Toward an understanding of avocado fruit abscission for increasing production

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Abstract
Average avocado yields are far below the estimated potential. Low yields are attributed to yield-associated traits that include extensive vegetative shoot growth, excessive flowering, low fruit set, high fruit abscission and a propensity for biennial bearing. Environmental conditions and management inputs influence the impact of these traits on yield. Climate models predict that the frequency of extreme climatic events will increase in the future, and as a result will impact yields. Therefore, breeding elite varieties and developing new management tools are essential for increasing production. The development of new management tools depends on the understanding of the physiology and regulation of yield-associated traits. Fruit abscission is a yield-associated trait that greatly contributes to irregular production patterns in avocado trees and orchards. Moreover, fruit abscission limits production in a diverse set of environments, including subtropical, Mediterranean, and cool climates. Therefore, research and development outcomes aimed at reducing fruit abscission will have a major impact on avocado industries throughout the world.

Introduction
The potential for avocado annual fruit production is estimated at 32 t/ha (Wolstenholme, 1987). However, actual average annual yields are approximately 10 t/ha, substantially lower than the estimated potential. Poor production levels are attributed to the semi-domesticated nature of avocado (Gama-Campillo and Gomez-Pompa, 1992), which includes several counter-productive traits such as vigorous vegetative growth, excessive flowering, biennial bearing, low fruit set and a high rate of fruit abscission (Goldschmidt, 2013; Lahav and Lavi, 2009). Moreover, the effects of climate change will further enhance these traits resulting in even more variations in annual yields. The additive effects of these yield-associated traits together with climate change are a major challenge for avocado production throughout the world.

Improving orchard performance through the development of new varieties and innovative management tools
Yield is a function of the interaction between the genetics, environment and management inputs (Hatfield and Walthall, 2015). In terms of avocado genetics, the dominant variety used in production throughout the world is ‘Hass’, which is a chance seedling identified in the mid 1920’s (Chen et al., 2009). While ‘Hass’ produces good quality fruit, it is not well adapted to many of the production areas around the world (Wolstenholme, 2013). Climate models predict that the environment will have a negative impact on production in many parts of the world (Howden et al., 2005); therefore, there is pressing need to develop new varieties for increasing orchard performance in the future. However, due to the long juvenile phase of avocado, breeding and evaluating new varieties takes a considerable amount of time.

To increase the yields of Hass and other varieties used in current production, new management tools must be developed to reduce the impact of yield-associated traits. In order to achieve this outcome, it is essential to develop an integrative knowledge base platform derived from a basic understanding of the physiological drivers that mediate these yield-associated traits. In Australia, avocados are produced in a wide range of environments including the subtropical regions of northern Queensland, to the hot and dry regions along the Murray River and the cool Mediterranean climate in the Pemberton region of Western Australia (www.avocado.org.au). While each region has its specific problems that affect production, such as the six-spotted mite in the southwest region of Western Australia, fruit abscission is a universal factor that limits production across all environments in Australia (Newett, 2013). Therefore, research and development outcomes aimed at reducing fruit abscission will have a major impact on avocado industries throughout the world including Colombia, Kenya and Tanzania.

Fruit abscission in avocado

Fruit abscission occurs throughout the growing season with a peak period of fruit drop occurring within the first five weeks after fruit set (Garner and Lovatt, 2016; Sedgley, 1980). During this high period of fruit drop, unfertilized fruits abscise within the first two weeks, while fertilized fruits ranging from 6-12 mm in size abscise for the remaining three-weeks (Sedgley, 1980). Growers estimate that 30-50% of the fertilized fruitlets that set abscise within this five-week period. The remaining fruit persisting on the tree have two developmental fates. A small subset of these fruits will continue to develop over the course of the growing season until the reach maturity for havest. The second set of fruits will develop and at some point, undergo fruit abscission. This later phase of fruit abscission can progress in a continuous manner or in a large wave based on the tree physiology, which is heavily influenced by the orchard environment and stress. The ability to identify key intervention time points throughout the growing season in order to minimize fruit abscission has been extremely difficult, as the factors that mediate fruit abscission are unknown.

Interaction between young fruitlets and the growing spring flush

The growth potential of avocado fruit increases over the course of the growing season, which is likely attributed to the development of the seed (Cowan et al., 2001). During the early stages of development, growth of the young fruitlets overlaps with the extension of the vegetative spring flush. Therefore, it has been hypothesized that the abscission of young fruitlets at early stages results from resource competition with the growing spring flush (Figure 1; Whiley et al., 2013). In support of this hypothesis, functionally determinate inflorescences are up to three times more productive than indeterminate inflorescences (Salazar-Garcia et al., 1998). In addition, indeterminate inflorescences retain more fruit when the terminal vegetative bud is removed (Lahav and Lavi, 2009).

The developing stems and leaves create a high growth potential for the spring flush. The high rate of cell wall biosynthesis in the growing stems results in a significant demand for carbohydrates for maintaining structural integrity of the vegetative shoots (Kebrom, 2017).

Growth retardants, such as paclobutrazole and uniconazole, are used in avocado industries to reduce the growth potential of shoots, as these plant growth regulators inhibit gibberellin biosynthesis required for stem elongation (Whiley et al., 2013). It has been hypothesized that reducing the growth potential of the vegetative spring flush will increase carbohydrate and nutrient availability required for fruit development, thereby reducing fruit abscission. In support of this hypothesis, experimental trials showed that applications of paclobutrazol at flowering reduced early fruit abscission (Adato, 1990; Kohne and Kremer-Kohne, 1987; Wolstenholme et al., 1990), increased fruit size (Whiley et al., 1992), as well as augmented yield (Adato, 1990; Kohne and Kremer-Kohne, 1987). However, other reports indicate that applications of paclobutrazol had little or no effect on yield (Penter et al., 2000; Stassen et al., 1999; Symons and Wolstenholme, 1990). In one study, applications of paclobutrazol reduced early fruit abscission; however, there was no increase in yield due to a heavy summer fruit drop event (Wolstenholme et al., 1990). The authors speculated that the paclobutrazol induced reduction in leaf expansion in spring flush limited the photosynthetic capability of the leaves. Therefore, the smaller leaf area was not able to supply the increased crop with photosynthates, which resulted in fruit abscission during the summer. Taken together, paclobutrazol is extremely effective at reducing the growth potential of the spring flush; however, variation in the effect on yield demonstrates the complexity of the mechanism(s) that regulate resource (carbohydrates) distribution during the spring and early summer.

The high volume of flowering and low rate of fruit set presents a major challenge for studying the physiological mechanism(s) that mediate the early fruit abscission (reviewed by Salazar-García et al. 2013). Creating a condition that increases fruit set and decreases fruit abscission would allow researchers to directly compare developmental profiles between developing (retained) and abscising fruitlets. Creating these conditions for profiling developing and abscising fruits is crucial, as studies in model plant systems demonstrate that early fruit development is marked by extensive changes in fruit physiology (Kang et al., 2013; Kumar et al., 2014). The inability to profile developing and abscising fruits at the same developmental stage will introduce artifacts that could obscure the ability to identify the key factors that mediate abscission.

The abscission of fruitlets during the summer

While a wave of fruit abscission is often mediated by stress-related events, little is known about the mechanism of the summer fruit drop that occurs in a continuous manner or in a wave independent of stress. It has been speculated that the summer fruit drop is mediated in part by tree resource levels, such as carbohydrates, which are essential for growth. If resource availability is reduced, the crop load is adjusted to an appropriate level that can be supported (Goldschmidt, 2013; Sawicki et al., 2015). Therefore, understanding how tree crop load is adjusted in response to resource availability and the physiological mechanism(s) that control fruit abscission may provide the knowledge necessary to develop advanced management tools aimed at reducing fruit abscission. Moreover, management tools aimed at reducing the summer fruit drop will likely be effective for reducing the early fruit drop event.

Role of seed coat in fruit abscission

Seed development is critical for fruit development and retention (Garner and Lovatt, 2016; Sedgley, 1980). The seed is composed of the embryo, endosperm and seed coat. While the embryo and endosperm are products of double fertilization, the seed coat is derived from the maternal integuments. Studies in model plant system show that the seed coat functions to provide the embryo with photosynthates and nutrients required for growth (Costa et al., 2012). Moreover, the seed coat also produces hormones critical for regulating embryo development (Bower and Cutting 1988; Robert et al. 2018). During the summer fruit drop, avocado seed coat senescence is associated with abscising fruits (Blumenfeld and Gazit, 1974; Garner and Lovatt, 2016; Figure 2). Therefore, the maternally derived seed coat appears to be a functional determinate that controls the fruit fate, to develop versus to abscise.

Model of fruit abscission

We propose a model that describes fruit abscission in avocado (Figure 3). According to this model, the physiology of the tree is a key determinate of fruit abscission. Tree carbohydrate availability and stress influence fruit abscission. Furthermore, mechanisms that control resource distribution target a subset of fruit to undergo abscission. While the mechanisms are not understood, competition for resources between fruits and with shoots can induce fruit drop. Furthermore, seed coat senescence is a key tissue that regulates fruit abscission. It should be pointed out inhibition of the summer/fall flush by high crop load likely involve a similar resource distribution mechanism. Therefore, understanding the mechanisms that mediate fruit abscission may also be applied to better understand biennial bearing.

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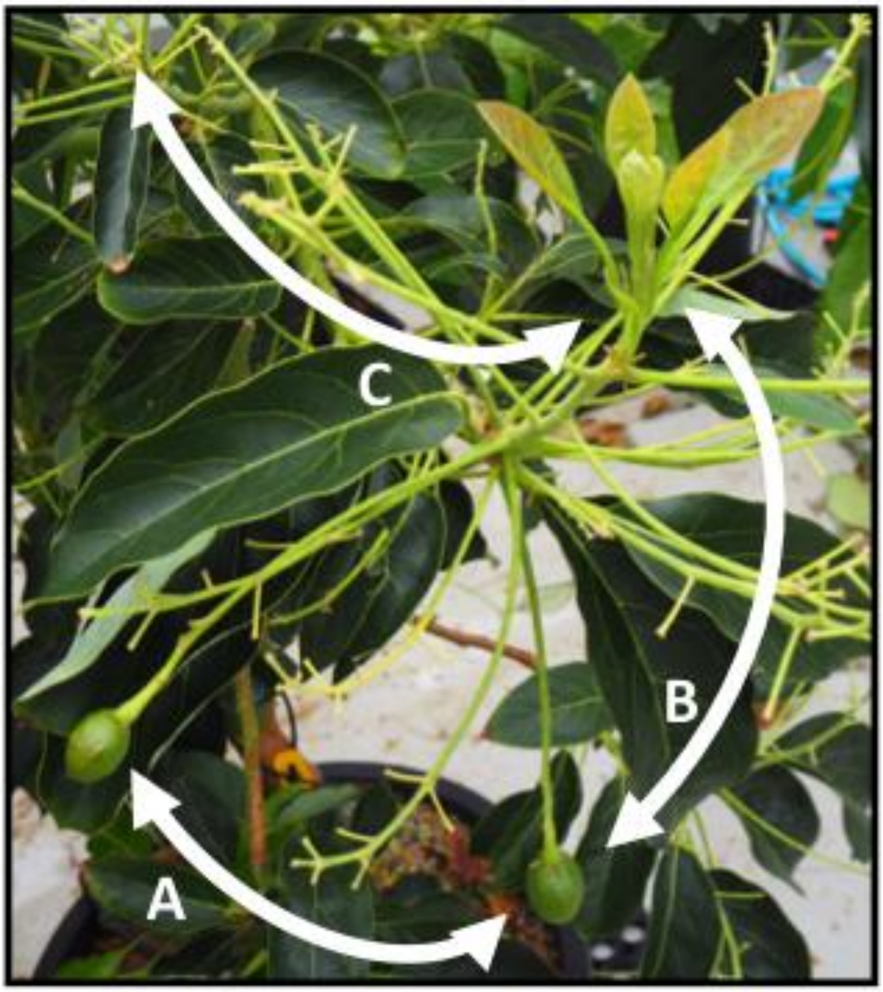

Figure 1: An illustration displaying the competition between the spring and developing fruitlets. The high rate of fruit abscission within the first five-weeks is mediated by three competition events: (Arrow A) fruitlet to fruitlet, (Arrow B) spring flush to fruitlet, and (Arrow C) branch – branch. All of these competition events results in the diversion of carbohydrates released from reserves away from developing fruitlets; thereby causing fruit abscission.

Figure 2: Abscising fruits display seed coat senescence. (A and B) Normal seed coat development is associated with developing fruits firmly attached to the tree. (C and D) Abscising fruits display varying levels of seed coat senescence. Note, the embryo has been removed from the fruits to visualize the seed coat with is marked with an asterisk (*).

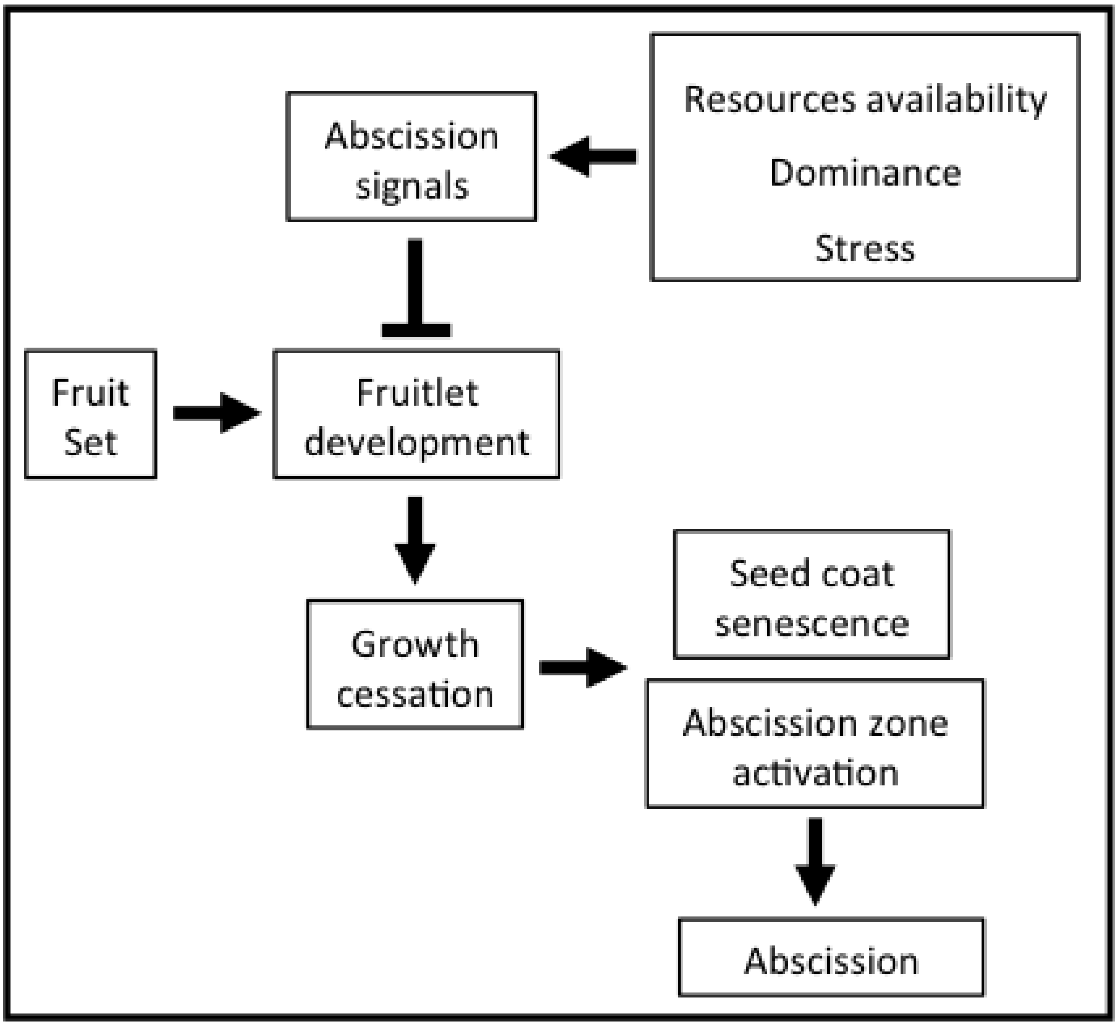

Figure 3: A model of the sequence of events for fruit abscission abscission. Abscission signals are produced in resonse to resource availability, dominance and stress, which target a subset of developing fruitlets in the tree. In response to the abscission signals, fruitlets undergo growth cessation. The senescence of the seed coat and activation of the abscission zone result in fruit drop.