Alternate bearing in olive initiated by abiotic induction leading to biotic responses

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Key words: alternate bearing, environmental control, fruiting metabolism, olive.

Abstract: Alternate bearing of olive trees is one of the most troublesome characteristics of this commodity, impacting its economy due to labor distribution, fruit and oil availability, oil mill capacity and marketing. The metabolic changes leading to alteration in fruit production are generally considered of direct genetic nature. In the present review this approach is challenged, showing that all the biotic-metabolic changes in olive leading to 'on' and 'off' years are the results of initial abiotic effects on the trees. The nature of the metabolic changes induced by the abiotic regional and annual conditions described are, no doubt, genetically controlled but initiated only as a result of adverse environmental abiotic conditions such as seasonal temperatures, water stress, and soil nutrition conditions.

Olive is one of the most alternating tree species among the commercially grown fruit trees and it is known as such worldwide. Fruiting alternation of olive is considered to be dependent both on environmental abiotic and endogenous biotic genetic factors. The degree of orchard fruiting alternation, even of the same cultivar, differs considerably between different areas and regions, thus an initial or independent genetic involvement is questionable. Fruit bearing alternation is particularly recognized in regions with climatic conditions that vary annually, particularly winter temperatures such as in the eastern Mediterranean basin (Fig. 1). In such regions alternate bearing is usually expressed and synchronized within the entire orchard, area or even region. Still, alternate bearing, although to a lesser degree, develops also in regions with a stable annual climate favorable for the olive tree's developmental cycle. The requirement of low, particularly varying temperatures between day and night in the winter to induce reproductive bud differentiation was established many years ago (Hartmann and Prolingis, 1957; Hartmann and Whisler, 1975). The buds of *Olea europaea* develop uniformly as they are of undefined nature and need to be induced to become either vegetative or reproductive (Fig. 2). Various studies describing the anatomical changes occurring in buds have been published and have mainly emphasized the changes leading to the reproductive state, though in some studies also leaf buds (Fabbri and Alerci, 1999). It is still controversial whether low temperature is required for the induction leading to differentiation, as during the process of vernalization (Lavee, 1989; 1996; Troncoso

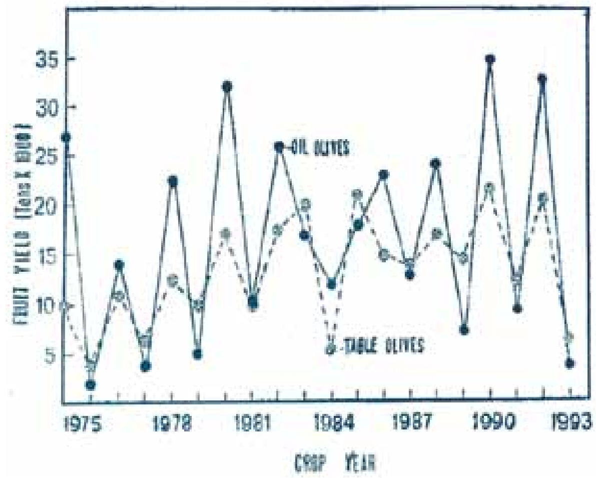

Fig. 1 - Alternate bearing over a period of six years in rain-fed and irrigated olive orchards (Lavee, 2006).

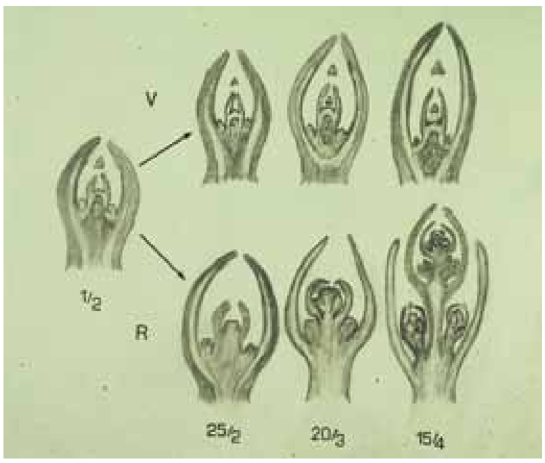

Fig. 2 - Differentiation of an undefined olive bud to a vegetative and reproductive state (Lavee, 1996).

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et al., 2012). On the other hand, it was suggested that low temperature is required mainly for predetermined reproductive bud opening, similar to the dormancy process in deciduous trees (Rallo and Martin, 1991; Rallo *et al*., 1994). Some bridging ideas related to that gap of the two approaches have recently been considered, though the need for a chilling period, or comparable conditions causing temporarily seasonal growth retardation for reproductive bud differentiation during the winter, has been well established.

Various growth and metabolic changes between fruiting ('on') trees and low or non fruiting ('off') olive trees have been described, as reviewed some years ago for "Olea" (Lavee, 2006) and fruit crops in general (Goldschmidt, 2005). The overall affect of olive alternate bearing is expressed by antagonism between the developing fruit and vegetative growth (Fig. 3). As olive fruit is initiated and develops from buds on shoots grown during the previous year, a reduction of vegetative shoot elongation and inhibition of lateral shoot out growth due to fruit development has a major effect on the general number of buds and thus on the potential reproductive buds in particular. As olive is a sectorial tree, the antagonism between developing fruit and vegetative growth might appear on a single scaffold, a tree section or a whole tree depending on the amount and distribution of the fruit in the 'on' year. It should be noted that the greater the amount of fruit in the 'on' year, the greater the chilling required for a return crop in the following year. Still, once the yield in the 'on' year exceeded a level specific for the growing conditions and the cultivar additional chilling will not be effective any more (Fig. 4A). Furthermore, if inflorescences are formed, the amount of male flowers (Fig. 5) usually increases and the fruit set potential of complete flowers is markedly reduced (Cuevas *et al*., 1994). A similar effect is induced by harvest time during current yield. Harvesting the current fruit late in the season will significantly reduce the level of return flowering in the following year with the degree of chilling having only a minor effect (Fig. 4B). All these phenomena are accompanied, and probably controlled by basic metabolic changes within the different organs of the tree. While in leaves during the 'off' year the level of proteins was considerable lower than in leaves during the 'on' year, the opposite trend was found in the bark of young shoots in which the protein level was significantly higher than in the 'on' year (Table 1). Recently, the molecular origin of some of those proteins, such as Ft which is involved in flower induction in Arabidopsis, were identified and their possible function in the process leading to flowering of olive was determined (Haberman, 2012; Samach and Smith, 2013).

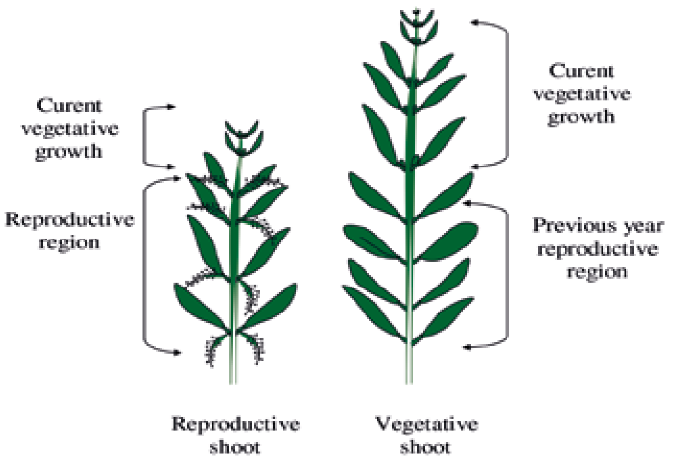

Fig. 3 - Comparison of the annual vegetative shoot growth of an 'on' year (left) and 'off' year (right) branch.

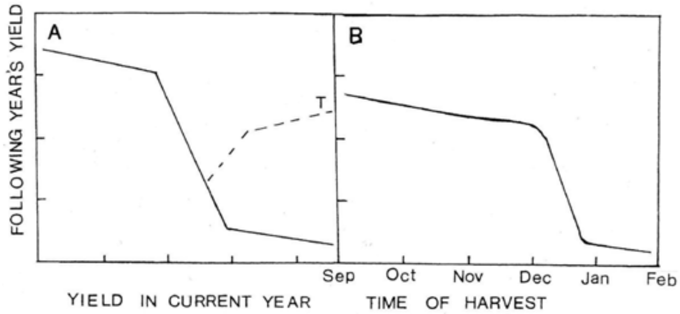

Fig. 4 - The effect of olive fruit yield level (A) and harvest time (B) in a current year on their fruiting potential in the following year (Lavee, 1989).

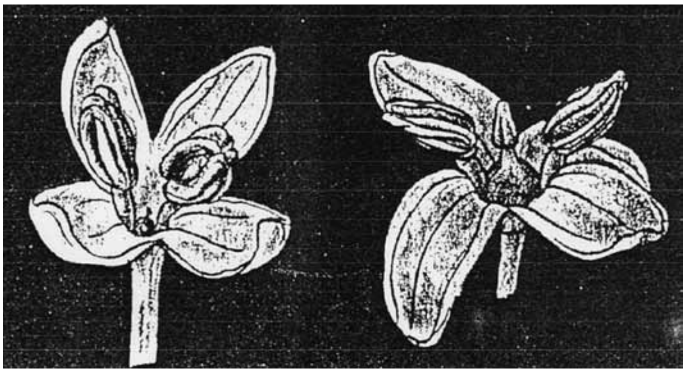

Fig. 5 - Open olive flower types. On the left a male flower, on the right a complete normal (open perfect) androgynous flower (Goor *et al*., 1960).

Table 1 - The protein content (mg/fw) of mature olive leaves of 4 cultivars in "on" and "off" years. Sampled in late summer

Koroneiki	Uovo di Piccione	Barnea	Manzanillo	Tree phase
		Leaves		
475 bc	370 a	310 a	295 a	"off"
530 b	510 b	405 c	510 b	"on"
		Bark		
490 b	490 b	500 b	440 b	"off"
370 a	360 a	370 a	360 a	"on"

From Lavee and Avidan, 1994.

Another major metabolic change in the leaves of olive trees in their ‘on’ and ‘off’ cycle was identified as a dynamic change of some phenolic compounds, particularly chlorogenic acid (CHA). This acid, which olive tissue responds to as a growth promoting auxin (Fig. 6), increases in the leaves during fruit-set and remains high throughout the ‘on’ year, inhibiting the differentiation of flower buds for the following year. The resulting low fruit set causes the level of CHA to drop again and remains low during the whole ‘off’ year (Fig. 7). The negating effect of CHA on reproductive bud differentiation was directly demonstrated by injecting CHA into scaffolds of cv. Manzanillo trees during the winter (Fig. 8) which resulted in a reduction of flower bud development for the following spring (Lavee *et al*., 1986). The amount of CHA developing in the leaves during the ‘on’ year fruit set is proportional to the amount of fruit developing on the trees (Fig. 9). Other biotic changes in the metabolism of olive trees leading to alternate bearing are the level or depletion of minerals, activity of endogenous and exogenous gibberellins, and the level of carbohydrates which, although controversial, were also reported to be involved in controlling alternate bearing.

Various schemes of biotic metabolic changes which lead to or inhibit floral induction were suggested and that indicate the sequences of events controlling vegetative or

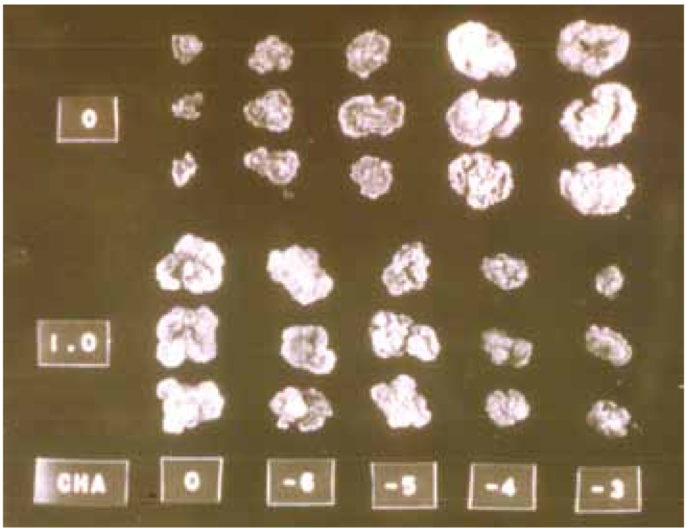

Fig. 6 - The effect of auxin (NAA) and chlorogenic acid (CHA) on the growth of olive callus tissue *in vitro* (Lavee, 1996).

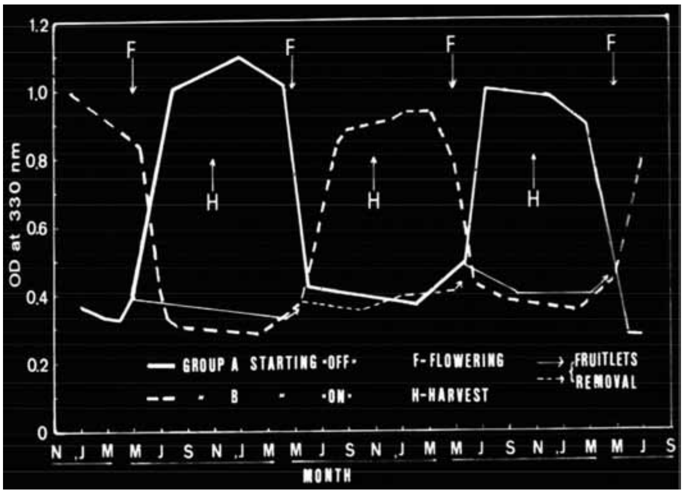

Fig. 7 - The change in content of CHA during the year in the leaves of ‘on’ and ‘off’ olive scaffolds and after inflorescences removal of cv. Manzanillo olive trees (Lavee and Avidan, 1994).

Fig. 8 - Pressurized winter injection of CHA in a scaffold of cv. Manzanillo causing a reduction in reproductive differentiation of buds.

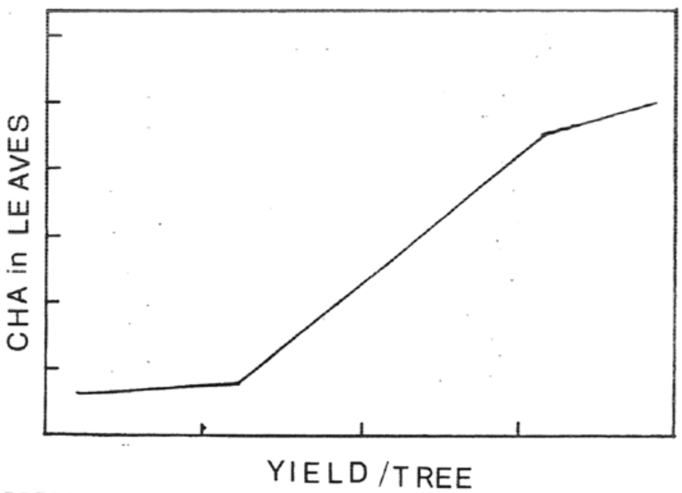

Fig. 9 - The relationship between the CHA level in leaves and fruit yield per tree of cv. Manzanillo (Lavee, 1989).

reproductive development during the tree growth cycle (Fig. 10). The thermal effect on the biotic processes at the different developmental stages was schematically presented (Fig. 11). Extreme abiotic conditions, particularly temperature, might change the developmental pattern of the reproductive bud, leading to abnormal organs. Juvenal seedlings one to two years old, when submitted to relatively extreme low temperatures, will induce metabolic changes that lead to semi differentiated abnormal reproductive buds (Fig. 12). A one- to two-day period of high temperature in mid winter, after the induction of the biotic metabolism leading to flower bud differentiation but prior to initial morphological changes of the buds, will lead to vegetative opening of all the buds along the shoots similar to that of the reproductive fully differentiated ones (Fig. 13). Thus, the abiotic pulse stopped and changed part of the normal biotic pathway of bud development. Long winter periods with insufficient chilling temperature to induce the biotic processes leading to bud differentiation will result in a lack of inflorescence development and therefore cause a fully synchronized alternant bearing, as is common in relatively warmer climates with variable winter temperatures (Fig. 14). However, in extreme high winter temperatures, rather uniform day length and no other abiotic factors to induce a winter period with growth cessation the abiotic environment will induce biotic conditions changing the entire reproductive development of the olive by developing single terminal flowers instead of the normal lateral inflorescences (Fig. 15). Such flowers are usu-

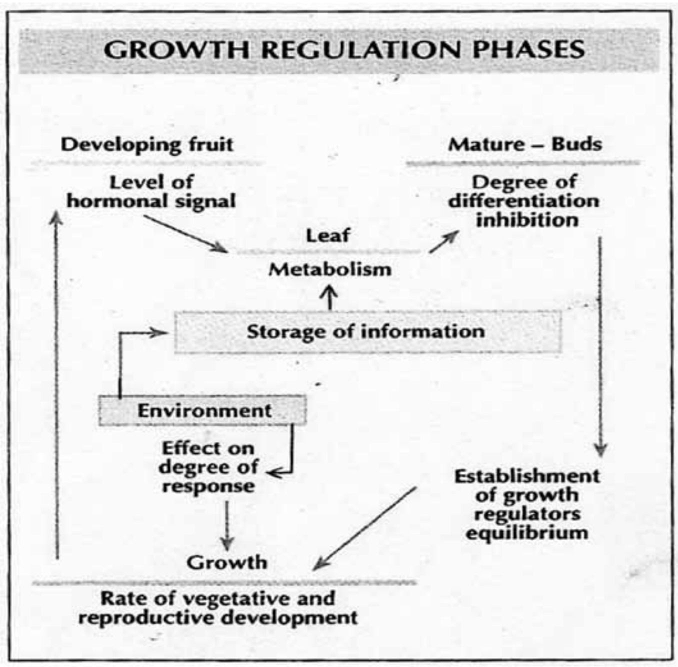

Fig. 10 - A short schematic presentation of the vegetative-reproductive growth cycle of olive (Lavee, 2007).

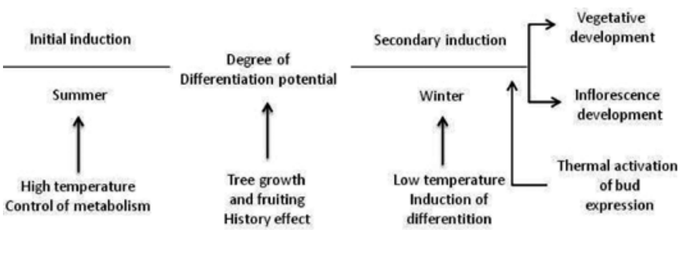

Fig. 11 - Description of temperature involvement in significant metabolic stages during olive vegetative and reproductive development (Lavee, 2006).

Fig. 12 - Abnormal semi-reproductive development of juvenile buds due to unusual strong abiotic thermal induction.

Fig. 13 - Illustration of a fully reproductive olive shoot (left) and a reproductive shoot reversed to vegetative development of all buds due to a period of high temperature during an early stage of winter reproductive differentiation (right) (Lavee, 1996).

ally malformed and those which set fruit, found to present, were all parthenocarpic.

Still, alternate bearing develops in olive also under the most suitable and annually repetitive climates. The alternate bearing under such climatic conditions is less spectacular as it is based on non synchronized alteration of each individual tree. This slowly developing alteration in fruiting is also not due to a genetic property. Various slight abiotic stimuli cause the initiation of the biotic processes leading in receptive buds to differentiation and small changes in fruit load which, accordingly, gradually amplify (Fig. 16). Various abiotic environmental events such as rain during the flowering period wash off the pollen and receptive compounds from the stigma, hot dry winds reduce the respectability of the stigma by drying it, lack of suitable pollen for the required cross pollination, as well as insufficient illumination might lead to the development of shot berries (Fig. 17), which are also, in part, instrumental in inducing alternate bearing in olive (Stutte and Martin, 1986 a, b). However these factors leading to alternate bearing cannot be considered genetic control of alternate bearing as they are all governed by abiotic environmental conditions inducing the onset of specific biotic activities. Furthermore, suitable exposure of the trees to light and radiation might create a period of retarded growth compensating for insufficient chilling starting the biotic endogenous processes which lead to fruit development as occurring in some semi tropical regions.

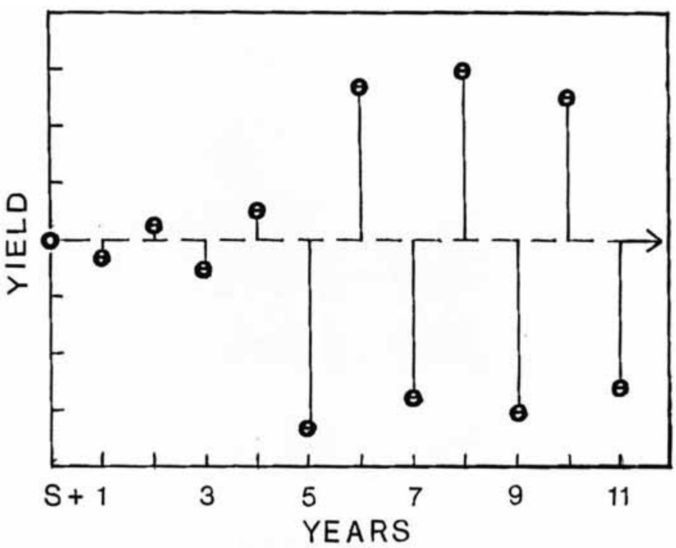

Fig. 14 - Sequence of synchronized alternate bearing development due to extreme high or low winter thermal conditions occurring particularly in regions with varying winter temperatures (Lavee, 1989).

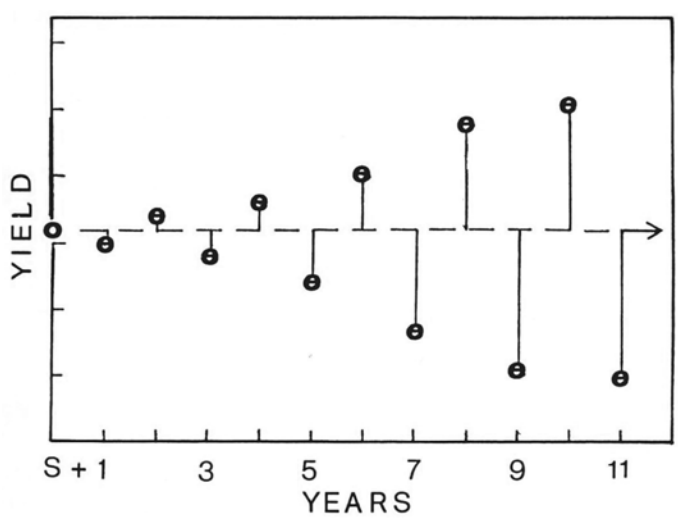

Fig. 16 - Scheme of alternate bearing development in individual trees under relatively stable low annual winter thermal conditions (Lavee, 1989).

Fig. 15 - Abnormal terminal bud differentiation developing a single flower due to high temperatures under semitropical environments.

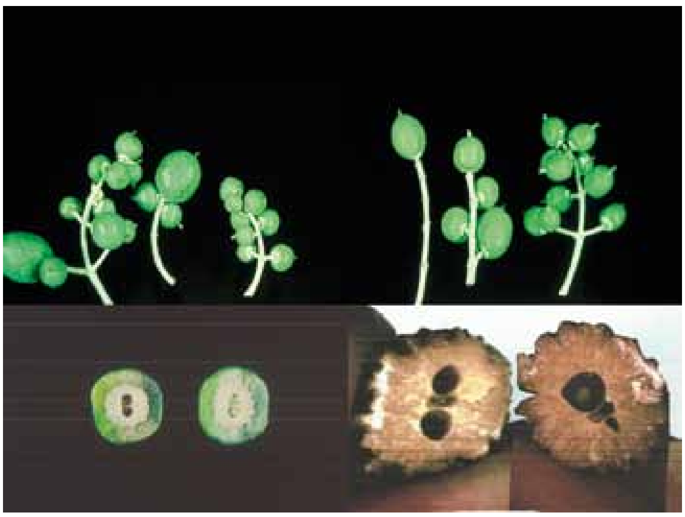

Fig. 17 - Parthenocarpic fruit (shot berries) development with aborted embryos due to unfavorable reproductive differentiation or mal conditions effecting fruit set in the spring.

To eliminate alternate bearing in olive, or at least reduce it, various horticultural techniques are applied such as fruit thinning, girdling, control of harvest time and, to a lesser extent, pruning. These interventions are selectively used for table olives, but in part also in olives for oil extraction. Controlled irrigation and mineral nutrition are helpful tools as well to reduce the biannual bearing, although it does not eliminate it.

Significant metabolic changes were found in various tree parts between ‘on’ and ‘off’ years during the development of the annual olive life cycle. These biotic changes, and their degree, are strongly affected by the environmental abiotic conditions. This close interaction between the endogenous metabolic processes and the environmental conditions at various olive growing sites led to the assumption that alternate bearing of olive is a basic genetic characteristic of this commodity which exists in close interaction with the surrounding abiotic conditions. There is no doubt that the biotic endogenous processes leading to alternate bearing are strongly affected, and in many cases even controlled, by local abiotic environmental conditions of olive growing regions. Thus, all the schemes describing alternate bearing clearly indicate the biotic-abiotic interaction (Fig. 18). This can be rather misleading as it is based on the nature and degree of the processes involved during the ‘on’ or ‘off’ phase of an already induced developmental cycle. However this approach deals with the level of alternate bearing and does not take into account its initial induction. Based on the various studies dealing with alternate bearing of olive, it should be concluded that the initiation of it is solely abiotic. Without an external, environmental and thus abiotic stimulus, alternate bearing of the olive tree is not initiated. Analysis of the currently available data clearly indicates that without an abiotic induction alternate fruiting of the olive tree would not occur.

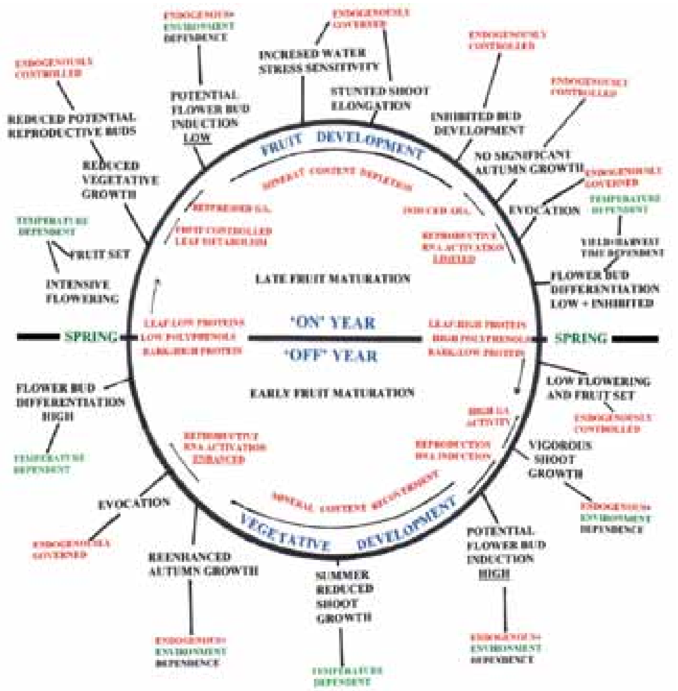

Fig. 18 - A general scheme showing initiation of the abiotic conditions on fruiting induction and subsequent biotic-abiotic interactions on the level of fruit differentiation and development in sequential ‘on’ and ‘off’ years (Lavee, 2007).

Conclusions

Alternate bearing in olive could result from an array of metabolic changes involving tree growth, fruit load, flower and pollen viability, etc., however these biotic changes were shown to occur only as a result of abiotic inductions. Thus, biannual bearing, at least in the case of olive, should not be considered a genetic trait developing as a stage of the growth cycle of the tree. On the other hand, the nature and degree of reproductive alternation and the metabolic changes involved are clearly based on an abiotic-biotic interaction.

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