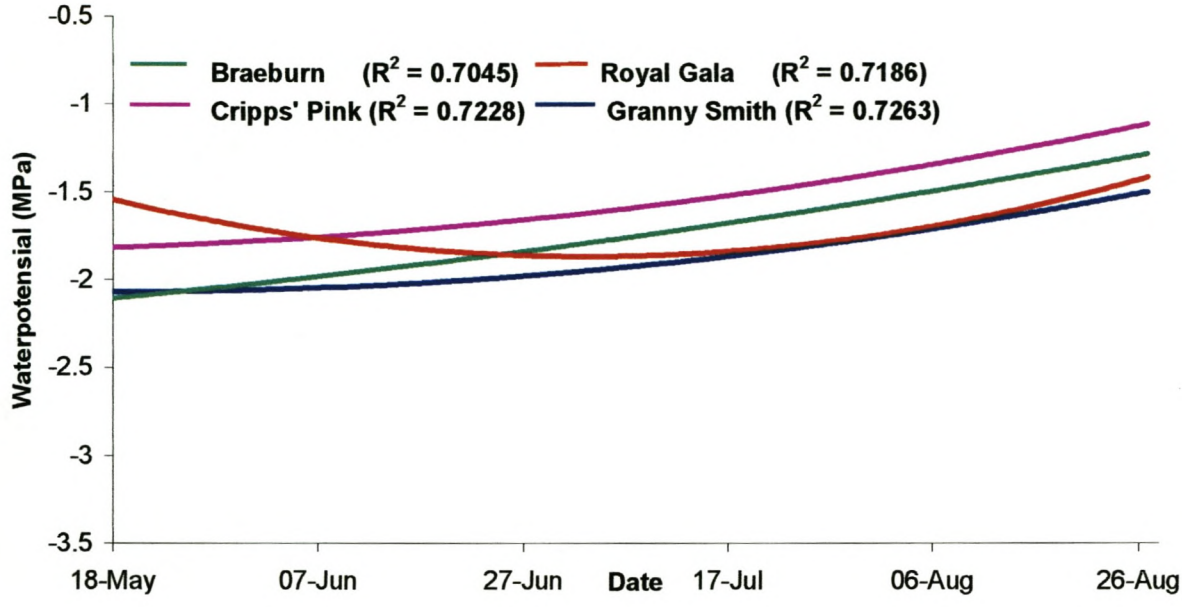


Table 1 Water potential of terminal buds of four cultivars from Elgin during winter of 2001.

	Date					
Cultivar	**5/18**	**6/7**	**7/17**	**7/27**	**8/6**	**8/26**
Braeburn	-2.11 a	-1.98 a	-1.85 ab	-1.69 ab	-1.47 ab	-1.29ab
Royal Gala	-1.55 b	-1.76 b	-1.86 ab	-1.85 a	-1.97 a	-1.42 a
Cripps' Pink	-1.81 ab	-1.76 a	-1.67 a	-1.53 b	-1.32 b	-1.12 b
Granny Smith	-.2.07 a	-2.05 a	-1.99a	-1.88a	-1.69a	-1.51 a

Mean separating within columns by LSD (5%).

Figure 2 Change during dormancy in the mean water potential values of terminal buds on extension shoots of four apple cultivars grown in Ceres (Koue Bokkeveld) (buds were harvested from orchards on a Northern and Southern slope for each of the cultivars).

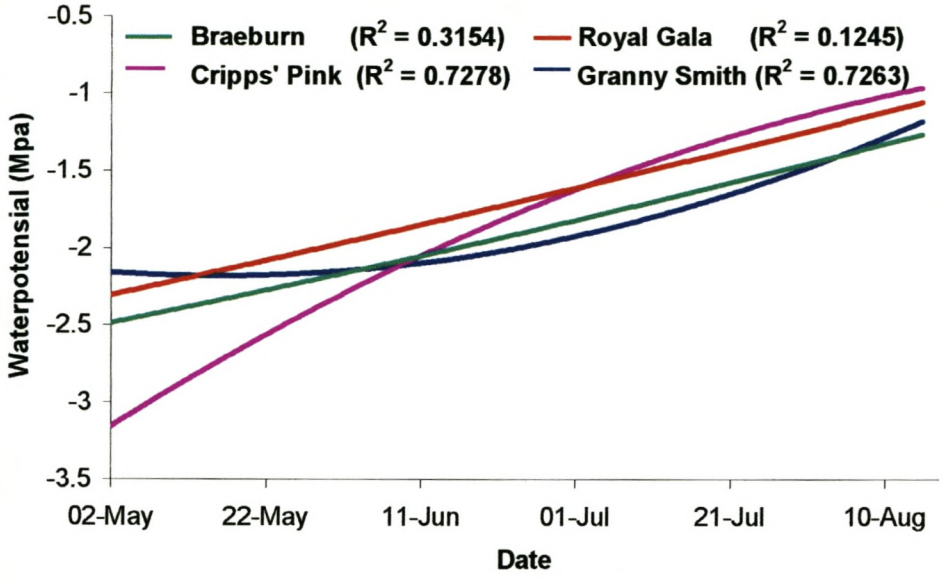


Table 2 Water potential of terminal buds of four cultivars from Ceres (Koue Bokkeveld) during dormancy during the winter of 2001.

	Date					
Cultivar	**5/8**	**5/22**	**6/11**	**7/3**	**7/23**	**8/15**
Braeburn	-2.48 b	-2.28 bc	-2.05 a	-1.80 a	-1.56 a	-1.27 a
Royal Gala	-2.31 b	-2.08 bc	-1.85 a	-1.59 a	-1.35 a	-1.06 a
Cripps' Pink	-3.05 a	-2.58 a	-2.13 a	-1.67 a	-1.28 a	-0.86 b
Granny Smith	-2.16 b	-2.17 ac	-2.01 a	-1.90 a	-1.62 a	-1.18 a

Mean separating within columns by LSD, p=0.05.

Figure 3 Mean water potential measurements of terminal buds and changes in daily temperature, during the trial period. Terminal buds from Royal Gala, Braeburn, Cripps' Pink and Granny Smith apple orchards growing on Northern and Southern slopes in Ceres and Elgin were used for measurements. The temperature data is shown as the mean daily temperature for each of the areas.

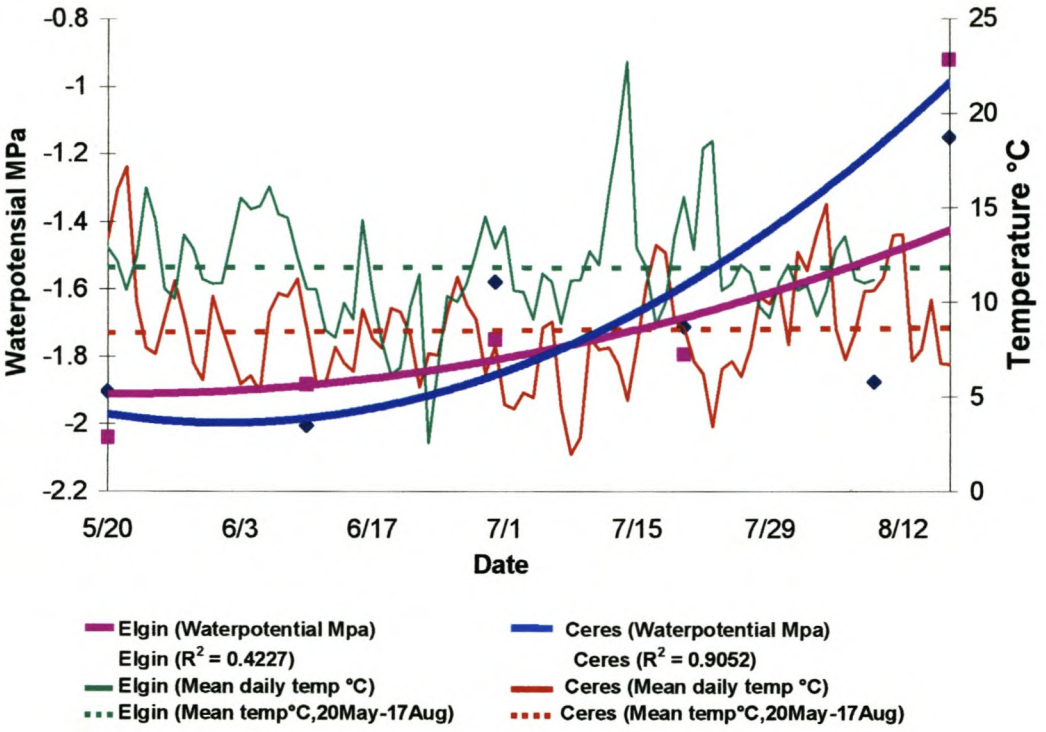
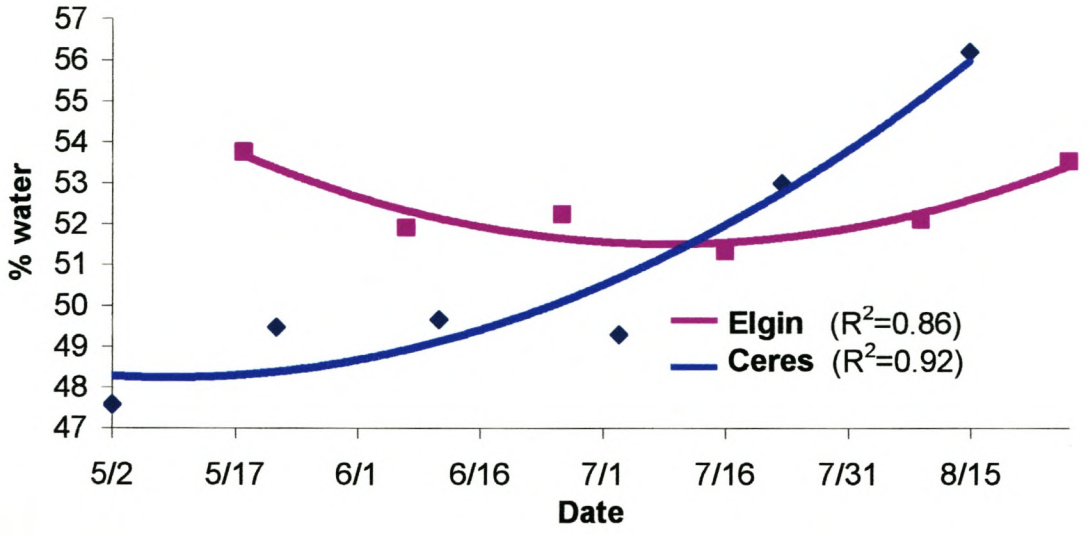


Figure 4 Changes in water percentage of terminal buds during the dormant period. Polynomial lines were fitted for the determined mean % water found in terminal apple buds of the four cultivars (Royal Gala, Braeburn, Cripps' Pink and Granny Smith) harvested from Northern and Southern slopes in Ceres and Elgin.



4. Paper 3: Pruning affects the development of correlative phenomena in 2-year-old 'Royal Gala' apple branches

Abstract

Two-year-old proleptic-branched shoots, ca. 50cm long, were selected from a 'Royal Gala' orchard in Ceres (Koue Bokkeveld) region (33°S, 945m, ca. 1300 Utah chilling units) in the Western Cape, South Africa. The shoots received two cold treatments; chilling in a cold room at 5-7°C and the natural chilling received in the field during 2000. In 2001, the trail was repeated, but only with the field chilling. The shoots received five dormant pruning treatments: control (not pruned), pruning back to the fourth lateral (heading) before or after chilling; and removal of the 2nd and 3rd laterals (thinning) before or after chilling. After pruning and chilling, the shoots were removed from the orchard or cold room every two weeks and forced in a growth chamber. The rate of bud burst (1/days to 50% bud burst) was calculated for the terminal buds of the lateral shoots, following categorization according to lateral position: the terminal extension shoot, the 4th lateral, and all other laterals pooled. Removing distal tissue by pruning (heading more than thinning) promoted bud burst on laterals. Pruning before chilling was more effective than after chilling. The correlative phenomena that inhibit bud burst on proximal shoots within two-year-old branches were manipulated by pruning.

Keywords: apple, pruning, correlative phenomena, dormancy.

Introduction

Apple shoots result from the unfolding of successive metamers, each consisting of a node, leaf, axillary bud and subtending internodal segment (Lauri & Térouanne, 1998). On vigorous shoots, some axillary buds may develop into shoots simultaneously with the extension of the main shoot axis (Hallé *et al.*, 1979). More generally, in temperate zone species axillary buds develop into shoots the following year after a dormant period. After adequate winter chilling, bud burst of the terminal and numerous lateral buds on the one-year-old shoot is proleptic (Cook & Jacobs, 1999).

The pattern of bud burst after dormancy resulting in lateral shoots forming on the year-old shoot is influenced by successive and linked regulating mechanisms. The combined effect can be seen under forcing conditions in the rate of bud burst, which is the sum of the endodormant (within the bud) and paradormant (from organs and tissues outside the bud) components. Whereas

endodormancy is an internal physiological block that prevents growth and appears to be removed by exposure to low temperatures, the paradormant component largely includes inhibition by distal shoot tissues (Champagnat, 1983; Cook *et al.*, 1998).

Following "adequate chilling", a well defined acrotonic bud bursting tendency develops before bud burst on the year-old shoot. Acrotony is the bursting and forming of extension shoots from the most distal or apical buds (Rauh, 1939). This acrotonic bud bursting tendency develops from the terminal bud that appears to exert primigenic dominance via an increased growth potential (Bangerth, 1989). The dominance is then further accentuated by inhibition by the distal shoot tissues. As a result of a positional advantage, the terminal bud, in the absence of paradormant inhibitions, is capable of establishing dominance and, thus a clearly defined acrotonic bud-bursting tendency (Cook *et al.*, 1999; Cook & Jacobs, 1999).

Apical dominance may play a role in acrotonic branching. Cline (1997) defines apical dominance "as the control exerted by the shoot apex over the outgrowth of the lateral buds". In the year of shoot formation it is thought that apical dominance leads to the paradormant inhibition of lateral buds, which normally grow only the following spring after adequate chilling (Cline & Deppong, 1999). In the second year, after bud burst of the dormant buds another mechanism, apical control, regulates the amount of elongation and diameter growth of proleptic shoots from previously dormant buds (Wilson, 2000). The terminal shoot via primigenic dominance rapidly establishes apical control over proximally located developing laterals (Bangerth, 1989). Bangerth, Li and Gruber (2000) suggested that the differences in IAA export from, and transport capacities of, dominant and dominated shoots, may be explained by a mechanism of auxin transport auto-inhibition (ATA), whereby the earlier and stronger export of IAA from the dominant shoot inhibits auxin export from the dominated shoot at the point where the two auxin streams converge. As each subsequent lateral bursts, it contributes to the inhibiting signal and thereby inhibiting shoot growth in the proximal direction, resulting in the most proximal shoots being reduced to spurs (Cook & Jacobs, 1999). It appears that after adequate chilling the bud-bursting pattern is synchronized on a shoot axis and correlative phenomena between buds appear to be conducive to the development of strong apical control (Cline, 1997; Cook *et al.*, 1998).

In areas with inadequate winter chilling, acrotonic branching is impeded by a modified bud burst pattern known as "delayed foliation" (Saure, 1985), which negatively influences tree growth. Firstly, there is a lower growth rate in the terminal as well as in the laterals buds (Crabbé, 1994),

which results in less branches forming. Furthermore, an increased basitonic bursting tendency is observed, with the proximal lateral buds bursting more readily than the distal ones (Jacobs *et al.*, 1981). An increased paradormant inhibition by the distal shoot tissues is also observed. Under inadequate chilling conditions, paradormancy largely amounts for the inhibition of lateral bud burst. The cause of this resides more in the shoot piece than the buds themselves (Cook *et al.*, 1999). This erratic bud burst pattern hinders apical control and the resultant hierarchic growth form. Proximally situated shoots become autonomous and lead to basitonic branching.

Limited information considering the interaction between endodormancy and paradormancy after the second rest period is available. The problems associated with inadequate winter chilling locally, and the importance of two-year-old branches in fruit production, require the examination of the development of correlative influences (paradormancy, apical control, and primigenic dominance) between shoots within in two-year-old branches. The role of commonly used pruning practices in the modification of these phenomena was investigated.

Materials and Methods

Two-year-old branches, ca. 50cm long were selected randomly from a commercial Royal Gala apple orchard in the Koue Bokkeveld region (33°S, 945m), near Ceres in the Western Cape. This area has moderately cold winter conditions receiving ca. 1500 Utah chill units.

The data were collected during two consecutive winters. In 2000 the shoots received two cold treatments; the natural chilling in the orchard or artificial chilling in a cold room at 5-7°C. In 2001, the trail was repeated but only with natural chilling. In 2001, the trail commenced earlier, 26 March, to observe the entrance into endodormancy in autumn as well as the exit in winter (Figure 2c). The shoots selected for the field chilling were tagged at the beginning of the winter (8 June 2000 and 26 March 2001). The shoots selected for artificial chilling in 2000 were cut from the trees on 8 June and transferred to the cold room. Every two weeks (seven dates in total), six shoots (replications) per treatment were cut from the trees (field chilling) or removed from the cold room. The shoots were placed into 5ℓ white plastic buckets with their bases in 1L of water containing $5ml \cdot \ell^{-1}$ household bleach (5% sodium hypo chlorite) and transferred to a growth chamber that maintained at a constant temperature of 25°C and 215 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photosynthetically active radiation. The water in the buckets was replaced three times a week and the basal 0.5cm of each shoot was cut weakly to avoid restrictions of water uptake.

For each of the chilling regimes the shoots received five dormant pruning treatments: control (not pruned), pruning back to the fourth lateral (heading) before or after chilling; and removal of the 2nd and 3rd laterals (thinning) before or after chilling (Fig. 1).

Shoots on the 2-year-old branches were numbered from the terminal (position 1) in a proximal direction; shoots with ten laterals were selected and the rest were removed. The bud bursting pattern was recorded for each shoot every two to three days until all, the terminal buds of all laterals had reached green tip (burst) or died. Shoot position on the branch was divided into tree classes; the terminal position (one), position four, and all other laterals (positions ≥5) except in the control treatment (positions ≥2). The rate of bud burst was calculated for the classes in each treatment as [1/(days to bud burst)], (Cannell, 1989). The rate of bud development of the different classes was compared by ANOVA using the GLM procedure of SAS version 6.12 (SAS Institute, 1996).

Results and Discussion

The change with time in the rate of bud burst [(1/days to budburst)] of the terminal buds on laterals in different positions was calculated for each treatment and is presented (Figure 2, Table 1). The exit from dormancy is observed in all years while in 2001 entrance and exit from dormancy are clearly observed. The cold room chilling (Fig 2b) resulted in the highest rate of budburst and chilling was clearly adequate. The rates of budburst in 2001 under field chilling was somewhat higher than 2000, and can be ascribed to the colder winter in 2001 (1077 and 1419 Utah Cold units received 2000 and 2001, respectively). During 2000 in the cold chamber a basitonic bud-bursting tendency developed in the control shoots (Fig. 2b). Terminal buds on lateral shoots had a slightly higher rate of budburst (not significant) than the terminal. This did not occur under field chilling (Fig. 2a, c). Under field chilling the laterals could not establish autonomy from dominance by the terminal.

By removal of distal shoots tissue (pruning) the rate of bud burst on lateral shoots was altered (Table 1). Heading removed the terminal and the first two laterals. The fourth lateral, as the new terminal position following heading (Figure 1) could establish dominance over the laterals. Heading compared to control and thinning resulted in the fastest budburst of the new terminal (position Four) as well as the laterals (Figure 2a, b, c).

Of the two pruning treatments, thinning removed less distal shoot tissue (Figure 1). In the thinning treatments, the terminal shoot was left intact and had a negative influence on the rate of budburst on laterals.

The rate of budburst differed if the treatments were done before or after chilling (Figure 1). The influence of time of pruning becomes evident when the rate of budburst after thinning and heading before chilling is compared to pruning after chilling. Pruning before chilling increased the rate of budburst on laterals most. The results could indicate that removing the distal inhibiting tissue after or at the end of endodormancy is less effective. These pruning effects indicate the presence of the correlative inhibition of budburst on laterals acting increasingly in a basipetally direction. Apical control may be involved

In order for a bud to dominate, it must have a positional (more distal) as well as a time advantage (primigenic dominance) over the dominated buds. In proleptic branches, after the first dormant period, the terminal bud can establish dominance as a result of being the first bud to burst (primigenic dominance). This growth pattern would lead to a well-defined acrotonic branching habit (Cook *et al.*, 1998). After the second dormant period, this acrotonic branching habit, although not significant, is still evident in the ex-field during 2000 in the control branches (Figure 2) where the terminal shoot exhibited a higher budburst rate resulting from the primigenic dominance and the paradormant effect it had on the more proximal buds. If the terminal shoot is lost as a result of pruning the next proximal shoot will become the dominating terminal (Wareing & Nasr, 1961). These results could indicate an inhibiting signal originating from the most distal tissue. Bangerth, Li and Gruber (2000) formulated in a recent publication a theory concerning IAA transport and the resulting effect on apical control. By using exogenous auxin and cytokinins on apple, pea and tomato plants, they formulated a hypothesis concerning IAA export and transport. They suggested those differences in IAA export from, and transport capacities of, dominant and dominated shoots may be explained by a mechanism called auxin transport auto-inhibition (ATA). This mechanism describes that where the two streams of IAA met in the transport pathway, the first stream of auxin (from the dominant organ, i.e., terminal meristem) inhibits the export stream of IAA from the other organ. This organ then becomes a dominated organ, which results in an inability to export the auxin produced in the organ, thus keeping the meristem inhibited. These authors found ATA to be sufficient to impose dominance without the need for other regulators.

To conclude pruning before chilling was more effective than after chilling. The correlative phenomena that inhibit bud burst on proximal shoots within two-year-old branches were clearly manipulated by pruning. These pruning effects indicate the presence of the correlative inhibition of budburst on laterals by distal shoot tissues acting in a basipetal direction. These effects may ultimately culminate in apical control.

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Table 1. Results of comparative analysis of the rate of budburst between Terminals (Term), Fourth lateral proximal from terminal (Four) and Laterals (Latr) with in treatments.

Cold chamber, 5-7°C (2000)		Term vs. Four	Term vs. Latr	Four vs. Latr
Control	Treatment		0.209	
	Time		0.0001	
	Treatment*Time		0.185	
Thinning before	Treatment	0.026	0.406	0.14
	Time	0.0001	0.0001	0.0001
	Treatment*Time	0.026	0.035	0.064
Thinning after	Treatment	0.008	0.06	0.133
	Time	0.001	0.001	0.001
	Treatment*Time	0.268	0.024	0.316
Heading before	Treatment			0.007
	Time			0.001
	Treatment*Time			0.908
Heading after	Treatment			0.123
	Time			0.0001
	Treatment*Time			0.921

Table 1(cont). Results of comparative analysis of the rate of budburst between Terminals (Term), Fourth lateral proximal from terminal (Four) and Laterals (Latr) with in treatments.

Field chilling (2000)		Term vs. Four	Term vs. Latr	Four vs. Latr
Control	**Treatment**		0.011	
	Time		0.001	
	Treatment*Time		0.718	
Thinning before	**Treatment**	0.0437	0.066	0.362
	Time	0.001	0.001	0.001
	Treatment*Time	0.641	0.027	0.569
Thinning after	**Treatment**	0.320	0.276	0.258
	Time	0.001	0.001	0.001
	Treatment*Time	0.69	0.254	0.872
Heading before	**Treatment**			0.003
	Time			0.001
	Treatment*Time			0.579
Heading after	**Treatment**			0.272
	Time			0.001
	Treatment*Time			0.976

Table 1(cont). Results of comparative analysis of the rate of budburst between Terminals (Term), Fourth lateral proximal from terminal (Four) and Laterals (Latr) with in treatments.

Field chilling (2001)		Term vs. Four	Term vs. Latr	Four vs. Latr
Control	**Treatment**		0.14	
	Time		0.0001	
	Treatment*Time		0.09	
Thinning before	**Treatment**	0.443	0.058	0.048
	Time	0.001	0.0001	0.0001
	Treatment*Time	0.033	0.058	0.012
Thinning after	**Treatment**	0.406	0.455	0.105
	Time	0.0001	0.0001	0.0001
	Treatment*Time	0.241	0.55	0.409
Heading before	**Treatment**			0.052
	Time			0.0001
	Treatment*Time			0.112
Heading after	**Treatment**			0.659
	Time			0.0001
	Treatment*Time			0.636

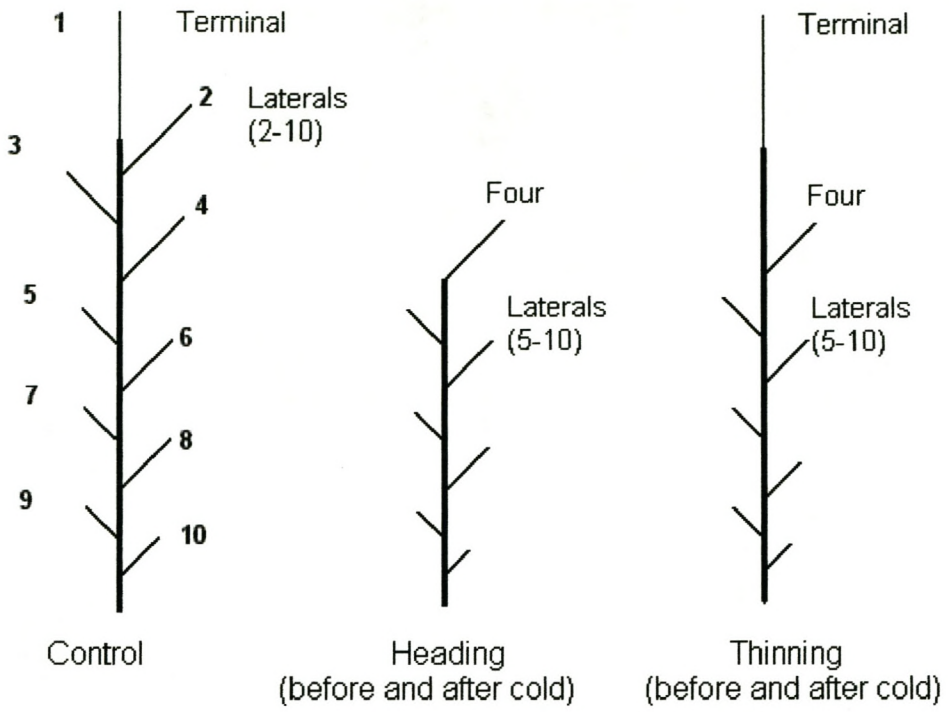

Figure 1 Pruning treatments done on two year old 'Royal Gala' shoots.

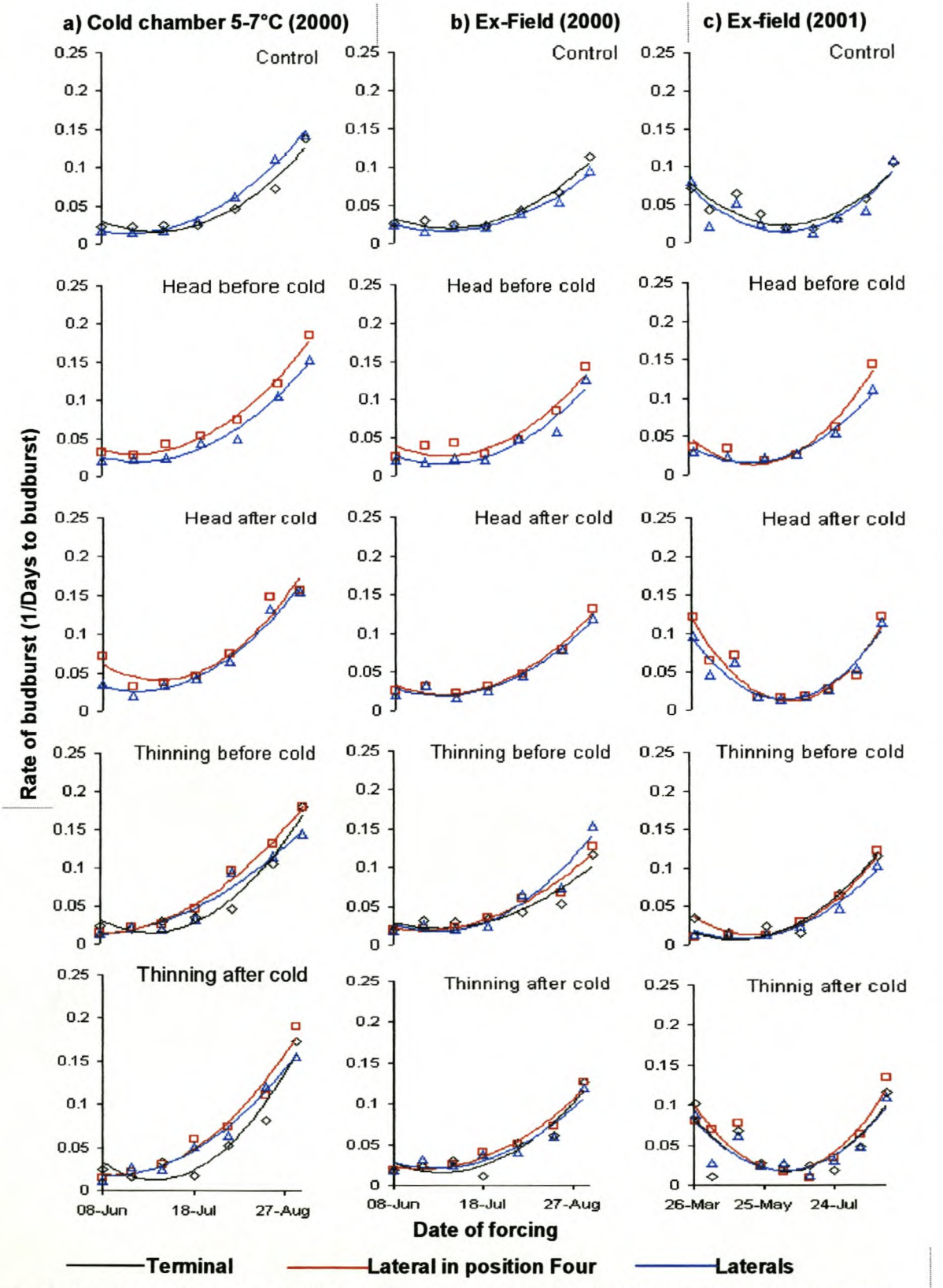

Figure 2 Dormancy patterns of different lateral categories (Terminal, Lateral in position Four and Lateral) of two year old 'Roval Gala' shoots.

5. Paper 4: Influence of bending and heading on the acrotonic branching habit of apple and pear shoots.

Abstract

The branching response of year-old unbranched shoots, 50cm long, from 'Royal Gala' and 'Cripps' Pink' apple and 'Rosemarie' pear were studied after physical manipulation treatments. Shoots for treatments a, b, c and d were re-orientated from either a horizontal or vertical growing position or left in the original position as control. Treatment d, e, f and h involved the same re-orientation and were headed (cut in half). The amount of growth (in mm) from each node was recorded as well as the position from the terminal bud. The 'Cripps' Pink' had a definite shift in the acrotonic branching pattern, (for the unheaded and headed shoots), towards a more basitonic response. The reduced effect on 'Royal Gala' and 'Rosemarie' suggest the difference in genotype response to bending. The response and lack thereof could also be a function of time of bending.

Keywords: Bending, heading, apple, pear, acrotony, basitony.

Introduction

Woody plants have characteristic branching habits. Lateral branches form, either the same season as the main shoot axis (sylleptic) or after a period of dormancy (proleptic branches). Laterals differ in length and orientation and are usually shorter than parent shoots. Proleptic branches of the same age generally decrease in length in a proximal direction on the parent shoot (acrotony). In contrast, basitonic branching occurs when proximal buds elongate to form extension shoots.

The acrotonic branching habit develops from an increased developmental rate of terminal buds compared to lateral buds from one-year-old apple shoots prior to spring budburst (Cook *et al.*, 1998a,b, Cook & Jacobs, 1999). This increase in growth rate of terminal buds result in a proximal inhibition of lateral bud burst by distal buds and shoot tissue, i.e., paradormancy (Champagnat, 1978; Cook *et al.*, 1998a,b). Acrotony is a prerequisite for trunk formation and allows maintained apical control of the terminal shoot or leader over seasons (Cline, 1997; Rauh, 1939). For basitonic branching to occur proximal buds needs to be released from inhibition by the distal shoot tissues. Basitony is seldom expressed in apple shoots except under specific conditions: gravimorphism (Wareing & Nasr, 1961); following conditions of sub-optimal chilling (Cook & Jacobs, 1999) or by the localized application of cytokinins in spring and autumn (Faust, Lui, Wang & Stutte, 1995) and in combination with gibberellins (Cook *et al.*, 2000).

Gravity is thought to play a role in facilitating transport of an inhibiting signal from organs in dominating (distal) positions (Mullins, 1965). Faust *et al.* (1997) concur with these earlier findings and stated that lateral branching on apple shoots is at least partially regulated by an auxin cytokinin interaction. The dominance of distal buds in shoots has been described as an effect of polar auxin transport and the primigenic dominance phenomena (Bangerth, 1989; Faust *et al.*, 1997). The differences in auxin export from, and transport capacities of, dominant (distal) and dominated shoots (proximal), may be explained by a mechanism of auxin transport auto-inhibition (ATA). The earliest and stronger export of auxin from the dominant shoot inhibits auxin export from the dominated shoot at the point where the auxin streams converge. Auxin from the dominated shoot thereby inhibits proximal shoot to develop (Bangerth, Li & Gruber, 2000). Re-orientation of a orthotropic shoot could disrupt the dominating pattern (distal tissue dominant over proximal tissue) and thereby facilitating the switch from an acrotonic towards a basitonic branching habit.

The branching habit of year-old apple shoots has been changed towards a basitonic habit by the application of TIBA (2,3,5-triiodo-benzoic acid) on distal shoot pieces and Promalin® [N-(phenylmethyl)-1H-purine 6-amine and gibberellins A4+A7)] on proximal shoot pieces (Cook *et al.*, 2000). This work showed the evident role of plant hormones in this growth response. In an attempt to reduce the dominance of the distal shoot piece and modify branching, bending and heading treatments were done on year-old shoots.

Material and Methods

On one year old unbranched shoots, ca. 50cm long, of 'Royal Gala' and 'Cripps' Pink' apple and 'Rosemarie' pear were selected from trees on at Wellgevallen experimental farm, Stellenbosch (34° Southern Hemisphere), in the Western Cape, South Africa. Eight bending and pruning (heading) treatments were conducted on dormant year-old shoots on trees on the 17 and 18 July 2000 (during winter after receiving ca.100 Utah chill units) as follows:

a) Vertical growing (orthotropic) shoots were left as a control; b) horizontal growing (plagiotropic) shoots were left as a control; c) vertical growing shoots were bent horizontal; d) horizontal growing shoots were bent vertical; e) vertical growing shoots were cut in half; f) horizontal growing shoots were cut in half; g) vertical growing shoots were bent horizontal and cut in half; h) horizontal growing shoots were bent vertical and cut in half (Figure 1). All treatments were conducted on branches on ten replicate 'Royal Gala' and 'Cripps' Pink' apple trees and 20

replicate 'Rosemarie' pear trees. The re-orientated shoots were kept in position with a wire. All treated shoots were removed from the trees on 5 January 2001 (after growth stopped) and measured. The length and position of new shoots (laterals) and the first year's growth was measured.

The parent shoots from treatments a, b, c, and d was divided into four quarters (Q1, Q2, Q3 and Q4) and in treatments e, f, g, and h into two halves (Q3 and Q4). The bud growth from the nodes was categorised into four classes: dormant (no growth ≤ 5mm); spur (≥5mm and ≤ 60mm); brindle (≤ 60mm and ≤ 200mm); and shoot (≥200mm). The growth per segment could be compared with growth in other segments and treatments. The growth was then analysed relative to position on the shoot (distance from apex). The data were subjected to an analysis of variance using the GLM (general linear models) procedure of SAS version 6.12 (SAS Institute, 1996)

Results

Bending

Bending vertical 'Cripp's Pink' (Table 1) shoots horizontal significantly reduced the amount of dormant buds, and increased budburst, the number of spurs and brindles. A significant decrease in the number of shoots was also found. Bending of vertical shoots flat significantly reduced the number of shoots in the distal quarter (Q1). Bending horizontal shoots upright did not change the branching pattern. The bending treatments had little effect on the branching pattern of 'Royal Gala' apple and 'Rosemarie' pear shoots (Table 2 and 3).

Bending and heading

The effect of bending with heading was generally similar to bending with 'Cripps' Pink' (Table 4). Bending flat and heading significantly increased the number of spurs as well as a higher total amount of buds bursting. The positional effect shows an acrotonic branching habit much the same as in the intact shoots. More and longer shoots developed from the most distal shoot piece (Q3). The bending treatments had little effect on the branching pattern of 'Royal Gala' and 'Rosemarie' shoots (Table 4 and 5).

Discussion

Acrotony in apple is the result of the positional effect of distal buds of dominance over proximal buds and has been ascribed to an increased ability of the dominant sink to export auxin (Cook *et al.*, 1998a,b; Bangerth, 1989). By autumn applications of cytokinins to the proximal lateral buds

and TIBA to the distal shoot half, increased basitonic branching (Cook *et al.*, 2000). These results provide evidence of a hormonal control of the branching pattern in a shoot.

By bending shoots away from their vertical position, a change in their normal acrotonic growth form has been found by Wareing and Nasr (1961), which proposed that the term gravimorphism should be applied to these effects of gravity on plant growth. By arching apple shoots in autumn and re-orientating them before spring, Crabbé (1987) was able to change the growth habit of shoots resulting in a disruption of the acrotonic form. These shoots were arched when conditions for polar auxin transport was still favourable, which is reported to stop at low temperatures (2-7°C) (Morris, 1979) and during endodormancy. Cook *et al.* (2000) argued that lateral buds, in advantageous positions for auxin transport secured some degree of autonomy to over come the distal inhibitions associated with acrotony in spring (possibly in terms off stored cytokinins).
This in addition to the notion that gravimorphism could be the consequence of an uneven distribution of endogenous auxin (Mullins & Rogers, 1971) and the primigenic effect. It would seem that conditions within the shoot that may lead to the dominance and/or autonomy of a bud could be determined prior to dormancy not merely the result of a bud's ability to export auxin when growth resumes in spring (Cook *at al.*, 2000).

The data reported show that in 'Cripps' Pink' shoots following re-orientation from upright to horizontal a charge in the acrotonic branching habit occurs. Distal branching is reduced. The reduced effect on 'Royal Gala' and 'Rosemarie' suggest the difference in genotype response to bending. The response and lack thereof could also be a function of time of bending. The bending was done in the middle of winter and bending earlier could have a more disruptive effect on the dominating effect of distal tissue.
Results of bending two different apple cultivars on three dates let Lauri and Lespinasse (2001) conclude that the effect of bending on the development and growth patterns of lateral shoots vary with genotype. They confirmed an earlier theory that the gravimorphic effect is progressively superimposed on the initial acrotonic tendency and that the longer bending is done before winter the greater its response could be.

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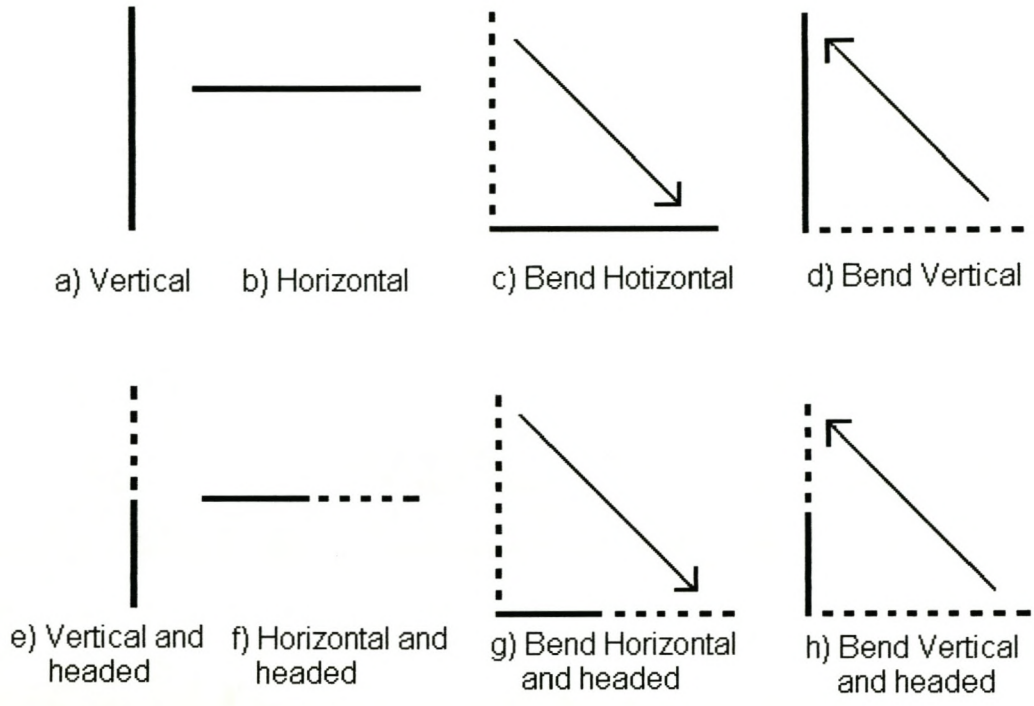

Figure 1 The eight treatments used on 'Royal Gala', 'Cripps' Pink' apple and 'Rosemarie' pear, cultivars. Broken lines in treatments c, d, g and h represent the original position of the shoot and in treatments e-h the original position as well as the removed shoot half.

Table 1 Effects of bending treatments on length of Cripps' Pink apple proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot	Burst buds
Vertical		3.3a	1.2c	0.1b	0.3a	1.7c
Horizontal		0.8c	2.2ab	0.5a	0.06b	2.7b
Bent Horizontal		1.7b	2.8a	0.5a	0.2b	3.4a
Bent vertical		1.1bc	2.0b	0.4ab	0.1b	2.5b
	Q1	1.9a	3.1a	0.9a	0.6a	4.6a
	Q2	1.2b	2.2b	0.1b	0.03b	2.3a
	Q3	1.5ab	1.8b	0.3b	0.00b	2.1b
	Q4	2.0a	1.1c	0.2b	0.01b	1.3c
Vertical	Q1	3.8 a	2.0 bcde	0.5 cd	1.3 a	3.8 bc
Vertical	Q2	2.6 abc	1.6 dcef	0.0 e	0.0 c	1.6 fgh
Vertical	Q3	3.9 a	0.5 f	0.0 e	0.0 c	2.4 def
Vertical	Q4	2.9 ab	0.8 ef	0.0 e	0.0 c	0.8 h
Horizontal	Q1	0.8 e	3.1 ab	1.0 ab	0.1 c	4.2 bc
Horizontal	Q2	0.6 e	2.2 bcd	1.1 de	0.1 c	2.4 def
Horizontal	Q3	0.4 e	2.0 bcde	0.4 cde	0.0 c	2.4 def
Horizontal	Q4	1.3 dce	1.4 def	0.3 dce	0.0 c	1.8 efgh
Bent horizontal	Q1	1.8 bcde	4.1 a	1.4 a	0.6 b	6.1 a
Bent horizontal	Q2	1.4 dce	2.9 abc	0.1 de	0.0 c	3.0 cde
Bent horizontal	Q3	1.3 de	2.9 abc	0.4 dce	0.0 c	3.3 bcd
Bent horizontal	Q4	2.4 bcd	1.1 def	0.0 e	0.0 c	1.1 gh
Bent vertical	Q1	1.7 bcde	3.2 ab	0.7 bc	0.4 b	4.3 b
Bent vertical	Q2	0.6 e	2.0 bcde	0.1 de	0.0 c	2.1 defg
Bent vertical	Q3	0.7 e	1.8 dcef	0.4 dce	0.0 c	2.2 defg
Bent vertical	Q4	1.7 bcde	1.1 def	0.2 cde	0.1 c	1.4 fgh
Significance (P>f)						
Orientation (O)		*0.0001*	*0.0002*	*0.0200*	*0.0050*	*0.0001*
Position (P)		*0.0600*	*0.0001*	*0.0001*	*0.0001*	*0.0001*
O x P		*0.5000*	*0.6900*	*0.2400*	*0.0001*	*0.2000*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

Table 2 Effects of bending treatments on length of 'Royal Gala' apple proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot	Burst buds
Vertical		1.8 a	2.5 a	0.3 a	0.03 b	2.8 a
Horizontal		1.2 b	2.5 a	0.2 a	0.2 a	2.9 a
Bent horizontal		2.1 a	3.1 a	0.3 a	0.1 b	3.5 a
Bent vertical		2.1 a	2.6 a	0.2 a	0.1 b	2.9 a
	Q1	2.3 a	5.4 a	0.7 a	0.4 a	4.7 c
	Q2	1.6 bc	3.5 b	0.2 b	0.01 b	2.9 b
	Q3	1.4 c	3.1 b	0.5 b	0.08 b	2.8 b
	Q4	2.0 b	1.3 c	0.5 b	0.05 b	1.7 c
Vertical	Q1	1.8 dce	3.4 ab	0.9 a	0.1 bcd	4.4 abc
Vertical	Q2	1.4 dce	3.3 abcd	0.0cd	0.0 d	3.4 bcde
Vertical	Q3	1.1 dce	3.0 bcd	0.0 cd	0.0 d	3.1 bcde
Vertical	Q4	3.1 ab	2.5 e	0.0 cd	0.0 d	0.3 f
Horizontal	Q1	2.0 bdc	3.2 abcd	0.6 a	0.6 a	4.4 abc
Horizontal	Q2	0.8 de	2.8 bcd	0.0 d	0.0 d	2.9 de
Horizontal	Q3	0.6 e	1.9 cd	0.2 bcd	0.2 bcd	2.1 e
Horizontal	Q4	1.3 dce	2.1 bcd	0.0 d	0.0 d	2.1 e
Bent horizontal	Q1	1.9 bcd	4.6 a	0.4 ab	0.4 ab	5.7 a
Bent horizontal	Q2	2.2 abc	2.8 bcd	0.0 d	0.0 d	3.1 dce
Bent horizontal	Q3	2.0 abc	2.9 bcd	0.1 dc	0.1 cd	3.1 dce
Bent horizontal	Q4	2.2 abc	1.9 cd	0.0 d	0.0 d	2.1 e
Bent vertical	Q1	3.3 a	3.3 abcd	0.3 abc	0.3 abc	4.1 bcd
Bent vertical	Q2	2.0 bcd	2.1 bcd	0.0 d	0.0 d	2.4 e
Bent vertical	Q3	1.6 dce	3.1 bcd	0.0 d	0.0 d	3.1 bcde
Bent vertical	Q4	1.5 dce	1.8 d	0.2 bcd	0.2 bcd	2.0 e
Significance (P>f)						
Orientation (O)		*0.0140*	*0.3000*	*0.7200*	*0.2300*	*0.2600*
Position (P)		*0.0200*	*0.0001*	*0.0001*	*0.0001*	*0.0001*
O x P		*0.0500*	*0.1100*	*0.7400*	*0.4000*	*0.1300*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

Table 3 Effects of bending treatments on length of 'Rosemarie' pear proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot[X]	Burst buds
Vertical		0.8 a	3.6 a	0.03 a	0	3.7 a
Horizontal		0.8 a	3.2 a	0.03 a	0	3.2 a
Bent horizontal		1.1 a	3.4 a	0.06 a	0	3.4 a
Bent vertical		0.9 a	3.0 a	0.06 a	0	3.1 a
	Q1	0.6 b	5.4 a	0.15 a	0	5.5 a
	Q2	0.4 b	3.5 b	0.03 b	0	3.5 b
	Q3	0.4 b	3.0 b	0.0 b	0	3.0 b
	Q4	2.1 a	1.3 c	0.0 b	0	1.3 c
Vertical	Q1	0.4 b	6.0 a	0.1 ab	0	6.1 a
Vertical	Q2	0.4 b	3.8 cd	0.0 b	0	3.8 cd
Vertical	Q3	0.5 b	3.1 d	0.0 b	0	3.1 cd
Vertical	Q4	2.0 a	1.6 ef	0.0 b	0	1.6 ef
Horizontal	Q1	0.8 b	5.3 ab	0.1 ab	0	5.4 ab
Horizontal	Q2	0.05 b	3.5 cd	0.0 b	0	3.5 cd
Horizontal	Q3	0.1 b	2.6 de	0.0 b	0	2.6 de
Horizontal	Q4	1.9 a	1.3 f	0.0 b	0	1.3 f
Bent horizontal	Q1	0.6 b	5.7 ab	0.2 a	0	5.9 ab
Bent horizontal	Q2	0.7 b	3.3 d	0.0 b	0	3.3 d
Bent horizontal	Q3	0.8 b	3.2 d	0.0 b	0	3.2 d
Bent horizontal	Q4	2.2 a	1.3 ef	0.0 b	0	1.3 ef
Bent vertical	Q1	0.9 b	4.7 bc	0.1 ab	0	4.8 bc
Bent vertical	Q2	0.2 b	3.4 cd	0.1 ab	0	3.6 cd
Bent vertical	Q3	0.3 b	3.1 d	0.0 b	0	3.1 d
Bent vertical	Q4	2.1 a	0.1 f	0.0 b	0	0.09 f
Significance (P>f)						
Orientation (O)		*0.5700*	*0.3000*	*0.9300*	*1*	*0.2900*
Position (P)		*0.0001*	*0.0001*	*0.0100*	*1*	*0.0001*
O x P		*0.8300*	*0.9400*	*0.9600*	*1.*	*0.8900*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

X, no shoot growth was found in this category.

Table 4 Effects of bending treatments on length of 'Cripps' Pink' apple proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot	Burst buds
Vertical and cut in half		3.8 a	0.9 b	0.2 b	0.6 a	1.6 b
Horizontal and cut in half		1.6 bc	1.7 ab	0.8 a	0.3 a	2.7 a
Bent horizontal and cut in half		2.8 ab	1.9 a	0.6 ab	0.6 a	3.0 a
Bent vertical and cut in half		1.3 c	1.8 a	0.2 b	0.6 a	2.6 ab
	Q3	1.5 b	1.8 a	0.7 a	0.9 a	3.4 a
	Q4	3.2 a	1.3 a	0.1 b	0.1 b	1.4 b
Significance (P>f)						
Orientation (O)		*0.0003*	*0.1000*	*0.0500*	*0.2800*	*0.0300*
Position (P)		*0.0001*	*0.1000*	*0.0001*	*0.0001*	*0.0001*
Ox P		*0.800*	*0.8000*	*0.3500*	*0.8000*	*0.8000*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

Table 5 Effects of bending and heading treatments on length of 'Royal Gala' apple proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot	Burst buds
Left vertical and cut in half		3.9 a	2.4 a	0.5 a	0.5 a	3.4 a
Left horizontal and cut in half		1.3 b	2.9 a	0.4 a	0.4 a	3.7 a
Bent horizontal and cut in half		4.0 a	2.4 a	0.6 a	0.6 a	3.6 a
Bent vertical and cut in half		1.4 b	2.9 a	0.2 a	0.3 a	3.4 a
	Q3	2.2 a	2.8 a	0.6 a	0.8 a	4.2 a
	Q4	3.1 a	2.5 a	0.2 b	0.1 b	2.8 b
Significance (P>f)						
Orientation (O)		*0.0001*	*0.7500*	*0.4500*	*0.4900*	*0.9700*
Position (P)		*0.0600*	*0.6000*	*0.0100*	*0.0001*	*0.0050*
O x P		*0.8200*	*0.8000*	*0.7000*	*0.9800*	*0.8500*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

Table 6 Effects of bending and heading treatments on length of 'Rosemarie' pear proleptic shoot growth relative to position.

Orientation	Position	Dormant buds	Spur	Brindle	Shoot	Burst buds
Vertical and cut in half		1.2 a	3.1 a	0.01 a	0.3 a	3.4 a
Horizontal and cut in half		1.0 ab	2.7 a	0.0 a	0.4 a	3.1 a
Bent horizontal and cut in half		0.1 b	3.5 a	0.06 a	0.3 a	3.9 a
Bent vertical and cut in half		1.5 a	3.0 a	0.0 a	0.2 a	3.2 a
	Q3	0.2 b	3.9 a	0.07 a	0.6 a	4.6 a
	Q4	2.0 a	2.3 b	0.0 a	0.0 a	2.3 b
Significance (P>f)						
Orientation (O)		*0.0900*	*0.3200*	*0.6800*	*0.5600*	*0.1690*
Position (P)		*0.0001*	*0.0001*	*0.2300*	*0.0001*	*0.0001*
Ox P		*0.6100*	*0.8700*	*0.6800*	*0.5600*	*0.8800*

NS.*.** Non significant or significant at P<0.05 or 0.01, respectively.

6. *GENERAL DISCUSSION*

Dormancy in woody species is induced naturally in autumn when day length and temperature decreases, and the dormant state is broken or released during the winter by exposure to chilling temperatures (Cannell, 1989). After completion of dormancy, apple bud burst occurs promptly and uniformly in genotypes that are adapted to the environment. However, dormancy symptoms may persist if winter is neither long nor cold enough to adequately break dormancy. "Delayed foliation" is a major symptom observed when deciduous fruit trees are grown in mild winter conditions (Rauh, 1939; Jacobs *et al.*, 1981).

Chilling models used in deciduous fruit production were found to be inadequate in warm winter conditions i.e., the Western Cape, South Africa, in predicting the end of dormancy and the resulting flowering period (Linsley-Noakes & Allen, 1994; Erez, Linsley-Noakes & Allen, 1990). A possible explanation was put forward to explain this failure. Haugge and Cummins (1991) found that there is a difference of dormancy patterns between apple cultivars. Their findings were supported by of Cook and Jacobs (2000) that suggested bud dormancy progression not only differs between cultivars, but also between cultivars growing in different areas. This lack in the understanding of the physiological processes in the apple bud during dormancy (endo- and paradormancy) has negative commercial implications. Production strategies, i.e., chemical and physical manipulations must address this problem to increase yield and quality. Thus, further research concerning the influence of insufficient chilling on endodormancy on different cultivars in two production areas was done. The trails concerned plant growth responses to chilling (artificial and field conditions) and physical manipulations (pruning, thinning and bending) as well as the changes in the status of water in the endodormant bud as an indicator of the physiological status of the bud during the dormant season.

6.1 Patterns of dormancy progression

The inadequate winter chilling in the apple production regions of the Western Cape South Africa has negative influences on the progression of apple bud dormancy. In order to characterize these endodormancy patterns, four apple cultivars from a warm and a colder production area were used to categorize cultivars into clusters showing a similar dormancy response.

The shoots were harvested from commercial orchards at the start of the winter and chilled at 7°C. By forcing bundles of tens shoots every two weeks and recording the growth rate (1/Days to 25% bud burst), the orchards were separated into cluster groupings each representing a

specific dormancy pattern. The first separation were made between high and low chilling varieties and the second and third split into clusters according to area differences. The clusters from the warmer production area initially entered deeper into dormancy before exiting whereas the bud burst rate those from the colder production area immediately increased. These data confirm that the chilling requirement includes a period of dormancy induction that is facilitated by the same range of temperatures (4-7°C) that is required by the bud to exit from endodormancy. The importance of a genotype and environmental interaction, were also evident and make better selection of cultivars very necessary.

6.2 Changes in water potential during endodormancy

The physiological and biochemical events that mark the end of dormancy are not well known (Faust *et al.*, 1997). The progress in the developmental stage of a dormant bud cannot be determined clearly by its appearance. However, some cellular components change during dormancy progression that can be used as a measurable indication of the physiological state of the bud. Therefore, the changes in levels of plant hormones (Seeley & Powell, 1981) starch (Felker *et al.*, 1983) and membrane lipids (Wang & Faust, 1990) have been documented during dormancy progression.

Water being the main solvent for cellular components that are responsible for physiological development, makes it logical to expect that any changes of its mobility in the bud tissue, will accompany the physiological changes associated with dormancy (Sugiura *et al.,* 1995). Water status of biological samples has been measured using different techniques: MRI (Faust *et al.*, 1991; Lui *et al.*, 1993), NMR and DSC (Sugiura *et al.,* 1995), in order to describe the physiological and biochemical events that mark the end of chilling. They found that there is a conversion of bound to free water occurring in dormant buds of low and high chilling cultivars. It appears that the processes involved in satisfying the chilling requirement of the bud, also converting water in buds from bound to free form (Faust *et al.,* 1991).

In this research, the water status was determined of four apple cultivars with a Dewpiont Potentiameter (Wp4, Decagon Devices, Inc, Pullman, WA, USA). The results from the trail confirmed the changes in the availability of free water in dormant buds. By using the water potential measurement, these changes could be illustrated. The influence of chilling and climate becomes evident. The water potential from buds in a cold production area behaved more "normally", i.e., a decreased availability of water in the bud during the progression of winter to a minimum and thereafter become more available with hours increased. In contrast, buds from a

warmer area did not change much in their water potential or content during the dormant season. Changes in water properties of apple buds are mainly a mechanism to avoid freeze injury. The changes in water potential from a bound to a free state in Koue Bokkeveld during the winter, could possibly be developed as a way to determine a cultivars "readiness" for dormancy breaking chemicals once a certain water potential is reached, irrespective of chilling hours. The lag in change of the water status in Elgin could be used as an indicator that bud application of breaking chemicals should wait until a certain value is reached.

6.3 Correlative effects in two-year-old branches

Apple branches generally develop proleptically (bud burst after a dormant period). After adequate winter chilling, buds bursting of the terminal and numerous lateral buds on the one-year-old shoot, is prolific (Cook *et al.*, 1998). Following "adequate chilling", a well defined acrotonic bud bursting tendency develops before buds burst on the one-year-old shoot (Rauh, 1939). The problems associated with inadequate winter chilling altering bud bursting patterns, and the importance of two-year-old branches in fruit production, require the examination of the development of correlative influences (paradormancy, apical control and primigenic dominance) between shoots within a two-year-old branch. The role of commonly used pruning practices in the modification of these phenomena was investigated.

'Royal Gala' two-year-old branches were subjected to two chilling regimes (field conditions and artificial chilling at 7°C) and five dormant pruning treatments: control (not pruned), pruning back to the fourth lateral (heading) before or after chilling; and removal of the 2nd and 3rd laterals (thinning) before or after chilling. The removal of distal tissue by pruning (heading more than thinning) promoted bud burst on laterals. Pruning before chilling was more effective than after chilling. The correlative phenomena that inhibit bud burst on proximal shoots within two-year-old branches were clearly manipulated by pruning. These pruning effects indicate the presence of the correlative inhibition of budburst on laterals by distal shoot tissues increasingly in a basipetally direction. These effects may ultimately culminate in apical control.

By manipulating these correlative effects in a potential fruit bearing branch it could increase the size of apples on the laterals due to increased dominance or even earlier bloom. Further study into the water potential and hand how it could potentially vary due to these paradormant effects in a two-year-old structure, could also give insight into the use of physical and chemical manipulations.

6.4 Manipulating branching pattern by re-orientating shoots

Woody plants have characteristic branching habits, and many deciduous fruit species have a branching pattern called acrotony, with long shoots at the distal end and short shoots at the proximal end, the short shoots producing leaves, but scarcely elongating (Wilson, 2000). In contrast with acrotony, basitonic branching occurs when proximal positioned buds elongate to form longer shoots than the distal situated buds. Acrotony being a prerequisite for trunk formation allows maintained apical control of the terminal shoot or leader over seasons (Cline, 1997; Rauh, 1937). For basitonic branching to occur proximal buds needs to be released from inhibition by distal shoot tissue. Basitony is seldom expressed in apple shoots except under specific conditions; gravimorphism (Wareing & Nasr, 1961) following conditions of sub-optimal chilling (Cook & Jacobs, 1999); or by the localized application of cytokinins in spring and autumn (Faust, Lui, Wang & Stutte, 1991) and in combination with gibberellins (Cook *et al.*, 2000). In an attempt to reduce the dominance of the distal shoot piece and enhance branching along the parent axis, bending and heading treatments were done on one-year-old shoots. The object of this trail was to change an acrotonic toward a basitonic branching habit in two apples and one pear cultivar.

'Cripps' Pink' show a definite change in the acrotonic branching form if vertical shoots were bend horizontal. That much less of an effect was seen on 'Royal Gala' and even more so on 'Rosemarie' suggests a difference in genotype response to bending. The response and lack thereof, could well be also a function of time of bending. Results of bending two different apple cultivars on three dates let Lauri and Lespinasse (2001) conclude that the effect of bending on the development and growth patterns of lateral shoots vary with genotype. They confirmed an earlier theory that the gravimorphic effect is progressively superimposed on the initial acrotonic tendency and that the longer bending is done before winter the greater it response is.

7. Conclusion

The Western Cape has inadequate winter chilling and the problem could get worse due to global warming. Inadequate chilling has a negative effect on apple bud dormancy and tree architecture. These effects impact negatively on the viability of apple production in the Western Cape. The economic significance of apple production in the areas necessitates research into ways of understanding and circumventing the problems in order to obtain export quality fruit. From the research reported on in this thesis, a twofold strategy is proposed that could lead to improved apple production in the Western Cape. The first focus should be on the betterment of genetic material through conventional and new breading programs that would make for correct cultivar selection for climate specific areas. Secondly, manipulation techniques (physical and chemical) that is used for improved production must be investigated in order to improve understanding of the physiological processes involved.

A better knowledge and understanding of cultivar behavior in varying climatic conditions is vital for quality fruit production. Categorizing cultivars into groups with the same dormancy pattern could have a number of applications in addressing production problems fruit production. Such knowledge would make it possible for selecting cultivar pollinator combinations suitable for a new orchard according to site-specific climate cultivar interaction. Thereafter, specific management plans, i.e., pruning, bending and girdling, for handling the vegetative/reproductive balance could be developed for these combinations. The grouping of different dormancy patterns illustrates the need to interpret dormancy of a cultivar not only as a certain amount of chilling units at the end of the season, but as a biological process which responds to temperature changes during the season. These different physiological phases, i.e., rate of entrance into endodormancy, maximum depth of dormancy and rate of exit are cultivar specific. These different phases and their response to a changing climate should be studied for potential manipulations during this vital chain of events. By integrating physiological measurements such as the water status of buds with growth response data (forcing shoots from orchards during winter), improved cultivar specific production practices should be developed. By linking the changes in water status and growth rate with dormancy and amount of chilling received show how the lack of winter chilling have a negative effect on the apple buds in Elgin compared to the Koue Bokkeveld. These combine information of water status and growth potential could give a guideline for deciding on the need to spray chemicals as well as the date of application. The selection and management of orchards in such areas is critical and calls for extra intensive physical and chemical manipulation techniques, in order to attain maximum production.

The correlative influences in the two-year-old branch are important in fruit production as they directly influence the quality of the apple (size and colour). The role of commonly used pruning practices (heading and thinning) resulted in altering these correlative influences in the branch. The results indicate that by manipulating the correlative effects in a two-year branch, earlier bud burst and flowering could be obtain and thus a longer growing season. This practice could thus lead to the ultimate aim of larger fruit. A difference between timing of pruning was found; pruning before chilling resulted in earlier responses compared to manipulation after chilling.

Bending is a physical manipulation to force shoots into a more reproductive growth pattern in order to increase the amount of fruiting units and thus the yield. Bending disrupts the apical control exerted over the lateral buds and results in a growth response called gravimorphism. Bending is a useful orchard practice in deciduous fruit production, especially if the natural growth pattern of a tree is altered due to inadequate winter chilling. Form the study the results show the importance of bending at the start of the dormant season, before a dominating gradient could be imposed via bud inhibiting hormones, possibly auxin. The correct time of manipulation could vary according to cultivar, but mainly bending could be most effective done prior to maximum dormancy.

Addressing the problems associated with inadequate chilling called for combining research into the physiology of the tree with climatic data. By this combination, structured approaches could be developed that are supported by mathematical models predicting bud burst and measurements of depth of endodormancy via forcing shoots and water potential. To develop a successful system their must be leniency for microclimate and cultivar specific effects.

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