Alternate bearing in avocado: an overview

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Abstract
Alternate bearing (AB) and irregular bearing (IB) present major challenges to growers and marketers of avocados. This problem is common to most tree fruit crops, and varies in intensity. It can manifest countrywide, regionally, on a specific farm and even in the branches of a single tree. AB is typically initiated by an abnormally heavy or light crop in young trees, followed by a light or heavy subsequent crop. This pattern then becomes entrained and difficult to change unless severe climatic events intervene, or drastic management interventions are made. A heavy "on" crop results in reduced vegetative shoot and root flushing, and less carbohydrate (energy reserves) build-up. Seed gibberellins may also reduce flower bud initiation. Fewer flowering and fruiting sites for next season's cropping are formed, and flowering intensity is reduced. Many complex, interacting factors affect AB intensity. A brief discussion is given of remedial measures such as pruning, girdling, growth retardants and management intensification. In future, new cultivars and rootstocks will reduce AB intensity. In the interim, revised growth cycle charts reflecting "on" and "off crop seasons are helpful in managing AB.

Introduction
Alternate (biennial) and irregular bearing are encoded in the avocado genome. Millions of years of evolution in montane highland tropical to subtropical (Guatemalan and Mexican 'races' or subspecies) and lowland tropical rainforests (West Indian 'race' or subspecies) probably resulted in occasional mast fruiting. With improved germplasm, vegetative propagation and better growing conditions in modern orchards, good fruiting can be expected in most years. However, the growth and fruiting habit of the avocado tree invariably leads to the setting of an unusually heavy crop in one particular year, followed by a poor crop. This pattern can then become entrained and, in the absence of climatic or other upsets, or strong management interventions, present management and marketing problems (Wolstenholme & Whiley, 1999; Scora et al. 2002).

Some degree of alternate bearing (AB) is common in fruit and nut tree crops, and Monselise & Goldschmidt (1982) gave a general review of the topic. Individual crop reviews exist for a wide range of crops. The subject is summarized for avocado by Whiley, in his chapter on Crop Management in Whiley et al. (2002). Since then new research has thrown additional light on factors affecting AB and irregular bearing (IB) in avocado.

This partial review summarizes our current knowledge of avocado AB and IB, particularly its manifestation in the warm, humid subtropics, and semi-arid Mediterranean production areas such as California and Israel. New Zealand production areas can be classified as cool to cold, very wet, maritime, with a winter rainfall peak. They present special problems, and here the author draws on the experience of local researchers and advisors. The emphasis is on scientific research results where available and applicable, with the grower in mind. The objective is to answer the question "why AB and IB?" with brief suggestions as to the practical control of AB in particular. Unfortunately, dedicated AB and IB literature for avocado is scarce and often coincidental.
Development and entrainment of AB

Bearing in well-managed young avocado orchards typically shows a rising trend, or only slight variation with increasing orchard age. An AB cycle will usually result from environmental and orchard management conditions that result in either an exceptionally heavy or a very poor (or no) crop (Monselise & Goldschmidt, 1982; Garner & Lovatt, 2008) in young trees. Prior to this, the vegetative: reproductive balance favoured vegetative growth. Even though the avocado fruit with its high and "energy-expensive" oil content (Wolstenholme, 1987, 1991) makes high demands on the leaf photosynthetic factory, low cropping is easily serviced by the relatively numerous and well-lit leaves. The first heavy "on" crop changes the balance in favour of reproductive growth (flowering, fruit set and fruit growth) which places the leaf canopy under heavy photosynthetic demand. Even the enhanced photosynthetic rates of leaves near fruits (Schaffer et al., 1987) cannot compensate for the high fruit "carbon" (energy) demands. Less carbon reserves are left for vegetative renewal (roots, growth flushes) and the new fruiting sites essential for the next season's fruiting. The result is an "off" crop. AB then becomes entrained because of the detrimental effect of the "on" crop on the subsequent crop's flowering and fruiting.

AB varies with environmental conditions, cultivar and rootstock, and management. It is worse in stressful (climate and soil) environments. It can be a problem and vary on a national scale, regionally, in different orchard blocks (Fig. 1) and even in different branches in a single tree. Once well entrained, it can only be reduced in extent (lower highs, higher lows - less of a boom-bust cycle) by a full package of management interventions. Alternatively, strong environmental upsets such as cyclones, severe storms/wind, drought and flood, hail etc, can change the pattern. Diseases (especially the proliferation of Phytophthora root rot, exacerbated by the stress of heavy bearing), and pests will aggravate AB.

Unfavourable climatic conditions at the critical flowering/fruit set period can cause crop failure at the start of an "on" year. In Israel and California, this can be the result of "hamsin" or Santa Ana conditions, viz. heat stress due to temperatures above 33C (and often over 40C) accompanied by very low humidity and strong winds (Lomas, 1992; Lomas & Zamet,
1994). In areas with cold winters, untimely cold spells can be just as devastating. Israeli work showed that minimum (night) temperatures of <10°C, especially for 5 or 6 consecutive nights, can dramatically reduce fruit set and cause seedless "cuke" production in cultivars prone to "cukedom" (Lomas & Zamet, 1994). It is suspected that this is a major cause of crop failure in some years in New Zealand (C. Partridge, pers. comm.). This is shown in Table 1, years 2003 and 2004, when heavy flowering occurred but cropping was low (Partridge, 2009).

Alternate bearing index (ABI)

The ABI is a useful measure of the extent of AB in scientific research (Pearce & Dobersek-Urbanc, 1967). $\text{ABI} = (\text{yield, year 1} - \text{yield (years 2)})/\text{yield, year 1} + \text{yield, year 2}$ in kg/tree for two consecutive (on/off) years. It ranges from 0 (no AB) to 1 (complete AB). In California research orchards, AB1 varied from 0.57 to 0.92 (Lovatt, 1997); Garner & Lovatt (2008) found a mean AB1 of 0.70 for all data 'Hass' trees in their trial. ABI can be expressed as a percentage by multiplying by 100.

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Causes of AB: Scientific theories

Two main theories have been proposed to explain why fruit development (a heavy "on" crop) inhibits flowering and fruiting the next season ("off" crop). The "starch depletion" theory resulting from a heavy "on" crop implies that flowering and fruit set for the "off" year takes place in trees with greatly reduced reserves of carbohydrate energy. This is certainly true for avocado trees, especially when harvesting is delayed (Whiley et al., 1996 a, b), but it is unsatisfactory as an over-arching explanation of AB. Reserve carbohydrate status is at best a useful integrator of overall tree condition, but too variable over different time scales, environments and management technology to justify routine predictive measurement. Scholefield et al., (1985) first established the close relationship between starch reserves and yield in avocado.

A more recent version of the "nutrient withdrawal" (primarily carbohydrates) hypothesis by a heavy crop, is that seeds inhibit flowering by exporting hormones, especially gibberellins (GA's) which have an anti-flowering effect. GA applications inhibit flowering in many tree crops, and GA concentrations in seeds are high. However, an alternative explanation that seeds compete with shoot apices for flowering hormones is equally tenable (Dennis &
Neilsen, 1999). In avocado, the inhibitory effect of heavy fruiting on flower bud initiation on a particular branch, as compared to a poorly fruiting branch, is easy to observe.

The writer believes that AB is best understood as a hierarchy of causative factors, controllable and uncontrollable, gradually getting closer to the proximate and ultimate factor(s) (Fig. 2). The latter may well reside in AB gene(s), yet to be identified. Inevitably, just about every possible factor will be involved, with complex feedback and feed-forward loops and interactions. Nevertheless, a better understanding of tree growth habit and phenological cycles suggests that there are some more amenable targets for AB management. This of course assumes that AB is in fact the main priority for growers.

Figure 2. Hierarchy of causative factors affecting AB.

Growth cycles as a guide to AB management

The well-known Whiley et al. (1988) avocado phenological growth cycle for the humid subtropics of Australia, with two shoot and two root flushes, and a typical "average, target" starch cycle, is shown in Fig. 3 (Whiley and Wolstenholme, 1990). This is the basis for orchard management, with fine-tuning for local conditions, in most of the Australian avocado industry, as well as South Africa and many other countries with similar climates (Whiley, 2002).

However, in subtropical Mediterranean growing areas such as California and Israel, with long growing season days and especially where cropping is relatively low (Whiley, A.W., pers. comm., 2009) an additional autumn shoot flush may occur. This is unlikely in Chile, where advanced management technology gives sustainable heavy cropping of 18-20 t/ha/an. In warmer production areas in subhumid, borderline tropical highland Nayarit State in Mexico, Salazar-Garcia et al. (2006) report a major winter shoot flush plus three minor summer flushes. Under these conditions the flowering intensity of all flushes is stable. A good vegetative: reproductive balance is maintained, with sufficient fruiting sites for return bloom. From an AB viewpoint, this would seem to be as close to Utopia as it is possible to come. The more tropical the climate becomes, the greater the number of growth flushes and the shorter the periods of quiescence. In contrast, the cool weather and short growing season of New Zealand results in delayed shoot flushing (and flowering), so that one prolonged "spring" (summer) flush is typical (from November, but sometimes delayed by heavy flowering). A second late summer/autumn flush may occur (Hardy et al., 2008). Thus the growth cycle varies in different growing areas (and for different cultivars), and should be independently determined.
Figure 3. The total growth cycle of cv. Fuerte showing the relationship between vegetative and reproductive growth and reserve starch in the trunks of trees (Whiley and Wolstenholme, 1990).

The growth cycle in Fig. 3 represents good-yielding orchards where AB is a minor problem. Where AB is deeply entrenched, the seasonal starch cycle will vary from the ideal. In "on" years there is a greater drawdown from a higher winter peak in spring and only a partial recovery through summer and autumn. In "off" years, spring starch reserves are low, but there is a strong build-up in summer and autumn, due to the poor crop (Fig. 4).

Figure 4. Seasonal starch reserves in trunk wood of avocado in "on" and "off" and "ideal" bearing seasons (diagrammatic) (Wolstenholme, 2001).

Fig. 3 is redrawn for an "on" year, to illustrate the distinct changes in key phenological events (Figs 5, 6). Flowering is more intense followed by proportionately greater spring and summer fruit drops. The heavy crop reduces the vigour of the spring flush, and especially the summer flush. Similarly, the two root flushes, but especially the autumn root flush, are less intense. In contrast, an "off" year has (lower intensity of reproductive and greater intensity of vegetative events (Fig. 6). Managing the vegetative-reproductive balance is the key to reducing AB, and these revised growth cycle charts graphically illustrate the changes which occur in "on" and "off" years.

A first attempt at graphically representing the two-year "on"/"off" bearing cycle in an avocado tree phenology chart was presented by Hardy et al. (2008) for the N.Z. Avocado Growers' Association. The accompanying 35pp. pamphlet "Spring: Tree Management, Phenology and Flowering" gives useful information, along with "Growing Productive Trees" by Barber et al. (2007), on how AB manifests in New Zealand, and suggested corrective measures. This however is for very different conditions, and for Hass trees which carry two crops due to the long fruit development period.
Rootstock effects on AB

Avocado rootstocks were reviewed by Ben Ya'acov & Michelson (1995) and in Whiley et al. (2002) by Newett et al. (2002). Seedling rootstocks were exclusively used until the mid-1970’s, when clonal rootstocks, selected primarily for tolerance to avocado root rot (*Phytophthora cinnamomi*) (P.c.) became available. Israeli and Californian researchers also selected stocks for salinity tolerance. Other horticultural attributes (yield, vigour, fruit quality etc.) received secondary attention until comparatively recently. Australian rootstock research was placed on a sound scientific footing some seven years ago (Whiley, 2009). Both the Australian and New Zealand industries are based on seedling rather than clonal rootstocks.
Mickelbart et al. (2007) reported on an important 10 year study of 'Hass' on 10 clonal rootstocks in California. Trees were spaced 6.1 x 6.1m on berms to improve soil drainage. P.c. and salinity were not problematical. Results would have differed substantially in P.c. infected soils, due to differing rootstock tolerances to P.c. Trees on all rootstocks showed AB, with ABI ranging from a low 0.33 on G755C to a high of 0.56 on Toro Canyon' and 0.55 on 'Topa Topa' (also high on 'G1033' and Thomas'). The 'G 755' series had the lowest mean yields, and are no longer recommended in spite of good P.c. resistance, 'Duke 7', with an ABI of 0.52, had the highest canopy efficiency (kg fruit per m$^3$ canopy), and highest cumulative yield along with 'Borchard'. Rootstock compatibility was not rated. The results confirm that clonal rootstock choice can significantly affect the expression of AB.

Although it is still too early for AB to manifest in Whiley's (2009) rootstock trials, an earlier report by Thomas (1997) gave useful leads to the importance of graft compatibility in 'Hass' on unknown seedling rootstocks. Six years of individual tree records showed that the six highest yielding trees had four times the cumulative yield of the six lowest yielding trees. They had fairly consistent yields, whereas the latter had a distinct "on""off" cycle. Perhaps most importantly, high yielding trees had smooth graft unions while poor yielders showed scion overgrowth. Scion overgrowth suggests a degree of root starvation for aerial resources, including carbohydrates. Whiley (pers. comm., 2009) has noted varying degrees of scion overgrowth on 'Zutano' seedling rootstocks in New Zealand, 'Lula' rootstocks in Argentina, and some seedling stocks in W. Australia, which seems to lead to aggravated AB. There is no doubt that healthy, compatible root systems reduce AB.

**Flowering and fruit set in "on" and "off" years**

Salazar-Garcia et al. (1998, 1999) have studied flower development of 'Hass' in "on" and "off" crop years in S. California. After an "on" year, flowering intensity the next ("off") season was greatly reduced (only 13% of shoots flowered, as compared to 46% in an "on" year, after an "off" crop). Thus the number of flowering/fruiting sites was reduced after a heavy crop. The spring vegetative shoots, growing from overwhelmingly indeterminate flowering shoots, did not flush in the "on" year if they carried fruits

It is clear that, at least in California and in the warm, humid subtropics, an "on" crop year has detrimental effects and greatly reduces crop prospects the following year due to:

- Fewer fruiting sites
- Reduced flowering intensity
- Impaired root growth

These seem to be the ultimate horticultural causes of AB.

Recent Californian research (Garner & Lovatt, 2008) found that the percentage fruit set in "on" and "off" crop years was not significantly different - crop size differed because flower number and intensity differed. In other words, the tree adjusts its crop up or down by influencing the number of flowers. This of course is in trees in which P.c. is under control, management is good, and fruit set is not compromised by severe stress including climatic extremes.

**Causes of variable flowering in "on" and "off" seasons**

Reduced "off season flowering is therefore a major expression of the AB syndrome, along with prolific flowering in the "on" season. Our discussion of the scientific literature suggests the following causes of reduced "off season flowering:

- Excessive previous "on" crop (skewed veg./reprod. balance, favouring fruiting)
- Reduced carbohydrate reserves at start of "off" flowering
- Reduced flushing (especially summer flush) previous "on" season
• Reduced root flushes (especially autumn flush) previous "on" season
• Reduced leaf and root replacement/renewal
• Fruit/seed gibberellins reducing floral induction previous summer and autumn
• Ultimately, fewer fruiting sites at flowering, serviced by compromised photosynthetic resources and a weakened root system.

In cool growing areas, the picture is complicated by late maturing cultivars such as ‘Hass’ requiring more than 12 months to mature their fruit, and by purposeful fruit storage on the tree to secure a market advantage. Whiley et al. (1996 a, b) showed that delayed harvesting of both ‘Fuerte’ and ‘Hass’ had progressively more severe effects on both average yield, as well as AB1. In ‘Fuerte’, AB1 increased from an average 0.06 (six years) for harvesting at 21% D.M., to 0.40 for harvesting at 30% D.M. Split harvests reduced the severity of these effects.

Management interventions to reduce AB severity

It is not the object of this paper to discuss control of AB in detail - several management interventions are dealt with in other sessions. I will briefly summarize current and possible future strategies.

Fruit thinning (reduction of crop load) in the "on" season is a logical option, since AB problems originate from overbearing. Early hand removal of smaller fruits, before the summer drop, has been shown to reduce AB. However, growers find this impractical (except in small trees) and distasteful. Perhaps they should revisit this attitude!

Pruning is a major management intervention to reduce AB, in particular to restore vegetative vigour where this has declined excessively due to overcropping. Increasingly, in conjunction with other tools such as girdling/scoring and growth retardants, it is being used in high density orchards to keep trees within their allotted space, and increase the number of well-lit fruiting sites. A comprehensive pruning research programme has recently been completed in Australia (Leonardi, 2009) and is a topic at this Conference.

Girdling is an ancient horticultural tool to reduce excessive vigour, and to improve flowering and fruiting - either of the whole tree or of selected branches or shoots. It can be used to improve fruit size, depending on timing and the size of the cut through the bark tissues. As movement of carbohydrates, metabolites and some hormones to the roots is temporarily reduced, some root starvation is inevitable, along with increased stress of treated limbs and even leaf yellowing. Girdling can be used to increase cropping in a branch renewal/rotation management system, where branches are treated as distinctive modules (mini-trees) which are re-cycled in an orderly manner by pruning. It is a practice which should be used with caution and a full understanding of the underlying science.

Growth retardants have been used in avocados to improve cropping and fruit size. Currently, uniconazole (Sunny Tm) has a proven role to play in reducing AB, in a management package for young intensively managed orchards where pruning, girdling and nutrition are integrated in well illuminated canopies (Whiley, A.W., pers. comm.).

Nutrition is an important component of "best practice" as determined by research on soil and leaf analysis, Lovatt (2001) researched nitrogen (the "manipulator element") timing and amount in California, and was able to reduce AB1 from 0.90 to 0.72 in a four-year study of 20 year old ‘Hass’ on ‘Duke 7’. The California standard is for six equal split applications according to phenological stage, totalling 168 kg/ha/annum. A double application at floral anthesis/early fruit set significantly reduced AB by encouraging spring flush growth in the "on" year. Although this is desirable from an AB viewpoint, there is a growing literature which warns against high fruit flesh N levels, especially in 'Pinkerton', resulting in fruit quality disorders. More research is needed on timing N applications to reduce movement into the fruit, while promoting shoot flushing in the "on" crop year and reducing it in the "off" year.
Gibberelins as anti-flowering agents ("on" crop year)

Salazar-García & Lovatt (1998, 2000) have investigated GA3 sprays to manipulate avocado flowering, both on individual branches and on whole trees. A 100mg/l GA3 spray applied in early winter before an "on" bloom reduced the number of inflorescences, increased the number of vegetative shoots, and reduced "on" yield by 47% - all desirable responses to possibly break or modify an AB cycle. More research is needed on GA3 concentration and timing.

The New Zealand situation

C. Partridge (2008, 2009, pers. comm.) has provided his insights on the AB and IB situation in New Zealand. These should be read in conjunction with two recent publications (Barber et al., 2007) and Hardy et al.(2008) by the N.Z. Avocado Growers' Association, which he co-authored. In this cold, wet environment, cold weather during flowering is the major cause of IB, assuming P.c. is under control. Heavy winter rainfall can cause flooding and root asphyxiation even on good volcanic soils. Site selection, shelter, pollinizers, provision for bees, and more intensive canopy management all reduce the risk factors in an environment that can be "pretty close to the wind." Israeli research showed that up to five or six consecutive nights below 10°C can be disastrous to fruit set is pertinent. Leaching of N and K from both leaves and soil by heavy winter rain is likely to be high, but root activity (soil temperature above ca 15C) is needed to take up nutrient elements. Inhibition and delay of shoot (and root) flushing will impact severely on AB and IB. Scion overgrowth above the graft union will also "starve" the vital feeder root system, and accentuate AB. Pruning from July to end September to force new growth for an expected "on" year may be helpful.

Conclusions

Alternate and irregular bearing are embedded in the avocado genome through evolutionary adaptation to montane cloud forest environments in Mexico and Central America. Current cultivars and rootstocks provide only partial assurance of regular bearing in most environments. Occasional severe climatic events can override the best efforts of management and cause crop failure. Horticulturally, the key is to attempt the maintenance of the ideal vegetative : reproductive balance as determined for the particular environmental conditions and management philosophy. Inevitably, this will swing towards excessive reproduction in "on" crop years, and excessive vegetative growth in "off crop years - to the detriment of shoot and root flushes in the former, and cropping in the latter. Choice of cultivar, rootstock, environment and management can all aggravate AB; late harvest also. Nevertheless, provided P.c. is under control, there is much that can be done, in a "package deal" that includes orchard intensification through closer spacing, pruning, girdling, provision for cross-pollination, and use of uniconazole, to reduce the intensity of AB. A Chilean management philosophy based on the above, with recycling of "modules" (branches) in an orderly fashion, is an example of a successful adaptive strategy that maintains high yield in a Mediterranean climate.

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References


