CHAPTER 2

LITERATURE REVIEW

2.1 Effects of inductive temperature periods and chemicals on flowering of some mango cultivars.

Floral induction is the basis for flowering and consequently fruiting. Unless the trees are sufficiently induced, there will be a reduction in yield. Low temperatures are the main inductive factor in mangoes. In places like around the tropics, sufficient low temperatures for mango floral induction may not be attained. Some growth regulators may intensify flowering of trees which were not adequately induced. In the following review, these aspects are addressed.

2.1.1 Floral induction process in mango

The flowering mechanism in Mango (*Mangifera indica* L.) is still poorly understood, although it clearly depends on environmental factors to bring about the transition from vegetative growth to reproductive growth, after causing a check in vegetative growth (Davenport & Nunez-Elisea, 1997). This transition is known to be induced by cold weather or combination of cold weather and water stress (Whiley, 1993). Other possible inductive factors in flowering can be photoperiod, carbohydrate and nitrogen status, plant hormones, and other yet undetermined factors (Bernier *et al.*, 1981).

Induction refers to the commitment of buds to evoke a particular shoot type, i.e. vegetative shoot (vegetative induction), generative shoot (floral induction) or mixed shoot (combined vegetative – floral induction) (Davenport & Nunez-Elisea, 1997). In addition, the inductive signal can be shifted from reproductive to vegetative or vegetative to reproductive by altering temperatures to which the plants are exposed during early shoot development (Batten & McConchie, 1995; Nunez-Elisea *et al.*, 1996).

2.1.2 The role of temperature on mango floral induction and differentiation

Although, the flowering stimuli of fruit trees are relatively less specific than those of herbaceous plants (Jackson & Sweet, 1972), temperature has been found to be the main factor on the flower formation of several fruit trees such as apples (Tromp, 1980; 1983), citrus fruit (Moss, 1969), litchis (Nakata &Watanabe, 1966) and olives (Badr & Hartman, 1971).

Studies in mango revealed the existence of a floral stimulus, which is continuously synthesized in mango leaves during exposure to cool, inductive temperatures (Davenport & Nunez-Elisea, 1990; Nunez-Elisea & Davenport, 1992). Unlike other plants requiring vernalization for induction (Bernier *et al.*, 1981) mango leaves appear to be the only site where the putative floral stimulus is produced (Davenport & Nunez-Elisea, 1992). Complete defoliation of girdled branches during inductive conditions results in vegetative shoots instead of generative shoots (Nunez-Elisea & Davenport, 1991b; Nunez-Elisea & Davenport, 1992). The putative temperature regulated floral stimulus is short-lived *in situ*; it's influence lasting only 6-10 days (Nunez-Elisea & Davenport, 1992; Nunez-Elisea *et al.*, 1996).

It is therefore clear that mango growth and development are strongly influenced by the environment as temperatures of below 15 °C readily promote floral induction; whereas vegetative growth is generally promoted by warmer temperatures (Whiley *et al.*, 1989; Nunez-Elisea *et al.*, 1991; Nunez-Elisea & Davenport, 1991a). Ravishankar *et al.* (1979), however, found that low temperature appears to exert a depressing effect on the further development of flower buds of mango. Similarly, Shu & Sheen (1987) showed that the longest period required for flower induction was when trees were exposed to $19/13^{\circ}$ C for more than three weeks. According to an experiment conducted by Robbertse & Manyaga (1998), there is also a difference in the number of cold units (days) required by different cultivars. Critical low temperature requirement and the minimum duration necessary for that particular temperature ("chilling period") for a certain plant is determined based on the time when floral differentiation is observed for the first time and it may be variable in different cultivars (Chaikiattiyos *et al.*, 1994). A similar variable minimum temperature requirement has been reported in other plants such as tomato, sweet pepper, eggplant and rice (Blum, 1988).

There is a general agreement on the principle that a growth check of sufficient duration is necessary for synchronous floral induction in mango (van der Meulen *et al.*, 1971). It is also agreed that vegetative growth and fruiting in mango trees are largely antagonistic and that excessive vegetative growth, especially in absence of a dry period, is likely to cause poor yields (Wolstenholme & Hofmeyer, 1985).

Attainment of floral induction does not necessarily ensure initiation of floral morphogenesis (Nunez-Elisea & Davenport, 1995). That means, growth of induced buds in the presence of cool temperature is essential for floral initiation, because induced apical buds that resumed

growth after trees were transferred to warm temperatures out-doors, produced a vegetative flush instead of an inflorescence. There is a certain threshold level where the buds are sufficiently induced for flowering and after attaining that level, they cannot be reverted to vegetative growth. Therefore it is decisive that buds are induced beyond the threshold level so that floral differentiation can occur. Temperature near 30 °C apparently counteracted floral development causing induced buds to continue vegetative development instead of initiating inflorescence. This response conforms to a statement by Shu & Sheen (1987) that, axillary buds that were previously exposed to cool temperatures but resumed growth in warm temperatures (31 °C day/ 25 °C night) expressed vegetative instead of floral morphogenesis.

Floral induction in mangoes, hence, is not a once off happening, but rather a continuous process lasting during the early stages of bud differentiation. The leafiness of an inflorescence would indicate the level of induction on a tree. Leafless inflorescences are an indication of total induction, while a leafy inflorescence indicates partial induction (Joubert *et al.*, 1993). Leafy inflorescences normally develop when the daily mean temperature during the induction period exceeds 15 ^oC. Van der Meulen *et al.* (1971) stated that leafy inflorescences reflect a lack of stress and excessive tree vigour, usually associated with high soil nitrogen. Similarly, Wolstenholme & Mullins (1982) concluded that adequately stressed trees would bear no leafy inflorescences. Stress of excessive tree vigour can probably contribute to a lesser leafy inflorescence but it cannot be a factor by its own.

Initiation of apical buds was stimulated at the start of temperature treatment by defoliating shoot tips (Nunez-Elisea *et al.*, 1991). Nunez-Elisea *et al.* (1993) observed that bud initiation was characterized as the swelling and initial elongation of the apex (about 5mm in height), which assures distinct conical shape, and had tightly clasped outer bud scales. Bud break is

considered the stage at which external bud scales loosened and began to open (Nunez-Elisea, 1985).

Flower sex expression

It is also apparent that temperature plays an important role in floral sex expression. Low temperatures (10 °C –15 °C) during flowering resulted in predominantly male flowers, while high temperatures favoured a higher percentage of hermaphrodite (bisexual) flowers (Tseng & Chang, 1983). Since the post-cold treatment of 25/20 ^oC imitates the natural conditions, it is generally expected that the total percentage hermaphrodite flowers of different cultivars would be in the region of 50-60%. Some researchers like Majumder & Mukherjee (1961); Randhawa & Damodaran (1961); Scholefield & Oag (1984) divided the inflorescence in three equal portions. As a result, they found that the apical portion had roughly 2 to 2.5 times more hermaphrodite flowers than the basal portions, but the total number of flowers in the basal portions was much higher. Joubert et al., (1993) indicated that in all cultivars that had taken cold temperature and produced inflorescences, the leafless terminal inflorescences had less hermaphrodite flowers (20.9-31.5%) than the leafy terminal inflorescences (32.7-43.7%). Shawky et al. (1977) found that most or all of the mature fruit were borne on the apex of the inflorescence. Male flowers compete with the hermaphrodite flowers for energy. The competition in the lower portion of the inflorescence, where at least four male flowers are competing with one hermaphrodite flower, is obviously stronger than in the apical portion where a higher fruit set could be expected (Joubert et al., 1993). As in the study of Joubert et al. (1993), Majumder & Mukherjee (1961) reported a higher percentage of hermaphrodite flowers on lateral inflorescences than on terminal inflorescences.

2.1.3 The role of growth regulators in induction

If evidence can be supplied that growth regulators can complement the process of differentiation in the induced buds or substitute the requirement of cold temperature, a farmer may escape the risk of failure of floral morphogenesis by spraying his trees with growth regulators. That is the purpose of testing growth regulators for their effect in the process of floral induction. Chilling and warm temperature treatments together with triazole retardants, PBZ and Uniconazole (UCZ), were included in an experiment on 'Tommy Atkins' mango trees, to study vegetative and reproductive developmental responses (Nunez-Elisea et al., 1993). The results of the study indicated that reproductive or vegetative morphogenesis in 'Tommy Atkins' mango can be affected by temperature (Nunez-Elisea et al., 1992; 1993). PBZ or UCZ, however, did not cause floral induction because vegetative, instead of reproductive (mixed or floral) buds were formed at 30/25 °C despite PBZ or UCZ pre-treatments. PBZ and UCZ sprayed trees did, however, produce nearly 20% more floral buds than non-sprayed (91 and 93% Vs 74%) and attained earlier bud break under chilling conditions. According to them, PBZ and UCZ possibly increased flowering rate by preventing shoot elongation prior to chilling treatment. They might have also caused rapid development of reproductive buds by interfering with gibberellin metabolism.

Environmental links to floral induction and evocation are generally well described (Davenport, 1993). Using such knowledge, flowering of mango can be enhanced during its normal season or manipulated to occur at other times of the year in tropical climates (Nunez-Elisea, 1985). One notable example is the use of potassium nitrate to stimulate out of season flowering of some cultivars growing at tropical latitudes (Barba, 1974); however, this treatment is not always dependable. There are a number of cultural practices (including

spraying of chemicals) that may assist in attaining of good flower development (both at on and off-seasons as well as inductive and non-inductive conditions) and consequently or directly affecting yield.

From the previous discussion in this chapter it is clear that cold temperature (below 15 °C) induces reproductive morphogenesis of buds in mango. Some growth regulators also reportedly enhance reproductive morphogenesis as a supplement to inductive temperatures even if they may not induce floral morphogenesis on their own. Under field conditions, especially in some places of the tropics, cool inductive temperatures for reproductive morphogenesis might not be attained at all or may be insufficient. These conditions only favour partial floral induction or complete vegetative morphogenesis. This is for the mere reported fact that attainment of floral induction does not necessarily ensure initiation of floral morphogenesis. Therefore, growth regulators and chemicals should be assessed for their complemental or total substitution effects (for specific cultivars) on the requirement of cold temperature for reproductive morphogenesis. The results may have special attributes to places with poor floral inductive climatic conditions or to places with frequent and sudden changes in temperature for sufficient floral induction to occur.

2.2 The impact of panicle and shoot pruning on vegetative growth, inflorescence and yield related developments in some mango cultivars.

Pruning of terminal panicles and activating axillary panicles may have advantages for better flowering and fruiting. This is basically due to a better chance of flowering in lateral buds and shifting of the flowering period to when more conducive weather conditions prevail. Post-harvest and renewal pruning of trees is also reported to be advantageous for enabling the tree to develop new vegetative growth, that will bear the coming season's crop and removal of excess and unnecessary vegetative parts.

2.2.1 The mango inflorescence

In the mango literature, the inflorescence is called a panicle although it is in fact a thyrse. Weberling (1989) explained the difference between a panicle and a thyrse as follows: The panicle is characterized by the fact that the main axis of the inflorescence is terminated by a flower, and similarly also for all the lateral axes. The degree of branching increases more or less regularly downwards from the uppermost lateral single flower below the terminal flower, so that the complete inflorescence has a conical outline, or at least primarily so. In a panicle, or inflorescence derived from a panicle, the terminal flower assumes a dominating position. The thyrse, by contrast to the panicle, is defined as an inflorescence "with cymose partial inflorescence". By "cymose branching" is meant a branching exclusively from the axils of the prophylls, which are developed as the only leaf organs preceding the individual flowers. They usually, as in dicotyledonous plants (and in some monocots), occur in pairs and inserted in more or less transverse fashion. The branching type of the thyrse may occur either in a determinate form, where the inflorescence is provided with a terminal flower or in an indeterminate form. It is therefore clear that the mango inflorescence is a thyrse rather than a panicle. Nevertheless, since all authors refer to the mango inflorescence as a panicle, it will also be called a panicle in this thesis.

The mango inflorescence is a much-branched terminal panicle with anything from a few hundred to over 6000 flowers (Wolstenholme & Mullins, 1982). The mango is andromonoecious, which means that each inflorescence bears both hermaphrodite and

staminate flowers (Coetzer *et al.*, 1995) where the staminate flowers predominate (Sedgley & Griffin, 1989). Each flower has one fertile stamen and varying numbers of staminodes, some of which are simply small thread like appendages (Coetzer *et al.*, 1995). Hermaphrodite flowers have a single ovuled ovary and one functional stamen. If they are normal and pollinated, they can set into fruits. It appears, however, that many flowers containing ovaries have defective internal reproductive ovules and are therefore sterile.

Terminal inflorescences normally develop from apical buds. These inflorescences may not develop adequately due to insufficient inductive temperature or shifting of the winter periods. Diseases and insects may also affect the developed inflorescences. Growers may have the desire to shift the production to a late harvest to take advantage of off-season markets. For these reasons, panicle pruning may be advantageous.

2.2.2 Induction of axillary panicles by terminal bud removal

In mango, the removal of the apical bud or inflorescence on terminal shoots just prior to or during the flowering period results in the development of normally inhibited axillary buds proximal to the point of cutting (Reece *et al.*, 1946). These buds usually develop into inflorescences, particularly if pruning is performed shortly before or after the start of normal floral bud development (Issarakraisila *et al.*, 1991). If inflorescences do develop, a delay in flowering of four to eight weeks is effected (Reece *et al.*, 1946), which gives rise to a delay in harvest (Issarakraisila *et al.*, 1991; Oosthuyse, 1995).

Several practical advantages have been found in the induction of axillary panicles after panicle pruning of mango (Shu, 1992). The primary advantage is to assure a good crop by escaping low winter temperatures or by compensating for the loss of panicles caused by prevailing low temperatures, frost and incessant rain (Singh *et al.*, 1974). Another benefit is to substitute malformed panicles (Majumder *et al.*, 1976; Pal & Chadha, 1982). Moreover, orchard owners in the central part of Taiwan have used this technique to produce off-season mango fruit (Shu & Sheen, 1987).

2.2.3 Effect of panicle pruning on flower development and cropping

Several chemicals like Cyclohexamide (Shu, 1993) have also been used in various geographical locations to de-blossom mango trees with the aim of delaying flowering to a period when conditions are more favourable for inflorescence development and fruit retention. The removal of inflorescences by chemical means was found to be useful to synchronize flowering, thereby, reducing variation in the stage of fruit growth and development prior to harvesting (Oosthuyse & Jacobs, 1996). The underlying principle in deblossoming is that the food reserves or any such substance as may induce flowering, are conserved by plucking off the inflorescence in its early stage (Singh, 1960). These reserves, according to him, are perhaps mostly depleted during later stages of fruit development. Thus the deblossomed tree, instead of developing panicles and producing fruit, puts on new vegetative growth, which flower and fruit the next year. According to Chang & Leon (1987), deblossoming of the terminal inflorescence can lead to inflorescence development from axillary buds, a 20-30 day delay in harvesting and higher yields. The yield of Mango mainly depends on the initial fruit setting and growth (Ploetz *et al.*, 1996). The large number of male flowers, a high percentage of perfect flowers which remain unpollinated and the failure of

pollen germination on the stigma are the main causes of the low percentage of set (Singh & Dhillon, 1990). Other factors reported include the failure of the gynoecium to develop properly, Thrip damage, reduction in the viability of the small quantity of pollen caused by low humidity, high temperature and bright sunlight. Despite tremendous efforts to elucidate the mechanism of this critical biological event (mango flowering) and the vast body of literature, which has resulted, many important details still elude scientists (Davenport & Nunez-Elisea, 1997).

2.2.4 Terminal shoot pruning

According to Gross (1996), pruning should maintain a good balance between growth and fruiting since a mango grower's objective is to harvest the maximum amount of marketable fruit at the lowest cost. This can be achieved, according to him, by selective pruning that will open the center of the tree, permitting air ventilation, sun for the colouring of fruit and better penetration during spraying.

Mango shoots do not flush while they are bearing fruit. In fact, fruiting appears to 'exhaust' the shoot, and it may not even flush post-harvest unless stimulated by pruning (Wolstenholme & Whiley, 1995). This is even more so in relatively cooler climates or with late harvest. Issarakraisila *et al.* (1991) found that in cool subtropical Australia only 4% of shoots that had matured a fruit, flushed after harvest. Shoots which flowered but lost their fruit had a 36% chance of flushing after harvest, while 49% of shoots which did not flower flushed after harvest.

It has been determined that the ideal time to apply terminal shoot pruning is directly after harvest (Mullins, 1986; Ram, 1993). The rationale for this inference is the allowance of maximum time for canopy recovery, shoot maturation and quiescence to maximize the likelihood of the new shoots arising after pruning to flower the next season. No direct evidence has been presented in support of this, although it has been demonstrated that older shoots are more likely to produce inflorescences than younger ones (Scholefield *et al.*, 1986). The need for quiescence after flushing might be linked to the reduction of endogenous gibberellin (Chen, 1987) and the accumulation of starch reserves (Suryanarayana, 1987). New shoot development after harvest on mango cultivars like Sensation is usually delayed, occurs unevenly, or may only materialize at flowering or soon thereafter (Oosthuyse, 1994).

Pruning by enhancing post-harvest flushing to occur uniformly, may effect earlier and more complete reserve replenishment (Oosthuyse, 1994; Davie *et al*, 1995) and reduce flowering variation (Oosthuyse, 1994). The benefits of 'heading back' cuts are firstly to remove 'carbon starved, exhausted' shoots which will not fruit the next season (Wolstenholme & Whiley, 1995). Secondly, old leaves with reduced efficiency are replaced and there is a better chance to build-up carbohydrate reserves. In the prominent late cultivars like Sensation, Keitt and Kent, the time available for new shoot development after harvest and before the onset of floral inducing cool temperatures is shorter (four to ten weeks) than that for the early cultivars like Irwin, Tommy Atkins and Zill (around twelve weeks) (Oosthuyse, 1995).

As to the observations of Thimmaraju (1966) (as cited by Pandey, 1988), the absence of flushing during February, March and April followed by flushing instead of flowering during August and September resulted in crop failure. Stassen *et al.* (1999) showed that pruning a late cultivar like Sensation early after fruit set (October in South Africa) stimulated early

vegetative growth, that enabled the tree to bear a normal crop the following season. Since this also acts as a fruit thinning treatment, fruit size was significantly increased over a three-year period. On an early cultivar like Tommy Atkins, they found no significant difference in yield over a two-year period, but fruit size and external fruit colour were significantly increased.

Lack of post-harvest flush after heavy cropping may be the result of tree "exhaustion" (Narwadkar & Pandey, 1982, cited by Pandey, 1988), and can be alleviated by post-harvest pruning (Ram & Sirohi, 1991). Oosthuyse (1994) also indicated that post-harvest pruning will effect prolific and synchronous re-growth shortly after its performance, and will result in slightly delayed and more uniform flowering. The result of the latter study supports the view that the vegetative re-growth caused by pruning after harvest, elevates the level of endogenous gibberellin, and thereby effects a delay in bud development and a delay in flowering is considered to be advantageous, since inflorescence development when temperatures are higher results in an increase in the proportion of perfect as opposed to male flowers formed (Singh *et al.*, 1965; Mullins, 1987), and gives rise to more effective pollination (Robbertse *et al.*, 1986; Shu *et al.*, 1989; Issarakraisila & Considine, 1994).

Oosthuyse (1994) indicated that many of the unpruned branches that did not produce new shoots, flowered as a result of floral development from axillary buds situated behind the scar of the previous season's inflorescences. In cultivars where a small fruit size problem occurs, as happens with Sensation, a rejuvenation pruning can be carried out on the bearing tree during October/November (Fivas & Stassen, 1995). In this case bearing shoots with weak, misshaped and small fruit are cut back. On the remaining bearers the fruit is thinned to numbers the tree can cope with, in order to get marketable sized fruit while maintaining the

annual yield. Contrary to the presumption of many researchers, pruning does not adversely affect cropping, which is, apparently due to the abundance of new shoots developing after pruning and the general ability of these shoots to produce inflorescence (Oosthuyse, 1994), provided it is done at an appropriate stage. In some instances, however, the depletion of reserves by excessive fruit produced in the previous season (especially in early cultivars) has been cited as a reason for the failure of trees to flower if pruned after harvest, despite the strong vegetative re-growth after pruning (Charnvichit *et al.*, 1991). On the other hand, the quantity of carbohydrate that a tree can produce (Oosthuyse, 1995) is directly related to the number of leaves on the tree. Removing leaves, "as" by pruning, one is reducing the tree's capacity to produce carbohydrates.

The concept of leaf: fruit ratio has been widely applied to deciduous fruit, most recently to kiwifruit, where 210-315 cm² of leaf area is required to produce 100 g of fruit which is a high figure compared to apple and grapefruit (Snelgar & Thorp, 1988). In mango, Chacko *et al.* (1982) noted that 30 leaves were inadequate to support the growth of a single fruit to normal size. Nevertheless, certain data expressly indicate that new mango shoots play an important role in replenishing carbohydrate reserves (Davie *et al.*, 1995). Pruning should not be so severe that sunburn of fruit occurs, but should rather result in a better coloured fruit (Fivas & Grove, 1998).

Cull (1991) indicated a relationship between fruit physiological problems such as 'Jelly seed' and excessive growth vigour during fruit development, caused by too much nitrogen fertilization. This is another point indicating the need for pruning to reduce excess tree vigour. Batten *et al.* (1988) also found a positive correlation between the incidence of "jelly seed" and the percentage of terminals flushing on 'Sensation' trees in subtropical Australia.

Therefore, environmental conditions that promote vegetative bias in trees, eg. high temperatures and soil moisture would reduce internal Ca allocation to fruit and increase the incidence of fruit disorders (Schaffer *et al.*, 1994).

De Jong *et al.* (1987) while studying the yield of peaches highlighted the concept of critical periods. They found that yields of early maturing peaches were considerably less than late cultivars, in spite of a longer post-harvest period to recoup reserves. The explanation was that the period of peak reproductive assimilates demand coincided with peak shoot growth in the early cultivars, but occurred after this period in the late cultivars. In other words, lower yield of the early cultivar was due to greater vegetative: reproductive competition during a critical period.

Therefore, vegetative against reproductive competition at critical periods can lead to allocation of resources away from the economic end product (Wolstenholme, 1990). This suggests that tree manipulation such as pruning needs to be considered in timely application, which should depend on certain physiological growth stages.

From the literature assessed in general and according to Oosthuyse (1992) in particular, much has still to be quantified concerning the effect of pruning on productivity; productivity being both a function of the quantity and quality of fruit produced. Intelligent pruning can open up the canopy and improve over all light relations and this is a fertile field for research (Wolstenholme & Whiley, 1995). It is of course essential that the benefit of pruning should always outweigh the additional cost incurred as a consequence of economic benefit.

2.3 Effects of Potassium Nitrate on flowering and yield promotions of mango.

Potassium nitrate can enhance flowering especially in tropical regions where cold temperature for floral induction may not be sufficient. That is due to its reported effect in supplementing nitrogen. It is also suggested that induction by potassium nitrate spray may occur as a result of ethylene synthesis. The overall effect of potassium nitrate when sprayed at different periods of plant phenological phases, concentrations and locations as well as the mechanism for its effect is reviewed.

2.3.1 Potassium nitrate stimulating flowering and factors affecting responsiveness of plants

Subsequent to the discovery and use of ethephon to replace smudging and stimulate flowering of mango, Barba (1974) reported the use of potassium nitrate (KNO₃) for the same purpose. In subtropical regions where winter conditions are usually sufficient for floral induction, flowering enhancement by KNO₃ has not been reported (Oosthuyse, 1992). KNO₃ sprays, however, have been used to stimulate off- season flowering of mango, especially in tropical regions (Bondad & Linsangan, 1979; Nunez-Elisea, 1985). Similarly, Davenport & Nunez-Elisea (1997) found that mango trees respond to KNO₃ applications when they are located in tropical conditions, but not in the subtropics. Goguey (1993) also asserted that the response of plants to different flower inducing treatments differs according to variety, climatic conditions and geographical location.

In the low- and mid- latitude tropics, receptive trees respond by initiating floral buds within two weeks after treatment and the effective spray concentration ranges from 1 to 10% KNO₃

with the optimum concentration varying with the age of the trees and climate (Davenport & Nunez-Elisea, 1997). KNO₃ concentrations of 2-4% or 1-2% NH₄NO₃ have been found to be effective for initiating floral buds (Nunez-Elisea, 1985; Nunez-Elisea & Caldeira, 1988).

Rojas & Leal (1993) stated that the concentration of KNO₃ used to induce mango flowering varies between 10-60 mg/L, while Maas (1989) found that foliar spraying with a 2% KNO₃ solution proved to be a very effective method of inducing mango trees to bloom. KNO₃ application, especially at 4% level, was slightly phytotoxic to the leaves and inflorescences that caused the distal margins of some of the leaves and the extremities of some of the inflorescence branches to become necrotic (Oosthuyse, 1996).

Astudillo & Bondad (1978) found that the results for KNO₃ sprays were influenced by the physiological age of the growth flushes, since aged vegetative flushes (5-8 months old) responded better to KNO₃ applications than young flushes. Bondad & Linsangan (1979), on the contrary, indicated a significant increase in number of panicles formed when KNO₃ treatments were applied in the initial stage of vegetative flush growth (younger flushes), in comparison with applications made at a later stage (matured flushes). They also found that trees that had low or no production in the previous season seem to respond better to the applications of KNO₃ than trees that were productive.

Recently, Davenport (2000) explained that, for successful stimulation of flowering, the nitrate salt must be applied after the resting buds of mango have reached sufficient age to overcome any inhibitory influence they may have on the flowering response

2.3.2 Mechanisms of potassium nitrate and other related factors in altering the physiology of mango trees

In line with other findings, Bondad & Linsangan (1979) elaborated that KNO₃ could modify the flowering behaviour of mango since KNO₃ makes it possible to produce fruit every year, breaking the biennial bearing habit (alternate or irregular) and can advance the flowering and fruiting periods of mango by several months. It is also shown that KNO₃ can induce flowering of trees that remain vegetative but are well beyond normal bearing age.

Accumulation of Nitrogen has also been observed before flowering (Phatak & Pandey, 1978) since it is known that nitrogen status could be affected by foliar applications of KNO₃, but whether or not this in turn influences flower induction must await further study. Protacio (2000) also discussed the need of nitrogen for flowering as follows: "From competent tissue, flower initiation can proceed. In this model nitrogen is crucial for flowering. Presumably, there is also a threshold for nitrogen concentration that if exceeded, will allow the plant to flower. Most probably, KNO₃ application triggers flowering by exceeding this threshold level."

Singh (1987) estimated that less than 0.1% of the hermaphrodite flowers develop into mature fruit while the rest falls to the ground. Assuming there are 100,000 flowers and each flower contains 10 micro gram of nitrogen, then each time a tree flowers, it loses 1 kilogram of nitrogen. The tree will, therefore, need to have adequate nitrogen reserves for flowering and subsequent fruit formation. Increased nitrogen fertilization via the soil has also been found to affect an increase in fruit retention and tree yield of mangoes (Smith, 1994). Hence, a nutritional effect cannot be discounted. Like nitrogen (N), phosphorous (P) has also been

reported to be associated with flowering processes (El-Hinnawy, 1956). The author emphasized the enhancement of the effects of thermo-induction by inorganic phosphorus. In mango, the high level of phosphorus in bearing shoots as compared to non-bearing shoots, further supports the above hypothesis (Thimmaraju, 1966 as cited by Pandey, 1988). The presence of higher levels of other elements like calcium, magnesium & potassium along with nitrogen & phosphorous have also been reported in bearing shoots in mango (Soni, 1967 as cited by Pandey, 1988).

Aerial applications of nutrients to mango trees have been found to be ineffective in increasing leaf nutrient status (McKenzie, 1995). This is probably due to the low absorptive capacity of the leaves. On the other hand, nutrient application when inflorescences are present may be effective in increasing the nutrient status of a tree, as the inflorescences may be more capable of nutrient uptake. KNO₃ spray application to 'Tommy Atkins' mango trees whilst the inflorescences were in full-bloom, was previously found to increase fruit retention, to reduce fruit size, and to increase tree yield and tree revenue (Oosthuyse, 1996).

The mechanism responsible for KNO₃ induction appears to be hormonally mediated but the exact relationship between KNO₃ and endogenous hormones in mango is unknown (Fierro & Ulloa, 1991). Protacio (2000) explained that the classical definition of the flowering hormone is a leaf-generated photoperiodic stimulus that induces a vegetative plant to attain the flowering state. Thus, there is a transition from a juvenile vegetative plant to a mature reproductive state due to the leaf-generated flowering hormone. He mentioned that, in a mature mango tree that has already flowered or in grafted trees, KNO₃ spray is an agent that initiates flowering from tissues already competent to flower but certainly not yet determined to be flowers. Nevertheless, the exact developmental stage, which KNO₃ affects, is still

controversial. Protacio (2000) explained further that a transitional change from juvenile vegetative to flowering state is not involved because the buds from bearing trees arose from tissues that already carry with in the flowering program. It can, therefore, be stated that KNO_3 may be a stimulus for flower initiation.

Despite poor correlation between KNO₃ application and panicle formation, hormones may establish a metabolic gradient that enhances panicle formation and uniform distribution of panicles (Fierro & Ulloa, 1991). Panicle induction by KNO₃ sprays has been suggested to occur as a result of ethylene synthesis (Barba, 1974). Chacko *et al.* (1972) has confirmed the same idea and said that this contention seems reasonable since the ethylene-releasing chemical ethephon has shown similar effects in Haden and other monoembryonic cultivars. The results from the research work of Davenport & Nunez-Elisea (1990), however, indicated that the effect of KNO₃ on flowering is not mediated by ethylene. Application of KNO₃ to scaffold branches had no influence on ethylene production either during or after the promotive period.

Results obtained with KNO₃ treatments in relation to flower promotion and fruiting has not been consistent in places such as India (Pal *et al.*, 1979 cited by Fierro & Ulloa, 1991), and Australia (Winston & Wright, 1986) or negative as in Florida (Davenport, 1987). The same was observed in experiments involving date of application, interval between applications, concentrations or component salt effects (Fierro & Ulloa, 1991). Sargent *et al.* (1996) also indicated the results obtained with KNO₃ treatments in relation to flower promotion and fruiting to be inconsistent. Some authors attribute the above-mentioned inconsistencies to the following factors: (1) inefficient application of the product; (2) physiological maturity of the plants; (3) production in the previous harvest and (4) age of the shoots. As mentioned earlier,

Goguey (1993) also asserted that the response of plants to different flower inducing treatments differs according to cultivars, climatic conditions and geographical location. The potential to increase flower formation by means of KNO₃ applications, have been suggested by a number of studies, yet more information is needed for an adequate understanding of the process (Fierro & Ulloa, 1991).

2.4 Effect of Paclobutrazol on the control of vegetative growth, leaf nutrient content, flower development, yield and fruit quality of mango.

Due to lack of pruning and factors that reduce vegetative bias (like water stress, reduced fertilization, cold temperature), trees may become excessively vegetative. The yield obtained from those trees is very low and usually bear in alternate years. Thus, the vegetative vigour of such trees should be suppressed. One method is the use of growth regulators like PBZ. Caution should, however, be taken with the use of growth regulators because of fruit residue limitations while fruit will be exported to different countries.

2.4.1 Mechanism of action towards suppressing vegetative growth and enhancing flowering

Paclobutrazol (1- (4-chlorophenyl) –4,4-dimethyl-2- (1,2,4- triazol-1-yl) pentan-3-ol) is a broad-spectrum plant growth retardant that selectively controls tree vigour without markedly affecting the size of apple, peach and plum fruit (Quinlan, 1980; Williams, 1982; Anon, 1984; Webster & Quinlan, 1984; Swietlik & Miller, 1985; Erez, 1986).

The cropping manipulations possible with PBZ ranges from off-season or early season harvests to simply increased yields (Voon *et al.*, 1991). Rademacher (1989) related flowering to the inhibition of plant gibberellin synthesis and to a lesser extent to other hormones, which interfere with the plant morphogenesis. The hormonal concept of flowering in mango implies that the cyclic synthesis of floral stimulus in the leaves and the difference between two such cycles would determine the flowering behaviour of a cultivar (Kulkarni, 1986). PBZ could promote flowering in two ways: it can speed up and increase the synthesis of the floral stimulus in an inductive cycle, or, it can plausibly affect the ratio between flower promoting and flower inhibiting factors (Kulkarni, 1988). He also explained that in young grafts, the shortage of a promoting factor (because of fewer leaves) favoured the inhibitor, and PBZ could reduce the amount of inhibitor and thereby shifting the balance in favour of flower promotion. Similarly, in the case of bearing trees, increased flowering earliness was noticed in the treated trees. In other words, the flower-inductive factor may commence earlier in the season.

In a related experiment, it was also found that the presence of GA_3 inhibits the expression of competence of mango to flower. Protacio (2000) explained that mango seedlings, even if still young, are competent to flower as early as right after grafting. Villanueva (1997) as cited by Protacio (2000) stated that mango seedlings flowered seven months after grafting in response to PBZ application, confirming that young grafted plants are competent to flower. One of the principal effects of GA_3 is to mobilize carbohydrates by stimulating their degradation to glucose (Jacobson & Chandler, 1987).

Therefore in an environment where GA levels are high, no starch accumulation can take place. Jacobson & Chandler (1987) also elaborated that; this may very well explain why GA

concentration needs to fall below a certain threshold level in order to accumulate starch within the tree. This is also true in the case of tuberization in potato (Ewing, 1987).

In mature mango trees, flowering is associated with reduced vegetative growth often induced by lower activity of gibberellins (Voon *et al.*, 1991). Exogenous application of GA as well as endogenous high levels of gibberellins has proved a major hindrance in the way of flower bud differentiation in a number of temperate as well as tropical fruits including mango (Tomer, 1984). These findings have contributed greatly towards better understanding of this phenomenon. Considering the above inhibitory role of GA for flower development in mango, PBZ, owing to its anti-gibberellin activity, (Quinlan & Richardson, 1984) could induce or intensify flowering by blocking the conversion of Kaurene to Kaurenoic acid. The latter is a precursor of gibberellins.

PBZ can considerably enhance the total phenolic content of terminal buds and alter the phloem to xylem ratio of the stem (Kurian & Iyer, 1992). Such alterations could be important in restricting vegetative growth and enhancing flowering by altering assimilate partitioning and patterns of nutrient supply for new growth.

2.4.2 Application methods of PBZ and reaction of species

PBZ can be applied to mango trees as foliar spray or by soil drenching (Tongumpai *et al.*, 1991). Davenport & Nunez-Elisea (1997) elaborated that unlike the other classes of growth retardants that are normally applied in foliar sprays, PBZ is usually applied to the soil due to its low solubility and long residual activity. It was shown that when PBZ was applied to the

soil, a portion is adsorbed onto the soil particles and is unavailable for immediate uptake; the chemical is also subjected to degradation by soil organisms (Pickard *et al.*, 1982).

Reports on PBZ in temperate tree fruit, show differences between species and locations in responses to methods of application. In England, soil treatment is generally effective in controlling shoot growth in cherry but not in apple (Quinlan, 1980; Quinlan & Richardson, 1984) whereas in the U.S.A., soil treatment was more efficient on apples (Williams, 1984). With plum, although foliar sprays were more effective than soil drenches in the season of application, soil drenching was more effective in the subsequent years (Webster & Quinlan, 1984).

In Israel, soil application was more effective than foliar sprays on peach (Erez, 1986). Failure or limited response to foliar sprays was generally attributed to reduced uptake in the dry conditions prevailing at that station, whereas higher efficacy of soil application in lighter soils and in irrigated orchards was attributed to better movement of the chemical towards the superficial roots (Anon, 1984).

PBZ is taken up through the root system and is transported primarily in the xylem through the stem and accumulated in the leaves and fruit if applied to the soil (Wang *et al.*, 1986). Voon *et al.* (1991) explained that PBZ is systemic and can be taken up by plant roots or through lenticels and bark perforations while foliar sprays uptake occurs through shoot tips, young stems and leaves. PBZ, being xylem mobile moves upwards with the transpiration stream (Lever *et al.*, 1982).

2.4.3 Application rates

A lot has been done to identify the best application rate of PBZ in different places. Factors like age of the trees, extent of vegetative growth and method of application should be considered when determining the rate of PBZ to be applied. The rates also affect the different tree parameters variously. In general, the amount of PBZ required to promote flowering and fruiting in fruit crops is very low (Browning *et al.*, 1992).

In general, rate of soil application is a function of tree size and cultivar. The rate is determined by multiplying the diameter of tree canopy in meters by 1 to 1.5 gram of active ingredients of PBZ (Tongumpai *et al.*, 1991). They indicated that other factors including soil type, irrigation system, etc. may affect PBZ activity and thus may be necessary to improve the effectiveness of the chemical. As to them, overdose may cause undesirable effects such as restricted growth, panicle malformation (too compact), and shoot deformity. They also asserted that to insure uniform flowering and reduce the detrimental side effects, the search for better application methods were investigated and one approach is to apply high volume of low PBZ concentration to improve better coverage.

2.4.4 Attributes on different tree aspects

Flowering

It is evident from the results of Burondkar & Gunjate (1993) that PBZ application increased the number of flowering shoots. In a related experiment, Tongumpai *et al.* (1991) noticed that the number of flowering shoots of all PBZ treated trees were twice as high as that of the

control. Kulkarni (1988) also observed increased flowering earliness in the treated trees. In other words, the flower-inductive factor may commence earlier in the season. Induction for an early flowering (Burondkar & Gunjate, 1993) may also advance fruit maturity and hence have another commercial advantage. Similar results were also reported in different important mango cultivars from Australia (Winston, 1992), Indonesia (Voon *et al.*, 1991), Thailand (Tongumpai *et al.*, 1991) and India (Kulkarni, 1988). It is probable that the application of PBZ caused an early reduction of endogenous gibberellins levels within the shoots (Anon, 1984), causing them to reach maturity earlier than those of untreated trees.

Vegetative growth

Excessive vegetative growth in the warm subtropical climates, like that of the South African lowveld results in large trees on most mango varieties, which promoted the evaluation of PBZ (Cultar) for growth suppression (Rowley, 1990) and PBZ has already proven to be an effective growth suppressant of stone fruit trees (Williams *et al.*, 1985). PBZ has the greatest effect on tissues, which are rapidly growing and developing (Steffens *et al.*, 1985), that could explain why PBZ predominantly affected the apical growth. Vijayalakshmi & Srinivasan (1999) found that, application of PBZ was found to be significantly superior in increasing the leaf area compared to other treatments like potassium nitrate, urea and ethrel recording an average area of 94.89 cm² where as the control was only 63.65 cm². According to them, the increase in leaf area has overcome the limitation of depletion for reserve food materials. As the reserve food materials were then plenty, the breaking up of alternate bearing cycle in the cultivars chosen has been achieved. However this was found to be contradictory to the findings of Embree & William (1987) and Kurian & Iyer (1993) who reported a decrease in leaf area with PBZ in pears and mangoes respectively.

According to the experiments of Kurian & Iyer (1993), PBZ at a concentration of 10.0 g per tree was the most effective and practically arrested tree growth but had some phytotoxic effects. In their experiment, when PBZ was applied at a rate of 2.5 or 5.0 g per tree, there was more than 50% reduction in tree volume expansion, with no phytotoxicity. While, independent of the methods (Spray or soil drench) and the concentrations, they found PBZ application to reduce size of leaves.

Leaf mineral content

Salazar-Gracia & Vazquez-Valdivia (1997) discussed that their results of an experiment with PBZ on mango trees support the work of Werner (1993) on young non-bearing trees in that soil application of PBZ decreased foliar levels of phosphorous. Leal *et al.* (2000), however, found that there was no effect of PBZ on the macronutrient content of the leaves and the statistical difference found were due to difference in tree phenological stages.

Yield

There is usually a yield increase associated with PBZ treatments, but Voon *et al.* (1991) emphasized the importance of supplying adequate nutrients, irrigation and generally good tree maintenance to maintain these high yields. In the experiments of Medonca *et al.* (2002), PBZ increased the productivity of 'Tommy Atkins'. Most other researchers also indicated that PBZ treated trees had a higher yield than non-treated.

Fruit quality

With the experiments of Medonca *et al.* (2002), there was no impact of PBZ on fruit quality parameters. On the other hand, a trial was conducted in India with 10 year old trees of Alphonso mangoes (Vijayalakshmi & Srinivasan, 2000). The trees were treated with 10 ml PBZ per tree, 1% KNO₃, 1% urea, 200 ppm Ethrel, 20 ppm NAA or 5000 ppm Mepiquat chlorode. They recorded data on ascorbic acid, carotene, total sugar and reducing sugar contents, TSS, acidity, and sugar: acid ratio in harvested fruit and concluded that applying 10 ml PBZ had the greatest effect, increasing all the parameters except for acidity. However, even if PBZ increased quality of fruits, it was ascertained that the accumulation of PBZ residues on the surface or inside mango fruit (especially due applications of higher rates) is unfriendly to human health (Singh & Ram, 2000).

The use of retardants for mangoes has not been sufficiently investigated (Werner, 1993). Whereas results for Asian and other mango varieties treated with PBZ are available and promising (Kulkarni, 1988; Voon *et al.*, 1991). Therefore, more investigation is expected to reach a final conclusion.

2.5 Effects of fruit thinning on some yield and fruit quality components as well as starch reserves of mango.

Production of excess fruit during initial fruit bearing stage is a common phenomenon in many fruit trees. The production of excess fruit beyond the tree's capacity leads to wastage of carbohydrate reserves and consequently reduces the final yield and quality of fruits as well as vegetative growth of trees.

2.5.1 Effect of excess fruit load on plant reserves and current assimilates

The mango has a worldwide reputation of being a poor yielding crop, and this poor yield may be worsened by irregular bearing (Wolstenholme & Robert, 1991). Many mango trees set a very large number of fruit that are normally nurtured to an advanced stage before abscission reduces the crop to a level the tree can handle (Davie & Stassen, 1997b). They also stated that if a tree that has set a large crop is left to its own devices, it will tend to abscise far more fruit than is necessary, thus reducing the yield to below levels the tree is in fact capable of supporting. Figures available for nine-year-old 'Haden' mangoes indicate that the maximum retention of fruit set was about five percent (Nunez-Elisea, 1985).

The delay in ridding itself of the excess fruit results in wastage of carbohydrate, which is eventually reflected in the smaller size of the remaining fruit. Commercially it is frequently desirable to have a smaller number of large fruit rather than a large number of small ones (Jackson, 1989). In general, there would appear to be an order of priority among plant sinks with developing fruit and seeds being the strongest (Wright, 1989). Janse van Vuuren *et al.* (1997) stated that as much as 65% of the starch of plants in an "on" year is finally channelled to the fruit. Fruit thinning may therefore be the answer for starch conservation. They also found that the bulk of the tree carbohydrate reserves are found in the roots, wood and to a lesser extent in the shoots. The heavy nutritional demands of fruiting distort carbon partitioning among vegetative parts including the root/shoot balance (Wolstenholme, 1990). As to the latter, the order of priority among sinks is a function of both growth rate (sink activity) and the size of the sinks. It is usually in order as follows: seeds > fleshy fruit parts as well as shoot apices and leaves > cambium > roots > storage. In other words, fruiting will firstly deplete storage reserves, then withhold assimilates from root growth (Cannell, 1985).

2.5.2 Effect of fruiting on flowering

The effects of fruiting on flower initiation are also well documented and most researches indicated heavy fruiting in one-year leads to poor flower initiation and light fruiting the following year (Wright, 1989). According to Wright (1989), developing fruit also compete with each other and the common effect of such competition is premature fruit abortion that occurs in a wide range of species.

2.5.3 Effect of fruiting on vegetative plant parts

A reduction in dry matter partitioning to shoots, leaves and roots due to fruiting has been demonstrated in a wide range of species (Wright, 1989). In apple, Heim *et al.* (1979) has shown a reduction in shoot and leaf production with increasing fruit load. He elaborated that the effects of fruiting on stem dry matter accumulation was specially severe, accounting for over 40% of the dry matter fixed in non-fruiting apple tree stems compared with just over 10% for heavily fruiting tree stems.

2.5.4 Effect of fruit thinning on fruit size and fruit quality

In thinning fruit by hand, the larger fruit are usually retained when differences in fruit size are apparent (Williams, 1979; McVeigh, 1994). In an experiment to determine the effect of fruit thinning on fruit drop and fruit size, Davie *et al.* (1995) found that the timely reduction in the number of mango fruit on the tree, to a quantity the tree can cope with, greatly reduced further fruit drop and at the same time resulted in a 15% increase in fruit size. Knight (1980) working with 'Cox's orange Pippin' apple found that

thinning by removing 70% of the fruit clusters significantly increased individual fruit size and did not affect total yield compared to unthinned controls. He also found that partial tree fruit thinning was not effective as selective whole tree thinning and the best results were obtained by thinning within fruit clusters suggesting that the competitive effects are rather localized.

Fruit thinning, by reducing competition for carbohydrates between fruit (Horscroft & Sharples, 1987), also improves fruit quality in terms of firmness, soluble solids content and anthocyanin formation hence red skin colour. The effects of fruit thinning on market quality appear to result from reducing competition for assimilates; its effect on biennial bearing seems to result from reducing the supply of seed- produced hormones which inhibit flower bud formation (Jackson, 1989).

2.5.5 The phenomena of tree reserves and its implication

Many of the problems associated with mango fruit production have been ascribed to insufficient carbohydrate reserves in the tree structures. It may also be due to the inability of the tree to supply sufficient carbohydrate from current photosynthate production in order to meet the demand of a heavy fruit load (Davie *et al.*, 1999). This is because the growth of a tree and the production of fruit depend on the ability of a tree to produce and store carbohydrates (Oliveira & Priestley, 1988).

Cull (1991) mentioned that the photosynthetic capacity of the tree regulates the supply of carbohydrate, with a high percentage of the photosynthate accumulated and being utilized by the respiration processes of the tree (Kozlowski, 1992). This process provides the energy for

the morphological development of the plant. Photosynthate also has to supply the structural units for innumerable organic compounds for which the proteins, sugars, colours and flavour compounds produced in the tree and fruit (Priestley, 1963). The excess carbohydrate is then stored usually in the form of starch (Stassen, 1980; Davie & Stassen, 1997a).

Developing fruit have often been reported to increase individual leaf photosynthesis rates in tree crops, including citrus, peach and apple (Wolstenholme, 1990). De Jong (1986) attributed this to increased stomatal conductance in the presence of fruit. However, a comprehensive study on sweet cherry (Roper *et al.*, 1988) found no differences in photosynthesis between fruiting and non-fruiting plants, although the former had lower carbohydrate levels.

The starch content of fruit trees follows an annual pattern of accumulation and utilization (Davie *et al.*, 1995) and the root and wood of trees are particularly important as storage organs (Davie *et al.*, 1999). It is clearly shown from their work that the starch reserves remain at their lowest levels during the period of rapid fruit growth. Results illustrate that the roots, wood, shoots, bark and even the leaves accumulate starch during the winter and that the reserves are then drastically depleted during the spring and summer (Stassen & Janse van Vuuren, 1997a; b). Davie & Stassen (1997a) generally concluded that the phenomenon of biennial or alternate bearing in subtropical tree crops stems primarily from the depletion of the starch reserves of the tree during fruit production and development. This drain in the tree resources leaves it unable to rapidly replenish its reserves in order to meet the demand of the new cycle of vegetative growth, flowering, fruit set and fruit development.

There would seem to be two sets of situations which may cause biennial bearing: either a very low fruiting year, often caused by adverse environmental factors at flowering, or a very heavy fruit set with too little fruit drop (Wright, 1989). Monselise & Goldschmidit (1982) stated that heavy crops produced during the on-year, is the most universally recognized cause of alternation and that starch levels in an off-year are much higher than in an on-year. Davie & van der Walt (1994) found that the point in time when the 'switch' to an on- or- off- year season is determined long before the fruit development stage and it may be just before or after harvest. Stassen *et al.* (1982) concluded, it is therefore clear that the canalising of carbohydrate reserves can be redirected by means of fruit and tree manipulation as well as with other cultivation practices. In other words, the depleting effects of fruit load on starch reserves can be altered by fruit thinning and tree pruning (Davie & Stassen, 1997a; Stassen *et al.*, 1999).

Generally, sufficient reports on fruit thinning in mango are lacking (Oosthuyse & Jacobs, 1995). This might be expected since poor fruit retention is still considered to be a major problem in mango. Most of the studies conducted to date, with regard to fruit thinning and tree manipulation are basic and encourage further study.