Avocado Alternate Bearing Research

Dr Grant Thorp
The New Zealand Institute for Plant
and Food Research Ltd

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Telephone: (02) 8295 2300
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Dr Grant Thorp *et al.*

The New Zealand Institute for Plant & Food Research Limited

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Project Leader: Dr Grant Thorp

Plant & Food Research
Mt Albert Research Centre
Private Bag 92169
Auckland 1142
NEW ZEALAND

T: +64 9 925 7290
M: +64 21 2268290

grant.thorp@plantandfood.co.nz

Key Personnel:

Andrew Barnett	Nick Gould
Brad Howlett	Helen Boldingh
Michal Blattmann	Ella Maxwell
Lisa Evans	Peter Minchin
Mark Goodwin	Darienne Voyle

This report provides an update on a series of on-going research projects established in Australia and New Zealand to provide the avocado industry with a better understanding of the causes of alternate bearing and a set of solutions to ensure growers can produce reliable fruit yields.

This project has been funded by HAL using a voluntary contribution from Plant and Food Research and matched funds from the Australian Federal Government.

Date: 31 May 2011

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Media Summary

All avocado producing regions encounter alternate bearing, with orchards producing variations in yields from one year to the next. In high cropping years prices to growers are low while in light cropping years marketers find it difficult to supply key markets. Environmental triggers such as frost or drought can initiate these ON/OFF cropping cycles, while internal physiological mechanisms are responsible for their continuation. Research in Australia and New Zealand by Plant & Food Research is aiming to understand better these mechanisms in order to provide solutions for growers wanting to produce consistently high yields.

Results from this study have demonstrated a close relationship between the supply of 7-carbon carbohydrates and boron to avocado flowers, with both nutrients being transported in the phloem. A shortage of 7-carbon carbohydrates will lead to a shortage of boron in flowers and thus potentially poor fruit set. High crop loads will compete with flowers for the available carbohydrates and boron and thus make the situation worse in ON cropping years. More careful timing of boron applications to match the requirements of growing fruit and canopy management to avoid over-cropping could therefore be important components in strategies to mitigate alternate bearing.

Hand pollination can increase fruit set fivefold, indicating that natural pollination systems may limit fruit set. It is important that insects visit all flowers and deposit sufficient quantities of pollen. This does not always happen. At one orchard, only 82% of flowers were visited by insects (honey bees) and of these only 32% resulted in pollen transfer. In a second orchard 100% of flowers had multiple visits by multiple insects but most pollen transfer occurred in the afternoon when polliniser trees were releasing pollen. These contrasting situations suggest that more hives are required at the first orchard whereas better overlap between female and male flowers is needed in the second orchard.

But even with hand pollination and a high number of pollen grains deposited on flowers this does not guarantee fruit set. Future research will continue to consider flower quality (carbohydrate and boron composition) and pollen viability as reasons for poor fruit set.

Technical Summary

All avocado (*Persea americana* Mill.) producing regions encounter alternate bearing to some extent, with unreliable yields from one year to the next. In high cropping years prices to growers are low while in light cropping years marketers find it difficult to maintain supply into key markets. Environmental triggers such as frost or drought can initiate these ON/OFF cropping cycles, while internal physiological mechanisms are responsible for their continuation. Much horticultural work has been undertaken in an attempt to understand these.

Previous research with avocado and other crops has implicated both tree carbohydrate status and boron (B) deficiency as drivers of alternate bearing. Poor pollination may also be important. Research in Australia and New Zealand is addressing these factors in an international research programme led by New Zealand's Plant & Food Research institute.

A continuous supply of B is vital for the formation of new cells, with reproductive growth being particularly sensitive to B deficiency. We have demonstrated that perseitol, the polyol transported in avocado phloem, can form a complex with B. So there is the potential for perseitol to complex with B in avocado phloem sap, to render B phloem mobile. We found that mature avocado leaves had a considerably lower B concentration than young tissues, consistent with other plant species in which B is phloem mobile. Also, ^{10}B was able to move from a mature avocado leaf into nearby young tissues, indicating phloem mobility, and we found B in phloem sap collected using the EDTA technique. We concluded that B can be phloem mobile in avocado and the ability for B transport may depend upon the amount of perseitol in the phloem sap.

Several results supported this close relationship between the supply of 7-carbon carbohydrates and B to flowers, with both nutrients being transported from leaves to flowers via the phloem. In both spring and summer flush shoots, leaf B concentrations decreased at a similar rate and timing as the decline in D-mannoheptulose. These are the shoot types which produce next season's flowers and fruit. Also, branch girdling during winter tended to increase B and D-mannoheptulose in flowers, by up to 50%. Therefore a shortage of 7-carbon carbohydrates could potentially lead to a shortage of B in flowers and thus poor fruit set. We found lower B concentrations in leaves from ON cropping trees compared with OFF cropping trees. High crop loads may therefore compete with flowers for the available carbohydrates and B and exacerbate alternate bearing. Investigating more strategic timing of B applications to match the requirements of growing fruit and canopy management to avoid over-cropping could therefore be important components in strategies to mitigate alternate bearing.

Fruit set has been shown to increase fivefold with hand pollination, indicating that natural pollination systems may be limiting. It is important that insects visit all flowers and deposit sufficient quantities of pollen. This does not always happen. Studies at one orchard showed that only 82% of flowers were visited by insects (honey bees) and of these only 32% resulted in pollen transfer. In a second orchard, 100% of flowers had multiple visits by multiple insects but pollen transfer was mainly limited to the afternoon when polliniser trees were releasing pollen. These contrasting situations suggest more hives are required at the first orchard whereas better overlap between female and male flowers is needed at the second orchard.

But even with hand pollination and a high number of pollen grains deposited on the stigmas of flowers this does not guarantee fruit set. Future research will continue to consider flower quality (carbohydrate and boron composition) and pollen viability as reasons for poor fruit set.

Introduction

This report describes ongoing research in Australia and New Zealand in Phase I of a programme to find solutions to alternate bearing in avocados. The projects are at various stages of completion with some projects completed and data about to be published in scientific papers while other projects are in their early stages of a multi-year programme. The main body of this report provides summaries of these projects. For copyright reasons, copies of the scientific papers are not included with this report.

The report concludes with recommendations for further research and how these recommendations can be incorporated into Phase II of the avocado alternate bearing programme. It is anticipated that Phase II will be facilitated by Horticulture Australia Limited (HAL) in partnership with Avocados Australia Limited (AAL) and jointly funded by HAL, AAL and the peak avocado industry groups in New Zealand and California.

Alternate Bearing Research

There are two scenarios that can lead to alternate bearing (Figure 1). The first is when there are "fruit but no flowers", which occurs when the presence of a heavy crop one year inhibits shoot growth and flowering in the next year. The second is when there are "flowers but no fruit", in this scenario there are sufficient flowers but very poor fruit set. Depending upon season and environment, these two scenarios may be additive or independent of each other. Research in Phase I of this programme has focused mainly on this second scenario.

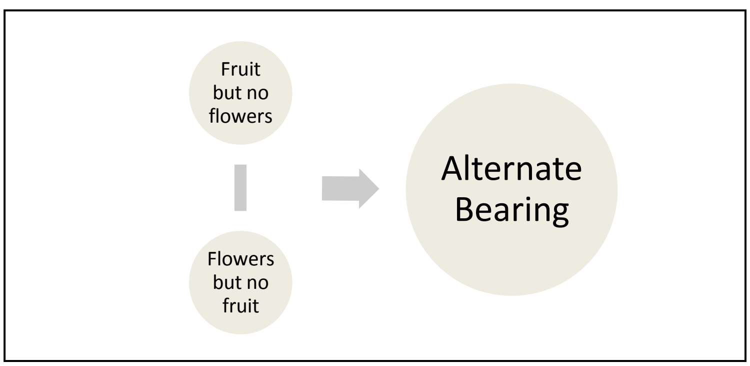

Figure 1. Alternate bearing can result from having too many fruit but not enough flowers for the following season and/or from having sufficient flowers but not the right conditions to set sufficient fruit.

While environmental triggers such as frost or drought can initiate these ON/OFF cropping cycles that are characteristic of alternate bearing, internal physiological mechanisms are responsible for their continuation. Much horticultural work has been undertaken in an attempt to understand these. Previous research with avocado and other crops examining reasons for low fruit set have implicated both low tree carbohydrate status and boron deficiency as drivers of alternate bearing (Whiley et al. 1996; Wolstenholme 2010). Poor pollination can also be important (Evans et al.

2010). In Phase I of our research we have considered both these aspects. A third project area is examining the opportunities to reduce the impact of alternate bearing at the orchard level by the use of high density orchard planting systems.

Carbohydrate and boron physiology

Is boron transported in the phloem of avocado trees?

A continuous supply of boron is vital for the formation of new cells during plant growth and development and reproductive growth is particularly sensitive to any deficiency in boron supply (Iwai et al. 2006). Insufficient transport of boron to flowers and developing fruitlets could be an important factor contributing to alternate bearing in avocado. In many plant species boron is not phloem mobile, as the mineral form of boron quickly leaks from the phloem into surrounding tissues, so distribution throughout the plant depends completely upon continuous xylem supply. Some plants have polyols (e.g. sorbitol, mannitol) as a component of their phloem sap. They form a complex with boron ions preventing its leakage from the phloem and making it phloem mobile. This has been well documented in many tree crops, such as apple and almond (Brown and Hu 1998). The major carbohydrates in avocado are the 7-carbon carbohydrates D-mannoheptulose and the polyol perseitol (Liu et al. 2002). Our hypothesis was that the presence of perseitol in the phloem sap of avocado may facilitate the transport of B via the phloem. While this had been previously suggested in the avocado literature, it had never been demonstrated. In this work we used mass spectrometry to demonstrate that perseitol, the polyol transported in avocado phloem, can form a complex with B. So there is the potential for perseitol to complex with B in avocado phloem sap, to render B phloem mobile. We used the methods of Brown and Hu (1998) to show that mature avocado leaves had a considerably lower B concentration than young tissues, consistent with other plant species in which B is exported from the leaf in the phloem. With nutrients such as calcium that are not transported in the phloem, concentrations in leaves increase over time as there is no export. We also demonstrated that ^{10}B was able to move from a mature avocado leaf into nearby young tissues, indicating phloem mobility, and we found B in phloem sap collected using the EDTA technique. We concluded that B can be phloem mobile in avocado and the ability for B transport may be related to the amount of perseitol in the phloem sap.

This work was led by Dr Peter Minchin and Helen Boldingh from Plant & Food Research, in collaboration with Mary Lu Arpaia, Eric Focht and Fayek Negm from the University of California Riverside and with Patrick Brown and Hening Hu from the University of California Davis.

The project has been completed, written up and submitted for publication in a scientific journal (Minchin et al. unpublished) and for presentation to the VII World Avocado Congress in Cairns in September 2011.

Variation in phloem sap composition in avocado trees

The phloem is a key structure in the supply of assimilates and remobilised minerals to developing plant tissues, including the flower. Inadequate supply of nutrients (carbohydrates and minerals) via the phloem could result in poor flower quality and low fruit set. Phloem sap composition is regulated by nutrient availability from the mature leaf in addition to the processes of loading, translocation and unloading of these nutrients along the supply pathway. There has been a wide range of assessments of phloem nutrient supply strategies for many different plant types, with the aim of understanding possible limitations of fruiting potential and subsequent production. In the case of avocado, it has been reported that there are unusual 7-carbon carbohydrates that are assimilated within the mature leaf and subsequently transported via the phloem (Liu et al. 2002). To investigate the role of the phloem in the supply of sugars and nutrients to the avocado flower, and how this may affect the processes of pollination and fruit set in different regions/environments, we monitored the phloem sap content (carbohydrates and nutrients) in the flower over 24-hour periods during flowering , in 'Hass' avocado orchards in New Zealand, Australia and California .We found that three major carbohydrates, sucrose, perseitol and D-mannoheptulose, plus boron were important nutrients supplied by the phloem for flowering and early fruit growth. We also made some preliminary observations of relationships between boron and perseitol concentrations in ON and OFF cropping trees and between samples collected after periods of very hot or relatively cool humid conditions. Examples of the types of relationships being investigated in this research are that high crop loads and/or cool conditions with relatively low evaporative demand may reduce the delivery of carbohydrates and boron via the phloem to flowers and developing fruit and that this limits fruit set. The implications of this would be that crop load and/or boron nutrition need to be better managed to ensure sufficient supply to developing flowers in ON cropping years. Low boron and carbohydrate concentrations in phloem sap during cool humid conditions could imply poor transport of these nutrients and thus explain poor fruit set in regions such as New Zealand where these conditions are prevalent over the flowering period.

This work was led by Dr Peter Minchin and Dr Grant Thorp from Plant & Food Research, in collaboration with Mary Lu Arpaia, Eric Focht and Fayek Negm from the University of California Riverside.

This work will continue under separate funding, with further samples required to determine variation in phloem sap composition over more than one season in Australia and New Zealand. Extremely high rainfall during avocado flowering in Queensland in 2010 limited the amount of work that could be completed in Year 1. Data was presented as a progress report to the VII World Avocado Congress in Cairns in September 2011.

Is boron transport to avocado flowers regulated by carbohydrate supply?

Our work has demonstrated that perseitol, the main transport sugar in avocado, can complex with boron to make boron phloem mobile in avocado (Minchin et al. unpublished). This suggests that boron transport from avocado leaves could be regulated by carbohydrate supply. Our hypothesis was that techniques, such as branch girdling (Whiley 2002), used to manipulate the supply of carbohydrates to flowers, would also affect the supply of boron. Branch girdling treatments were applied at different phenological stages to manipulate carbohydrate supply to flowers on 'Hass' avocado trees with high (ON) and low (OFF) crop loads. Few differences were found between leaf carbohydrate concentrations in ON and OFF cropping trees. However, leaf boron concentrations were consistently lower in ON cropping trees, which suggests that fruit are an important competing sink for boron. Leaf boron concentration declined during winter at a similar timing to that of D-mannoheptulose, the storage form of perseitol. Girdling treatments applied to ON cropping trees increased the rate of boron loss from leaves and increased the boron content of flowers immediately before anthesis. This is consistent with boron supply to flowers being regulated by carbohydrate supply.

Branch girdling has often been used by avocado growers to increase flowering and fruit set, but with inconsistent results (Davenport 1986). Essentially, girdling is a means of altering the allocation of the supply of carbohydrates and thus boron from leaves to other parts of the tree. Regulating crop load in ON cropping trees could have a similar effect by reducing the size of the fruit sink thus making more carbohydrates and boron available for next season's flower and fruit development. Future studies will consider this aspect to develop more sophisticated crop regulation strategies to mitigate the effects of alternate bearing.

This work was led by Dr Grant Thorp from Plant & Food Research, in collaboration with Toni Elmsly and Henry Pak from the New Zealand Avocado Industry Council.

The project has been completed, written up and submitted for publication in a scientific journal (Thorp et al. unpublished) and for presentation to the VII World Avocado Congress in Cairns in September 2011.

Role of carbohydrates and boron in determining flower quality in avocado

One of the arguments for why carbohydrate and boron resources are implicated as a possible cause of alternate bearing is that when trees are carrying high crop loads there are insufficient carbohydrates and boron available to support floral development and ensure successful fruit set (Scholefield et al. 1985). This implies that there can be poor quality flowers, characterised by being deficient in carbohydrates and/or boron. Projects in Spain and New Zealand have been examining this possibility.

Earlier work in Spain by Iñaki Hormaza and Librada Alcaraz showed that flowers with high starch content were more likely to set fruit than flowers with low starch content (Alcaraz et al. 2010). In collaboration with the Spanish scientists we undertook to expand on this result and quantify the concentrations of individual carbohydrates and boron in avocado flowers and relate these to the probability of flowers setting a fruit. In New Zealand, we hand pollinated 2959 'Hass' flowers and 24 hours later collected styles from these same flowers for subsequent carbohydrate and boron analysis. Of the hand pollinated flowers, 69 continued development to produce a fruit to give 2.3% successful fruit set. The styles from these flowers/fruit, plus comparable samples from early, mid and late-blooming flowers that did not result in successful fruit are now being analysed for carbohydrate and boron composition. A similar project was established in Spain during their flowering period in 2010 and tissue samples were extracted and shipped to New Zealand for analysis.

This work was led by Dr Grant Thorp from Plant & Food Research, in collaboration with Iñaki Hormaza and Librada Alcaraz from CSIC in Spain.

This work will continue under separate funding with further flower samples to be collected New Zealand in October 2011. Future work and publication of data will depend on the results of carbohydrate and boron analyses. Possible implications of this work is that it will provide new knowledge on flower quality, which will contribute to the development of more sophisticated flower thinning strategies to regulate crop load and mitigate the effects of alternate bearing in avocado.

Use of molecular techniques to study utilisation of boron and carbohydrates by avocado flowers

Related research projects have examined whether carbohydrate and boron concentrations in flowers have a role in determining flower quality and the levels of fruit set in avocado. However, there is also the possibility that flowers may have sufficient carbohydrates and boron, but poor fruit set occurs because the flowers are not able to utilise these nutrients. In this project, we were interested in gaining a better understanding of factors affecting the utilisation of carbohydrates and boron by avocado flowers. The first step was to identify key genes involved in the utilisation of carbohydrates and boron by floral tissues. Genes of interest were Trehalose Phosphate Synthase 1, a key enzyme controlling the metabolism of glucose (Schluepmann et al. 2003), and Glucuronyltranferase 1, a key enzyme required for boron binding in cell wall construction during pollination (Iwai et al. 2006). These genes have previously been identified in at least six other plant species. This work has enabled the construction of degenerate primers to conserved regions for amplification of the genes from avocado. Once the genes are sequenced, variations in gene expression in avocado flowers will be examined for possible explanations of the very low fertilisation rates typical of avocado. This information will improve our understanding of factors contributing to poor fruit set in avocado and aid development of methods to improve yields, especially in OFF-flowering years.

This work was led by Dr Nick Gould from Plant & Food Research.

This work will continue under separate funding. Candidate genes have been identified; the next phase is to sequence these genes, for the first time, in avocado. Preliminary data was presented as a progress report to the VII World Avocado Congress in Cairns in September 2011.

Role of insect pollination of avocados in Australia and New Zealand

Fruit set on avocado trees is generally < 0.1% of flowers. However, research in New Zealand has shown that hand pollination can produce fruit set greater than 5% (Evans et al. 2010). This suggests that pollination by honey bees (and other insects) is limiting. If open pollinated flowers could reach 5% fruit set this would mitigate many of the effects of alternate bearing, especially in OFF flowering years. The purpose of this current study is to better understand why application of pollen grains to avocado flowers markedly increases fruit set and to use this information to improve the efficiency of pollination systems. The study has been conducted in a New Zealand (with pollinisers) and in two Australian orchards (one with and one without pollinisers) to determine the number of pollen grains required on the stigma to set fruit, types and numbers of insects visiting avocado flowers, the length of their visits, the numbers of pollen grains transferred, and proportions of insect visitors carrying avocado pollen.

In Israel it has been estimated that between 7 and 20 pollen grains are required per stigma for a fruit to be produced, but this is based on insufficient evidence and the number required is likely to vary with climate. In New Zealand, hand pollinated flowers produced more fruit than open pollinated flowers, with 2.9% and 0.76% fruit set, respectively. On average those flowers that set fruit had significantly more pollen grains ($P = 0.014$) than those that did not produce fruit. In Australia, only 0.68% of the hand pollinated flowers and none of the open pollinated flowers produced fruit. On average there were significantly fewer pollen grains ($P = 0.035$) on the hand pollinated stigmas in Australia compared with those in New Zealand. The lower number of pollen grains on stigmas in Australia may be due the polliniser flowers having less pollen (a different polliniser was used in Australia and New Zealand), or perhaps weather conditions and/or the pollens compatibility affected the pollen ability to adhere to the stigmas. Further studies are necessary to investigate this.

Video footage showed that in New Zealand 97.4% of flower visits were by honey bees, while in Australia 49.7% of the visitors were hover flies, 37.9 % were honey bees, and 12.4% of the visits were from other insects (flies other than hover flies and native bees). In New Zealand, 17.7% of flowers did not receive any insect visits while open during the female phase, and no pollen grain deposition was recorded on a further 68% of visited flowers. In Australia, 100% of flowers observed at the female stage received an insect visit and pollen was transferred as long as there was overlap between female and male flower opening. However, the total number of pollen grains transferred onto female phase flowers by visiting insects was low in both countries, c. 1.7 and 0.72 pollen grains in New Zealand and Australia, respectively.

Honey bees were caught on flowers in their female phase in the New Zealand orchard (which had polliniser trees) and in two different blocks in one of the Australian orchards. Block 1 at the Australian orchard had no polliniser trees and was 400 metres away from block 2 which had 16 polliniser trees. It is unlikely that were any male-phase 'Hass' flowers open at the time the bees were caught. In New Zealand, 84% of the bees were carrying pollen available for pollination (pollen on the body of the insect not its corbiculae), compared to 68.6% and 87.7% in block 1 and 2 in Australia, respectively. Bees from flowers in block 1, with no polliniser trees, were carrying less pollen than bees from block 2, with polliniser trees (4.7 and 18.2 pollen grains, $P=0.007$). Bees collected from the New Zealand orchard were carrying 38.7 pollen grains. This number of avocado pollen grains carried by honey bees foraging on female avocado flowers is very low compared to the number of pollen grains found on bees foraging on other crops such as kiwifruit and carrots (Mark Goodwin, unpublished data).

In block 2 in Australia a small number of hover flies and a species of stingless bee were also caught on flowers open in their female phase. 50% percent of the hoverflies and 94% of the stingless bees were carrying avocado pollen, in similar amounts to that carried by honey bees.

The low numbers of pollen grains transferred to flowers by pollinators may be a factor that limits fruit set in these countries. The contrasting situations between the New Zealand and Australian sites suggest that perhaps more bees are required at the New Zealand orchard whereas better overlap between female and male flowers is needed at the Australian orchard. However, other factors may have influenced pollination and insect behaviour; these factors may include climatic conditions and/or the compatibility and/or viability of pollen. Future studies will consider these aspects.

This work was led by Lisa Evans from Plant & Food Research.

This work will continue under separate funding, with data collection over more than one season. Only limited data could be collected in Queensland in 2010 because of extremely high rainfall events during the flowering period. These data have been analysed and results presented hereand were presented as a progress report to the VII World Avocado Congress in Cairns in September 2011.

High density planting systems

All avocado producing regions encounter alternate bearing to some extent with unreliable yields from one year to the next restricting the ability of industries to establish new markets. Ultimately the most cost-effective and sustainable solutions to alternate bearing in avocado orchards may come from the adoption of high density growing systems (Thorp et al, 2001), as used by apple and stonefruit growers.

Orchard productivity is proportional to the total intercepted radiation (Monteith 1977). This means growers need to manage the shape and size of their trees to maximise the total amount of incoming radiation intercepted by the orchard. Schaffer and Whiley (2003) emphasised this point when they said growers need to shape avocado trees so that a greater proportion of leaves receive sufficient light to attain their maximum photosynthetic potential. With apples and other crops that use high density planting systems the ideal tree shape is a “slender pyramid” shape by which the tree is slightly wider at the base than at the top (Tustin, 2000).

There is a common belief that alternate bearing cycles are more prominent in older avocado orchards with large trees that are difficult to manage. New “high density” orchards established with fast track development systems to promote early yields from “small trees” may provide growers more options to apply sophisticated and precise management interventions needed to achieve consistently high yields in avocado groves and thus avoid extreme alternate bearing (Hofshi, 1999). Previous work in New Zealand, California and Chile has demonstrated the proof of concept for high density orchards. However, there remain two key requirements to the success of these systems.

- Nurseries need to provide growers with single-leader trees suitable for high density orchards; this requires a radical re-think of the type of tree produced by avocado nurseries.
- Renewal pruning systems need to be tested and confirmed so that growers can contain trees size and maintain consistent yields over the life of the orchard.

An additional requirement, not encountered in California or Chile but that has been a barrier to the success of high density plantings systems in New Zealand is to get high yields from young trees (Thorp, unpublished data). The key to promoting the growth of a single leader tree with a slender pyramid shape suitable for high density plantings is to encourage vigorous growth from a single growing point from the grafted scion. If there is sufficient vigour in the primary growth axis then a new lateral shoot will be produced at every leaf node as the primary axis extends (Figure 2). These shoots form by syllepsis as they emerge and extend at the same time as the primary growth axis without an intervening period of rest (Thorp et al, 1994). A high proportion of sylleptic shoots is a good indicator of vigorous shoot development.

Unfortunately, the economics of growing plants in nurseries mean plants are closely spaced on the propagation benches and this inhibits the number and growth of these sylleptic lateral shoots (Figure 3).

One option is for nurseries to sell the plants soon after grafting, before shading reduces the production of lateral shoots developing from the primary growth axis. This would mean it is then left for the grower to promote the required vigorous growth in the field from a single growing point that will produce a single leader tree with a lateral branch at every leaf node. Growers can do this by removing at an early stage any competing shoots arising below the primary growing point that is being promoted to form the trunk (Figure 4). These are generally proleptic shoots that develop from resting buds below the terminal bud being promoted as the primary growth axis (Thorp et al, 1994). These proleptic shoots reduce the vigour of the primary growing point and so it is important that they are removed as soon as possible once the primary growing point has been identified.

Another option tested for the first time in New Zealand in 2010/11 was to take a larger plant from the nursery, plant it into the field and then pin it down to create a bend just above the graft union to force the development of a new growing point (Figure 5). This new growing point forms within a few weeks and quickly becomes vigorous, producing the desired growth habit with a new lateral shoot at every new leaf node to give a slender pyramid tree shape that is slightly wider at the base than at the top. This new shoot does not need to be staked as it immediately develops a very strong, tapered trunk. The original section of tree is kept for a few months before it is removed, in the meantime the leaves on this section will be supporting growth of the root system and of the new trunk.

This option of pinning down the tree at planting and promoting the growth of a new trunk works better than just using a heading cut to cut back the trunk in order to promote a new growing point. This heading method removes all leaf growth needed to support root growth and growth of the new trunk, so that the new growing point is slow to develop and lacks the required vigour to produce the desired single leader growth habit.

This project led by Dr Grant Thorp from Plant & Food Research, is ongoing with planning in place with nurseries and growers in Australia and New Zealand to test plots of high density 'Hass' avocado trees using young plants produced using the methods described here.

Figure 2. The desired growth habit for single leader trees, note the new lateral shoot (arrowed) produced at each leaf node along the primary growth axis.

Figure 3. It is difficult to promote vigorous growth from a single growing point with a new lateral shoot at every leaf node when trees are closely spaced on nursery benches.

Figure 4. Growers have the option of planting out smaller trees and promoting the growth of a single, vigorous growing point in the orchard. This is done by removing at an early stage any competing shoots arising below the primary growing point that is going to be promoted. Arrows mark the shoots that need to be removed.

Figure 3. Strong single leader tree with the desired slender pyramid shape produced by pinning down the main stem of the tree and forcing a new stronger growing point from above the graft union. The original section of plant (arrowed) can be seen pinned down to the left.

Recommendations for further research

We recommend that further research on alternate bearing in avocado is linked with the International Avocado Alternate Bearing Programme being developed by Plant & Food Research for the international Avocado Research Council (ARC), involving the peak avocado industry groups from Australia, New Zealand and California.

Dr Grant Thorp led the development and submission of a substantial research proposal for this programme, valued at US$2.6 million over five years. Feedback from the ARC was positive and a funding recommendation is expected in August 2011. The programme will be managed by Plant & Food Research and it is anticipated that ARC will approach HAL for contributory funding to support the recommended research projects. The proposed programme would involve science groups from Australia, New Zealand, Chile, California, Florida and Spain, and cover five project areas:

1. Research integration, model development and Decision Support System (DSS) delivery
2. Determining environmental and biological triggers for alternate bearing in avocado
3. Regulating the transition from vegetative to floral meristems in avocado
4. Improving flower quality, pollination, fertilization and fruit set in avocado
5. Management strategies to mitigate alternate bearing in avocado.

A summary of this proposal is provided at the end of this report (Appendix I). A full copy of the proposal can be obtained from Dr Dan Ryan, Business Manager at Plant & Food Research (Dan.Ryan@plantandfood.co.nz).

Outputs

Two scientific papers have been prepared for publication in the Journal of Horticultural Science and Biotechnology:

1. Phloem transport of boron within avocado trees. By Minchin PEH, Thorp TG, Boldingh HL, Cooney JM, Negm FB, Focht E, Arpaia ML, Hu H and Brown P.

2. Is boron transport to avocado flowers regulated by carbohydrate supply? By Thorp TG, Barnett AM, Boldingh HL, Elmsly TA, Pak HA and Minchin PEH.

Two popular articles have been prepared for publication in the next issue of Talking Avocados and Avoscene. These are industry journals published by the Australian and New Zealand avocado industries, respectively.

1. Alternate bearing research – an update on progress in New Zealand and Australia. By Thorp TG, Minchin PEH, Boldingh HL, Gould N and Evans L.
2. High density planting systems for 'Hass' avocados. By Thorp TG and Barnett AM.

Communications/extension activities:

1. Grant Thorp and Peter Minchin attended the International Alternate Bearing Summit held in California on 27-29 September 2010. The purpose of this Summit was to engage an international group of scientists to promote discussions on alternate bearing in fruit trees, mostly focused on avocados, which would develop themes for future research and facilitate international collaboration. A draft summary of this meeting was prepared by Grant Thorp as a first step towards developing a framework for a co-ordinated programme of research on alternate bearing. This summary was circulated among scientists who attended the meeting and responses collated and incorporated into the international Alternate Bearing research proposal submitted to the Avocado Research Consortium (ARC).
2. Lisa Evans, Nick Gould, Helen Boldingh and Ella Maxwell visited Queensland and northern NSW avocado orchards during flowering in October 2010 to undertake project work on pollination and phloem sap composition, with the assistance of John Leonardi from AAL.
3. The New Zealand avocado research teams from Plant & Food Research and AIC (New Zealand Avocado Industry Council) met in New Zealand on 24 November 2010 to review research progress and plans for the next 6 months of activity in Australia and New Zealand. Librada Alcaraz, our collaborator from Spain also attended this meeting.
4. Grant Thorp met with Henry Pak (AIC Technical Manager) on 30 November 2010 to provide AIC with an update on Alternate Bearing research activities.
5. Grant Thorp attended a Planning Meeting in Riverside California on 5 February 2011 of the lead scientists from New Zealand, California, Spain and Israel contributing to the international Alternate Bearing research proposal submitted to the Avocado Research Consortium (ARC).
6. Grant Thorp and Lisa Evans visited avocado growers and nurseries in southern and central Queensland and northern NSW in March/April 2011 to complete pollination project work and to develop plans for high density planting trial sites in Australia. During this visit, meetings were held with Antony Allen (CEO), John Leonardi (Technical Manager), Lachlan Donovan and Daryl Boardman (Directors) from AAL to provide them with updates on progress with alternate bearing research projects and the development of the international alternate bearing research proposal and preparations for Avocado Brainstorming 2011.
7. Grant Thorp visited West Australia in April 2011 with John Leonardi from AAL to meet with avocado growers in Pemberton and Busselton, and Alec McCarthy from the WA Department of Agriculture to provide them with updates on progress with alternate bearing research projects and the involvement of West Australian growers and R&D staff in this research. Russell Delroy (AAL Director) was also provided with an update on the international alternate bearing research proposal and preparations for Avocado Brainstorming 2011.
8. Grant Thorp continues to contribute to planning for Avocado Brainstorming to be held in New Zealand in August/September 2011. The purpose of Avocado Brainstorming is to

provide a forum for avocados scientists from around the world to participate in detailed scientific discussions on current topics relevant to the international avocado industry. Alternate Bearing in avocados will be a key theme for this meeting. Avocado Brainstorming is held every 4 years in conjunction with the World Avocado Congresses.

References

Alcaraz ML, Hormaza JI, Rodrigo J 2010. Ovary starch reserves and pistil development in avocado (*Persea americana*). Physiologia Plantarum 140 (4): 395–404.

Brown PH, Hu H1998. Phloem boron mobility in diverse plant-species. Botanica Acta 111: 331–335.

Davenport TL 1986. Avocado flowering. In: Janick J ed. Horticultural Reviews Volume 8 AVI Publishing Co. Inc. Westport, CN. Pp 257–289

Evans LJ, Goodwin RM, McBrydie HM 2010. Factors affecting 'Hass' avocado (*Persea americana*) fruit set in New Zealand. New Zealand Plant Protection 63: 214–218.

Hofshi R 1999. High-Density Avocado Planting – An Argument for Replanting Trees http://www.avocadosource.com/papers/research_articles/hofshireuben1999.htm.

Iwai H, Hokura A, Oishi M, Ishii T, Sakai S, Satoh S 2006. The gene responsible for borate cross-linking of pectin rhamnogalacturonan-II is required for plant reproductive tissue development and fertilization. Proceedings of the National Academy of Sciences 103: 16592–16597.

Liu X, Sievert J, Arpaia ML, Madore MA 2002. Postulated physiological roles of the seven-carbon sugars, mannoheptulose, and perseitol in avocado. Journal of the American Society of Horticultural Science 127(1):108–114.

Monteith JL 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society, Series B, 281: 277–294.

Schaffer B and Whiley AJ 2003. Environmental regulation of photosynthesis in avocado trees – a mini-review. Proceedings V World Avocado Congress (Actas V Congreso Mundial del Aguacate): 335–342. http://www.avocadosource.com/wac5/papers/wac5_p335.pdf

Schluepmann H, Pellny T, van Dijken A, Smeekens S, Paul M 2003. Trehalose-6-phosphate is indispensable for carbohydrate utilization and growth in Arabidopsis thaliana. Proceeding of the National Academy of Sciences 100: 6849–6854.

Scholefield PB, Sedgley M, Alexander DM 1985. Carbohydrate cycling in relation to shoot growth, floral initiation and development and yield in the avocado. Scientia Horticulturae 25: 99–110.

Thorp TG, Aspinall D, Sedgley M 1994. Preformation of node number in vegetative and reproductive proleptic shoot modules of Persea (Lauraceae). Annals of Botany **73** (1): 13–22.

Thorp TG, Woolf A, Boyd L, Ferguson I, White A, Everett K 2001. Avocado canopy management - sustainable production of top quality fruit. Australian and New Zealand

Avocado Growers' Conference "Vision 2020" (Proceedings), 3–7 June 2001, Bundaberg. Australia. http://www.avocadosource.com/journals/ausnz/ausnz_2001/1063p020.pdf

Tustin DS 2000. The evolution of central leader apple tree management in New Zealand. Compact Fruit Tree 23 (3): 83–92.

Whiley AW 2002. Crop management. In: Whiley AW, Schaffer B, Wolstenholme BN eds. The Avocado; Botany, Production and Uses. CAB International Press, Wallingford, UK. Pp 231–258.

Whiley AW, Smith IE, Wolstenholme BN, Saranah JB 1996. Boron nutrition in avocadoes. South African Avocado Growers' Association Yearbook 19: 1–7.

Wolstenholme BN 2010. Alternate bearing in avocado: an overview. Cited from http://www.avocadosource.com/papers/southafrica_papers/wolstenholmenigel2010.pdf.

Appendix I. International Avocado Alternate Bearing Research Programme

Background

An international Avocado Research Consortium (ARC), involving the peak avocado industry groups in Australia, New Zealand, California and Israel was established specifically to address alternate bearing research for the benefit of the global avocado product group. ARC agreed to establish an international funding stream specifically to support a number of science projects aimed at developing new knowledge and practical solutions to the problem of alternate bearing and started a process by which they requested research proposals from various research providers.

To start the process, an International Alternate Bearing Summit was convened by the ARC in California on 27-29 September 2010 to engage an international group of scientists with an interest in alternate bearing in avocado and other crops. The Summit Objectives were to promote discussions on alternate bearing in fruit trees, mostly focused on avocados, which would develop themes for future research and facilitate international collaboration. A second meeting involving lead scientists willing to form an international collaboration and prepare a joint proposal to ARC was held in Riverside California on 5 February 2011. A summary of these discussions was prepared to provide a research framework that highlights the key hypotheses and likely experimental approaches required to provide solutions to alternate bearing. A research proposal document was prepared on the basis of this research framework and submitted to the Avocado Research Consortium (ARC) on 4 March 2011. This proposal represents the strongest international collaborative research effort ever dedicated to avocado science and the search for industry solutions to alternate bearing. The proposed experimental programme involves 14 collaborating research organisations from six countries, with more than 30 scientists representing a mix of experienced and young, emerging scientists and several non-avocado scientists who have experience with alternate bearing research with other fruit crops.

Research Hypothesis

The key research hypothesis considered during the International Alternate Bearing Summit was that:

"The presence of a fruit on a fruiting shoot determines the fate of the meristem on that shoot"

What this means is that if a fruit is present then meristems remain vegetative and do not produce an inflorescence in the following season (Figure i). If there is no fruit, then meristems become reproductive and produce an inflorescence and fruit in the following season. There exists some plasticity around this, arising from the timing of growth processes of the meristem relative to fruit development and the timing of the perceived signal from fruit that induce alternate bearing.

Considered at the whole tree and orchard level this simple hypothesis can be re-written as:

"Crop load determines the level of return bloom on avocado trees"

Thus, if trees have a high crop load then that has a negative effect on resources available to support strong shoot and root growth (Figure ii). The number of buds that can potentially produce inflorescences and/or the percentage of buds that will go through transition to flowering are reduced. Fewer buds and reduced floral signalling, resulting possibly from seed-produced gibberellins inhibiting floral induction, will result in diminished flowering and a low crop load in the following season. The argument is then that trees with a low crop load should have sufficient resources to support strong vegetative development, the number of buds that can potentially produce inflorescences is increased and the percentage of buds that will go through transition to flowering is increased, both leading to heavy flowering in the following season. With each of these steps, two groups of hypotheses based on "signalling" and "resources" can be developed to question the mechanisms involved.

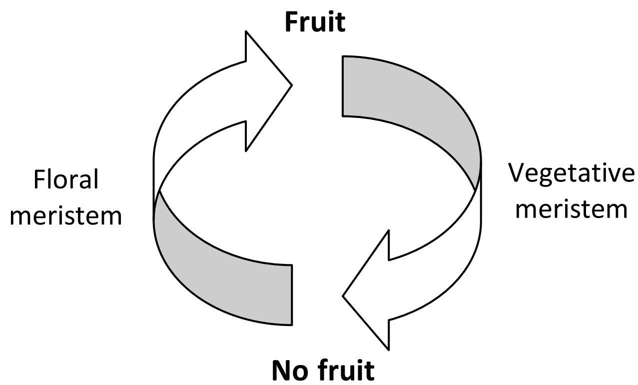

Figure i. Key hypothesis showing that with avocado the presence of a fruit on a fruiting shoot determines the fate of the meristem on that shoot.

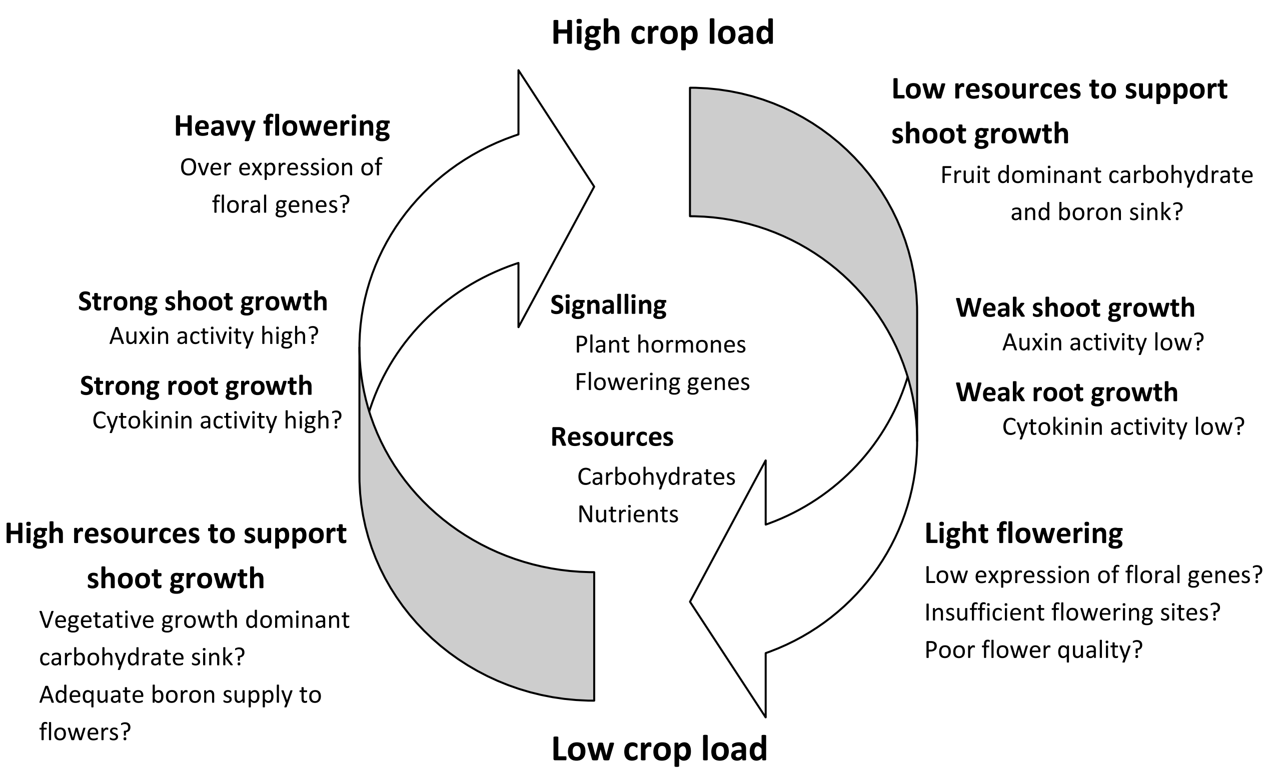

Figure ii. Combined hypotheses describing the role of signalling and resources in determining the effect of crop load on the level of return bloom in avocado trees.

Signals may be produced that turn flowering on or off. For example, a leaf may produce signals that generate and maintain floral development, while a fruit may produce a signal that negates these floral signals as apparently happens in an OFF flowering year (Figure iii). Either way, these signals determine if a meristem will change from a vegetative to floral state. Signalling could involve one or more of the following: plant hormones, sugars, metabolites, small RNA's or proteins which have been shown to travel in the phloem. Once the signal has been generated, it needs to be transported to the target tissue and then either it is maintained through flower development until anthesis (flower opening) and fruit set or it can initiate a change in state which is then stable until another signal is received.

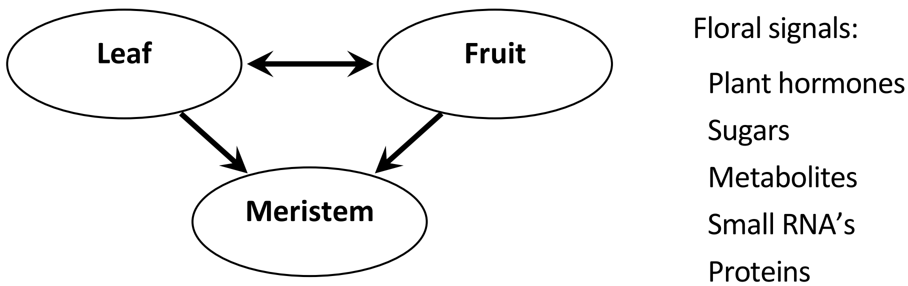

Figure iii. Signals may be produced in a leaf that generate and maintain a floral signal or possibly in a fruit that negates this signal as in an OFF flowering year.

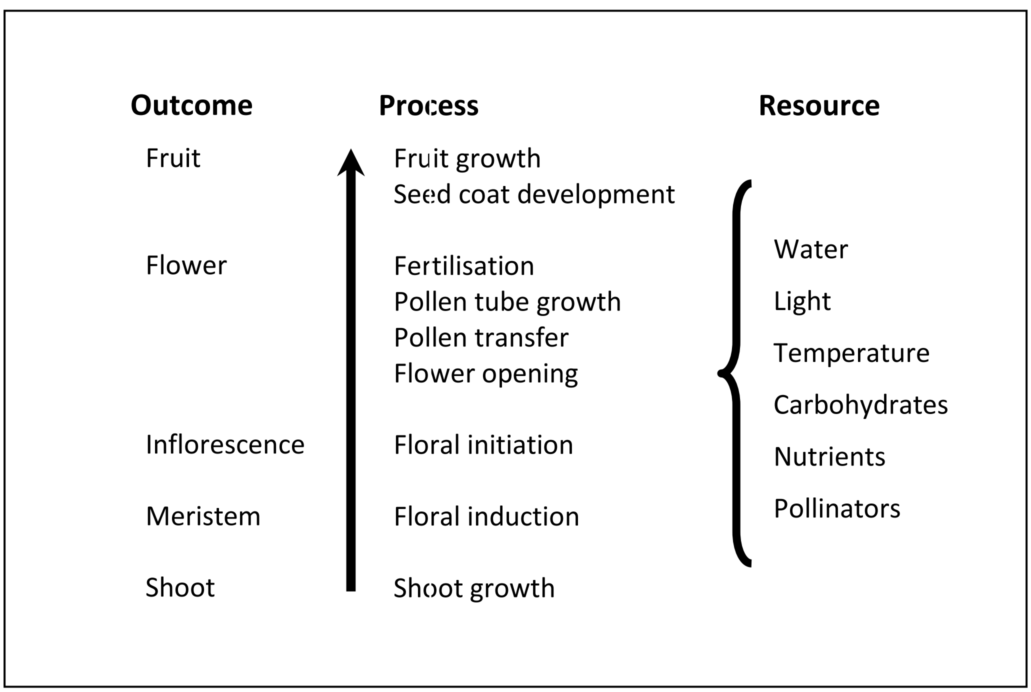

Figure iv. Sequence of development, processes and resources required for successful flowering, fruit set and growth leading to a commercial crop of fruit.

Once a developmental pathway from flower induction to fruit has been determined, certain resources are needed to maintain that pathway; important among these are water, light, temperature, carbohydrates and nutrients and of course pollinators to ensure successful pollen transfer (Figure iv).

This approach to hypothesis building is based on a virtuous circle with fruit having a direct impact on flowering and trees alternating between heavy and light crops. With avocados, however, some otherwise healthy trees can produce few flowers and/or few fruit for several years before setting an ON crop. This is frequently observed with young trees and heavily pruned trees. Alternate bearing is also more extreme with some rootstock/scion combinations than with others and environmental conditions such as drought or low temperatures can trigger alternate bearing. Hypotheses have been developed to better understand mechanisms involved in these situations in order to develop solutions that promote regular cropping from all trees.

Several experimental approaches have been developed and presented in this proposal to cover what we believe are the key factors and knowledge gaps that need to be researched in order to provide solutions to overcome alternate bearing in avocado. This research, which includes both applied physiological approaches together with basic research, aims to identify the nature and molecular identity of the flowering signals and the resources and environment required to maintain floral development and obtain successful fruit set. It is a balanced approach designed to take advantage of international collaborations, with work to be included in both hemispheres to take advantage of 'two seasons in one year', while identifying solutions that can be adapted/modified to suit specific regional conditions. A set of common field experiments regulating crop loads to better understand the drivers of alternate bearing and to help identify grower solutions are proposed to be established on private grower properties in Australia, New Zealand, California and Spain. These will provide local focus points **for early interaction with growers and industry in general**.

The proposal begins with a review then **design and development phase for a Decision Support System (DSS)**. Here we will use modelling and DSS tools to integrate information, both current and new, so that we get rapid dissemination of information to grower. The first step is to review the wide range of DSS platforms currently available, including AVOMAN in Australia, www.avocadosource.com in California and others developed to manage alternate bearing in other fruit crops. This information will then be used to investigate the opportunities for delivery of a single DSS platform or support of multiple systems in different jurisdictions. The meta-analysis included in this proposal to be completed in Year 1; will provide a comprehensive historical database that will form the basis of any DSS platform.

Programme Outline

The programme structure will be based around five integrated science project areas with a Project Leader appointed to each:

Part A. Research Integration, Model Development and DSS Delivery

Project Leader: Dr Hamish Brown (Plant & Food Research, New Zealand)

Activity 1 DSS design, development and delivery

Activity 2 Avocado structural, functional model development

Activity 3 Light model development

Part B. Determining environmental and biological triggers for alternate bearing in avocado

Project Leader: Dr Patrick Brown (UC Davis, USA)

Activity 1 Meta-analysis of alternate bearing

Activity 2 Analyzing available data on avocado yield and phenology, deriving environmental relationships and defining standards for data collection, analysis and integration

Activity 3 Validation and targeted experimental manipulation

Activity 4 Data analysis, interpretation and utilization

Part C. Regulating the transition from vegetative to floral meristems in avocado

Project Leader: Dr Mary Lu Arpaia (UC Riverside, USA)

Activity 1 Establishing and monitoring the growth and development of a population of ON and OFF trees

Activity 2 Determining the time of floral induction in avocado

Activity 3 Identification of phloem derived signals that correlate with alternate bearing

Part D. Improving flower quality, pollination, fertilization and fruit set in avocado

Project Leader: Dr Iñaki Hormaza (CSIC, Spain)

Activity 1 Characterization and management of flower quality

Activity 2 Improving pollination, fertilization and embryo development in OFF cropping trees

Part E. Management strategies to mitigate alternate bearing in avocado

Project Leader: Dr Grant Thorp (Plant & Food Research, New Zealand)

Activity 1 Crop regulation

Activity 2 High density planting systems

Programme Management

Innovation Partner: The New Zealand Institute for Plant & Food Research Ltd

Collaborators: Universdad Viña del Mar (UVM, Chile)
Consejo Superior de Investigaciones Cientificas (CSIC, Spain)
Universidad de Almería (UA, Spain)
University of California, Davis (UC Davis, USA)
University of California, Riverside (UC Riverside, USA)