Review article
Received: 2006-10-09

UDC 633.852.73

BIENNIAL BEARING IN OLIVE *(OLEA EUROPAEA)*

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ABSTRACT

Alternate bearing is a wide spread phenomenon in many fruit tree species and causes severe labor, marketing and thus economical problems. The domestic olive (Olea europaea) *is genetically highly alternating in fruit production. The expression of alternate bearing in olives involves a wide range of changes in activation and repression of endogenous metabolic pathways. The degree of alternate bearing is highly dependent on the environmental conditions and might be very different in accordance with the climate in each growing region. The objective of this work was to present the main endogenous and environmental factors and their interactions that lead to alternate bearing and to review approaches with which alternate bearing is reduced.*

Key words: *Olea europaea*, physiology, flower bud induction, alternate bearing, biennial bearing reduction

PRODUTTIVITÀ BIENNALE DELL'OLIVO *(OLEA EUROPAEA)*

SINTESI

La produttività alternata è un fenomeno molto diffuso negli alberi da frutta e causa notevoli problemi lavorativi, di marketing ed economici. L'olivo (Olea europaea) *è geneticamente altamente alternante nella produzione di frutti. L'espressione della produttività alternata degli olivi include un'ampia sfera di cambiamenti nell'attivazione e nella repressione delle sequenze del metabolismo endogeno. Il grado di produttività alternata dipende in gran parte dalle condizioni ambientali e può variare a seconda del clima di ogni singola regione di crescita. Lo scopo di tale studio era quello di presentare i principali fattori endogeni ed ambientali e le interazioni fra essi che portano alla produttività alternata. L'articolo fornisce inoltre una revisione degli approcci con i quali la produttività alternata viene ridotta.*

Parole chiave: *Olea europaea*, fisiologia, induzione a fiore delle gemme, produttività alternata, riduzione biennale della produttività

INTRODUCTION

Biennial or alternate bearing is a widely spread phenomenon in many fruit tree species and causes severe labor, marketing and thus economical problems. Still, the metabolic processes, their induction and the messengers involved are only very partially known. There is no doubt, however, that the processes involved are not universal and rather different in the various fruit tree species (Goldschmidt, 2005). Although different horticultural practices have been developed and are being used to minimize the alternate bearing in many species, their effect is in most cases only partial (Monselise & Goldschmidt, 1982).

The domestic olive *(Olea europaea)* is genetically highly alternating in fruit production. In non-irrigated olive groves the yield may vary between 7–8 tons/ha and a few hundreds kg. The occurrence and development of alternate bearing is potent also in intensive orchards with controlled irrigation, nutrition and training techniques, though the level of fruit production is higher and better controlled (Lavee, 1989). Without specific intervention, the gap between 'off' and 'on' years may vary between 5–30 t/ha. As the olive is an industry dependent commodity, the problems rising from alternate bearing are of particularly high economical severity. The degree of alternate bearing is highly dependent on the environmental conditions and might be very different in accordance with the climate in each growing region (Morettini, 1950; Hartmann, 1951). The impact of the environmental conditions is not only of direct nature on the reproductive organs – the flowers – but have also a major impact on the endogenous metabolic processes of the tree. This impact involves metabolic changes induced by specific gene activation or repression.

THE EFFECT OF FRUITING AND VEGETATIVE GROWTH ON ALTERNATE BEARING OF OLIVE TREES

To address this problem, it is necessary to clarify first the fruiting habit of the trees. The olive fruit develops on inflorescences developing from the buds borne on the previous year's shoots. However, inflorescences will develop only on well lignified wood, thus stronger and longer vegetative shoots grown in the previous year have a better potential to develop inflorescences in the present one. Olive shoots grow throughout the summer and in many regions from very early in the spring to late fall and in extreme cases even in the winter. The buds developing in the leaf axils will be therefore at different ages in the following spring at time of bloom. Still, all the buds on well-lignified parts of the shoot reach about the same level of development at the end of the summer and can potentially differentiate to form inflorescences. In extreme cases (years or regions) even the very late growth may be lignified and terminal inflorescences can be found. The number of flowers per inflorescence varies between 10–32 according to variety and year. The potential number of flowers per tree particularly in 'on' years is extremely high. A varying number of the flowers on each inflorescence are non-producing male flowers. The amount of fruit per tree is not dependent on the percent of male flowers in either the 'on' and 'off' years, as only 1–3 flowers per inflorescence (and not on all of them) set fruit (Tab. 1). The reproductive and vegetative buds are of the same origin. Once its inflorescent developed, a reproductive bud cannot form a vegetative shoot even when it did not set any fruit. At a very high fruiting event even the few lateral buds, induced to develop extension growth and generally vegetative terminal buds, are inhibited and develop rather weak shoots. Under such conditions the amount of shoots, their length and thus the number of buds available for differentiation and fruiting in the following year is very low. The potential of the buds on such shoots to differentiate into reproductive buds is low even under favorable environmental conditions. This is due to endogenous metabolic changes leading to inhibition of flower bud differentiation in general and viable flowers in particular (Cuevas *et al.*, 1994; Kitsaki *et al.*, 1995).

The 'off' year, which will result, is usually characterized by an establishment of vigorous vegetative growth. The relatively long and strong shoots during that year bear a large number of well-developed buds, which under suitable environmental conditions are ready to undergo reproductive differentiation. The large number of buds that potentially could differentiate into reproductive ones is the basis for reestablishing an extensive number of inflorescences, which will usually lead to the development of the next 'on' year.

It could be concluded that fruit production in the olive is mainly dependent on the vegetative growth of the previous growing season. On the other hand, the degree of vegetative growth in any particular season is a function of the amount of fruit present on the tree at the same time. Thus, the balance between the amount of developing fruit and the vegetative growth in any given growing season will effect and control the potential fruit production for the following season.

THE EFFECT OF FRUIT ON FLOWER BUD INDUCTION

In addition to the effect of fruit on the level of vegetative growth, the developing fruits were shown to have also a significant effect on the development of flower buds for the following season. For various fruit species it was suggested that the developing fruit is a strong sink competing for metabolites with the vegetative growth (Monselise & Goldschmidt, 1982). In olive, this relation is not clear and seems to be not particularly significant. Some workers found a correlation between 'on' and 'off'

Tab. 1: Relationship between the percent of perfect flowers and fruit-set per 100 inflorescences in three olive cultivars.
A, B, C = groups of shoots with different levels of perfect flowers within each of the three cultivars tested.
Tab. 1: Razmerje med odstotki popolnih cvetov in nastavkom plodov za 100 socvetij pri treh oljčnih kultivarjih.
A, B, C = skupine poganjkov z različnimi stopnjami popolnih cvetov znotraj posameznega testiranega kultivarja.

Inflorescence Group	**cv. Sevillano**		**cv. Suri**		**cv. Mazanillo**	
	Perfect flowers (%)	Fruits/100 inflorescences	Perfect flowers (%)	Fruits/100 inflorescences	Perfect flowers (%)	Fruits/ 100 inflorescences
A	**5**	**12**	**25**	**27**	**35**	**72**
B	**20**	**14**	**45**	**26**	**55**	**69**
C	**35**	**13**	**65**	**28**	**75**	**71**
MSE		**4**		**6**		**6**

Tab. 2: The protein content of mature olive leaves and one year old bark of four cultivars in 'on' and 'off' years (sampled in late summer, expressed in µg/g f.wt). Different letters represent significance at the P=0.05 level.
Tab. 2: Vsebnost proteinov v odraslih oljčnih listih in lubju enoletnega poganjka v rodnem in nerodnem letu (vzorčeno pozno poleti, izraženo v µg/g svežih listov). Različne črke ponazarjajo statistično značilnost pri P=0,05.

Tree phase	**Manzanillo**	**Barnea**	**Uovo**	**Koronaiki**
		Leaves		
'off'	295 a	310 a	370 a	475 bc
'on'	510 b	405 c	510 b	530b
		Bark		
'off'	440 b	500 b	490 b	490 b
'on'	360 a	370 a	360 a	370 a

years with primer metabolites, such as carbohydrates (Seyyednejad *et al.*, 2001) and polyamines (Pritsa & Voyiatzis, 2004). An increase in the starch content during the winter in the central axis of lateral potentially reproductive buds was also reported (De la Rosa *et al.*, 2000). Others, however, did not find a competitive effect for basic organic metabolites between the developing fruiting and vegetative growth (Fernandez-Escobar *et al.*, 1999, 2004). Stutte & Martin (1986a) found a uniform level of carbohydrates in the leaves of bearing and non bearing trees. They also found that destruction of the seeds (embryos) in intact fruits before stone hardening allowed a seedless development of the fruits. Such "partenocarpic" fruits had only a small effect on the returned bloom and crop development in the following year (Stutte & Martin, 1986b). It could be concluded that the effect of the developing fruits on reducing flower bud differentiation for the following season is of regulatory nature via signals produced by the developing embryos. Such signals could be involved in developing the significant differences found in the protein content and its quantitative changes during the growing season in both leaves and young shoots of fruiting and non-fruiting trees (Lavee & Avidan, 1994). Seasonal change in the amount of total proteins in the leaves and young shoots found during 'on' and 'off' years revealed opposite trends (Tab. 2). These differences in the protein content seem to be more of regulatory nature, as specific and different proteins were induced during the 'on' years and others in the 'off' ones. The nature of these proteins and their possible role in controlling alternate bearing are presently investigated at the Volcani Center in Israel.

Lately, specific changes in the mineral content of leaves between 'on' and 'off' years were reported and related mainly to the potential activity of growth regulating systems (Fernandez-Escobar *et al.*, 1999, 2004). Troncoso *et al.* (2006) showed a considerable depletion of the N and K contents in the leaves at the end of the 'on' year, while at the end of the 'off' year these values were high (Tab. 3). They concluded that a recovery of the mineral content is required for flower bud differentiation to reoccur. Growth regulators and particularly gibberellins were shown to reduce flower bud induction in the olive as in many other fruit species when applied during the major growing season in the summer or in the fall (Lavee, 1989; Fernandez-Escobar *et al.*, 1992; Lavee & Haskal, 1993). In an old paper, however, Badr *et al.* (1970) showed that at least two gibberellins increased during the winter in lateral expected flower buds, while abscisic acid was higher in the terminal vegetative buds. Differences in the content of various growth regulators in leaves and buds during 'on' and 'off' years were reported by various workers (Navaro, 1990; Ben-Tal & Wodner, 1993; Baktir *et al.*, 2004). The major changes

Tab. 3: Leave-nutrient contents in different phases of the production cycle.
Tab. 3: Vsebnost hranil v listih v različnih obdobjih rodnega cikla.

Biannual cycle phase		**% d.w.**					**ppm**		
		N	**P**	**K**	**Ca**	**Mg**	**Fe**	**Mn**	**B**
Winter stop after harvest		1.45	0.07	0.50	2.10	0.14	70	27	12
Recovery after harvest ('off' year)	Spring	1.67	0.10	0.60	1.70	0.15	40	24	13
	Summer	1.65	0.12	1.00	1.20	0.10	35	22	25
	Autumn	1.67	0.13	0.90	1.20	0.13	50	20	18
Winter stop before harvest		1.75	0.12	0.80	1.30	0.13	50	20	14
Fruit development ('on' year)	Spring	1.64	0.09	0.60	1.30	0.12	55	23	14
	Summer	1.56	0.08	0.50	1.60	0.13	65	30	20
	Autumn	1.40	0.06	0.40	2.20	0.14	70	30	14
Optimal Nutritional Level		1.95	0.11	0.86	1.42	0.20	39	50	15

Tab. 4: The effect of winter and spring applications of exogenous chlorogenic acid (CHA) on flower bud differentiation and fruit-set on cv. Manzanillo trees. (CHA was pressure injected in scaffolds.)
Tab. 4: Vpliv zimskega in pomladnega tretiranja s klorogensko kislino na diferenciacijo cvetnih brstov in nastavek plodov pri drevesih cv. Manzanillo. (CHA je bila dodana s škropljenjem.)

Treatment of branch	**Inflorescences**		**Fruit set (%)**	**Fruitlets**	
	No./branch	**% of control**		**No./branch**	**% of control**
	4 injections 10 Dec – 10 Feb				
Untreated	227	100	26	59	100
CHA injected	118	52	23	27	46
	3 injections 15 Feb – 25 Mar				
Untreated	220	100	28	62	100
CHA injected	215	98	30	65	105
MSE	10	–	–	4	–

in the various growth regulators content and the ratio between them were found during specific developmental periods. These periods could be related to bud differentiation, such as mid summer, early and late winter and before bud opening in the early spring (Bakir *et al.*, 2004). The involvement of growth regulators and the balance between them regulates the current vegetative and fruit development but at the same time act as vectors to initiate the specific metabolic activity controlling the fruiting potential for the following year.

A significant change in the content of secondary metabolites, such as chlorogenic acid in the leaves of olive trees between 'on' and 'off' years, was noted. It is assumed that the signal inducing the synthesis and accumulation of these phenolic metabolites in the leaves is initiated in the developing embryos in the fruits. This could be partially verified by removing the young developing fruit-lets and preventing there by the increase in the level of chlorogenic acid in the leaves, keeping it at a similar one as found in the leaves on 'off' year trees (Lavee & Avidan, 1981; Lavee *et al.*, 1986; Ryan, *et al.*, 2003). Injection of chlorogenic acid during the winter before an 'on' year into the xylem of trees in the field reduced flower bud differentiation on the treated scaffolds by more than 50% (Tab. 4). A similar application in the early spring before bud opening had no effect on bud differentiation and inflorescences development (Lavee *et al.*, 1986). A rather high positive correlation was found in mid summer between the amount of fruit per tree and the level of chlorogenic acid in its leaves. It could be concluded therefore that the developing fruits in the present year are not only in competition with the vegetative growth but have also a direct effect on the metabolism leading to reproductive induction and differentiation of the buds for the potential yield in the following year (Fig. 1).

Generally, the negative correlation between the amount of yield in the present year and that in the following one was already well established in the past as the basis for alternate bearing, as was also the effect of late harvesting in the second half of the winter. In the case of late harvesting it might be speculated that an additional independent effect on bud growth inhibition can be active on top of the earlier induced effect of yield on bud differentiation leading to the reduced flowering and some times fruit set in the following spring. The quality and viability of flowers developing in the year following a heavy yield was considerably reduced (Cuevas *et al.*, 1994).

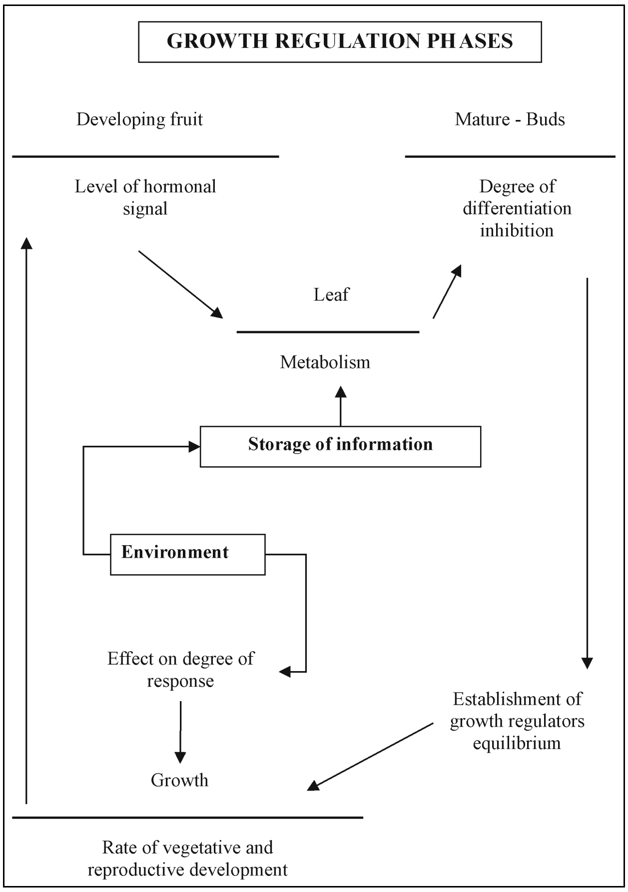

Fig. 1: A flow diagram of the stages involving growth regulators in controlling the level of alternate bearing in olive trees.
Fig. 1: Prikaz stopenj, ki vključujejo regulatorje rasti v procesu alternativne rodnosti oljčnih dreves.

EFFECT OF CLIMATE ON ALTERNATE BEARING DEVELOPMENT AND EXPRESSION IN OLIVE ORCHARDS

Under normal environmental conditions suitable for olive development, alternate bearing develops gradually and on an individual tree basis. At a young age and particularly under good growing and intensive conditions yield is increasing gradually during the first 3–4 fruiting years and alternate bearing usually does not develop. Thereafter, olive trees will gradually start to alternate in their production, unless specific horticultural practices such as adequate pruning, thinning etc. will be applied. The alternate bearing will be under annual favorable climatic conditions very light and often even unnoticed for the whole orchard or a region. Under such conditions it is independent of the climate and develops individually for each tree based on the balance between its previous individual growth and fruit production. As a result, the mean production of the orchard could be rather uniform with only slight fluctuations for many years, particularly when adequate horticultural care is given to the trees. This will not be the case in regions where the climate is unstable and might in some years be limiting and in others particularly favorable for flower bud differentiation and fruit set. Such conditions occur mainly in the warmer growing regions where winter temperatures (particularly the schedule and amount of chilling) vary significantly from year to year. Regions with occasional spring frost, heavy rains or dry and hot desert winds during flowering will also initiate the onset of a sudden orchard or regional biannual bearing. The gradual development of alternate bearing of individual trees is controlled by their endogenous metabolism, while the sudden synchronized beginning of orchard or regional biannual bearing is primarily induced by external environmental factors.

Temperature is the major environmental factor influencing the process leading to flower differentiation. The requirement of adequate amounts of winter chilling (below 9 °C) for flower bud differentiation was suggested many years ago (Morettini, 1950; Hartmann, 1951). Unfavorable temperature regimes particularly in the winter are instrumental in inducing alternate bearing in general and orchard or regional synchronized one in particular. In regions with uniformly cool winter temperatures, the potential for flower buds to differentiate in the trees is high. Small differences in vegetative growth or fruit production between years will gradually lead to alternate bearing development with an individual schedule for each tree. In regions with relatively warm winters and marginal chilling hours, years with somewhat increased chilling conditions will induce an abundant amount of reproductive buds in all trees. This potentially leads to a high uniform fruit production that will result in an overall low flower bud differentiation for the crop of the following year and there cause the beginning of a synchronized alternate bearing. More common though in inducing synchronized alternate bearing will be the opposite situation, starting with an 'off' year caused, *i.e.* by lack of enough suitable chilling conditions (Hartmann & Prolingis, 1957). The climatic conditions have a major impact on olive tree fruiting and development at different stages during its annual developmental cycle. In non-irrigated trees, the amount of rain and its distribution is governing the level of tree development and its potential fruit production together with the thermal schedule. Any extreme condition leading to a water or thermal stress at any stage during the growth cycle of the tree may induce a misbalance between vegetative development and fruiting, which could result in an initiation of alternate bearing. Even a single and short stress incident when occurring at a critical developmental stage can create such a misbalance and start a biannual bearing syndrome. A most severe initiation of alternate bearing will occur in both non-irrigated and irrigated orchards when flowering or fruit set are climatically damaged. High temperatures and dry winds on the one hand and heavy rain or frost on the other might lead to a fruitless, highly vegetative season, which in turn will result in over-cropping during the following year. The resulting biannual bearing might persist for many years, if horticultural means to minimize it are not taken. In irrigated orchards, the major climatic parameter effecting fruit production is the temperature as water stress can and usually is avoided by the controlled water supply. It is commonly assumed that biannual bearing in intensive orchards is less severe; this, however, is usually not the case. Furthermore, in many regions it is even more extreme due to the vigorous vegetative growth in the 'off' years and thus followed by an extensive fruit production in the 'on' ones creating a vicious cycle of extreme alternate bearing.

Temperature conditions are closely involved in the processes leading to flower bud differentiation and viability of the flowers. In warm growing regions, winters with insufficient chilling for normal flower bud development are rather frequent. The nature of the low temperature effect on reproductive bud development is not yet resolved. In various studies, different interpretations were suggested for the effect of temperature and particularly the low ones during winter on the reproductive development of the olive. Some workers suggested that the winter chilling is required to release pre-determined flower buds from a dormant phase enabling the inflorescences development for a forthcoming yield (Rallo & Martin, 1991; Rallo *et al.*, 1994). Other workers associated the effect of winter chilling requirement with a metabolic phase similar to vernalisation required in most cases for both stages of inflorescence induction and avocation (Hackett & Hartmann, 1967; Lavee, 1989, 1996; Troncoso *et al.*, 2006). The range of low winter temperatures effective in fulfilling the chilling requirements, their amount, inductive period and daily cycle dynamics are not yet clear enough. In an older work, Hartmann & Whisler (1975) indicated that a daily gradual change between low and high temperatures is required for reproductive bud differentiation. They also showed that for some cultivars a moderate uniform temperature period of 12 ^{o}C was inductive for flower bud differentiation. Considerably more information is needed to evaluate the different daily and seasonally temperature cycles required for efficient although balanced, reproductive bud differentiation. Both the thermal conditions in the spring and early summer and the amount of developing young fruits on the tree are tightly linked in their effect on the potential level of bud differentiation for the yield in the following season (Lavee, 1989, 1996; Fernandez-Escobar *et al.*, 1992; Cuevas *et al.*, 1994; Fabri & Alerci, 1999; Baktir *et al.*, 2004). But at the same time it is also obvious that it is not the only induction time, as in many cases buds which developed considerable later during the summer and autumn, might also be induced to differentiate into flower buds. Lately it has been shown by Lavee & Troncoso *(unpubl.)* that buds induced to grow in the autumn will develop vegetative shoots, while the same buds when forced later, in the winter, developed inflorescences.

As already indicated earlier, the vegetative growth following warm winters, causing reduced flower bud differentiation, will be abundant due to lack of developing fruit. Synchronized biannual bearing in such regions is normal and commonly expressed in olive industry. The temperatures in the spring, autumn and probably also during the summer are continuously involved in the induction and avocation processes governing flower bud differentiation. The thermal effect on the nature of bud development can be demonstrated in a simple flow diagram regardless of the endogenous metabolism involved (Fig. 2).

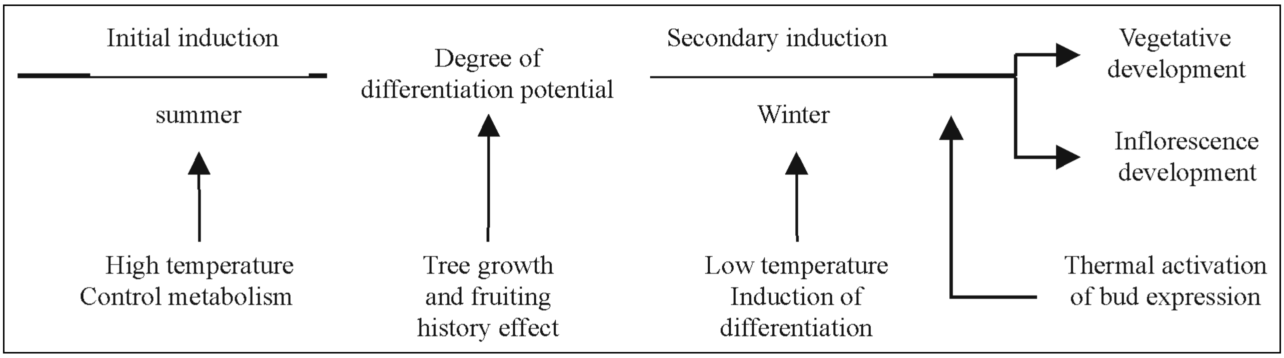

Fig. 2: A flow diagram of the effect of environmental conditions on the stages leading to reproductive and vegetative development in olive trees.
Fig. 2: Prikaz vpliva okoljskih dejavnikov na proces rodnosti in vegetativni razvoj oljčnih dreves.

INTEGRATION OF ENDOGENOUS AND ENVIRONMENTAL EFFECTS LEADING TO ALTERNATE BEARING

Bud transformation leading to reproductive and vegetative stages is based on a continuous interaction between environmental inducing conditions and endogenous metabolic response. This integration is effect resulting in expression of different levels of growth and fruit production. The degree of phase expression determines the severances of alternate bearing and its long term development. As shown earlier, both endogenous and environmental factors are controlling the dynamics and level of each developmental phase of the tree leading to the degree of alternate bearing developing. The environmental conditions and particularly the temperature regime are instrumental in gene activation and repression initiating the metabolic activity leading to phase development and expression of the tree. Still, the developing organs were shown to have an independent controlling effect on the future phase development of the tree.

An attempt was made to summarize the timing and nature of involvement of both environmental and endogenous factors during the olive developmental cycle in consecutive 'on' and 'off' years (Fig. 3). The controlling factors, environmentally and or endogenously, on organ development are indicated. The circle is describing a biannual alternate bearing situation with the upper half representing the 'on' year and the lower half the 'off' one. Starting from the spring, the sequence of events during the 'on' year till the following spring has been recorded, from where the events in the 'off' year are described. Along the inner side of the circle, the timing of some of the major metabolic inductions was indicated. Outside the circle, the sequences of the developmental stages are shown as well as their major dependence on environmental effects, endogenous induced conditions, or both.

It should be emphasized that each stage during the developmental cycle is affected by the previous one, but at the same time it also affects the potential expected expression of the one that follows. The level of fruit set will affect not only the differentiation ability for the following year but also the characteristics of the fruit in the present one such as fruit size, time of fruit maturation and, as a result, the rate of oil accumulation. A heavy yield is leading in the present year to small, late maturing fruit with a slower rate of oil accumulation. Under such conditions the negative affect of the developing fruit on bud differentiation for the following year is amplified, while the quality of the present fruit products is reduced. Alternate bearing has therefore a negative effect not only on labor distribution, oil mill capacity, storage requirement etc., but also on product quality in the 'on' year. Even on a two year quantitative basis the production of a fully alternating orchard is in the order of 10–20% lower than that of a non or only partially alternating one (Tab. 5). The commonly raised question of increasing alternate bearing and having half the orchard producing one year and the other half in the next one is usually problematic. In most regions, the annual climatic conditions are not uniform enough to allow such a stable long term production control. Once alternate bearing develops for the whole orchard, most of the expenses saved in cultivation and harvest costs (and even more) have to be spent on storage and increased oil mill capacity. But above all the probable quality reduction of at least part of the olive products is unfeasible for today's market.

Tab. 5: Production of fruit, oil yield and oil mill efficiency in alternate and uniformly bearing irrigated cv. Barnea olive orchards. (Calculations are based on 24 hr work and 1.5 t/hr machines.)
Tab. 5: Pridelek plodov, pridobitek olja in izkoristek oljarne za alternativno in redno rodne, namakane oljčne nasade cv. Barnea. (Izračuni so osnovani na 24-urnem obratovanju oljarne s kapaciteto predelave 1,5 t/uro.)

Year	Fruit yield (t/ha)	Oil yield (t/ha)	Oil mill (hrs/100 ha)	Ha/machine
Alternate bearing orchard				
'On'	22.0	4.4	1467	150
'Off'	3.0	0.6	200	–
Total for 2 years	25.0	5.0	1667	–
Uniformly bearing orchard				
'On'	15.5	3.1	1030	225
'Off'	12.5	2.5	836	–
Total for 2 years	28.0	5.6	1866	–

APPROACHES AND METHODS TO REDUCE ALTERNATE BEARING

Due to the high dependence of the processes leading to flower bud differentiation and fruit set on the environmental conditions, there are regions where alternate bearing can only be partially overcome. Drastic changes in climate common particularly in the eastern Mediterranean basin will re-induce biannual bearing even after or during continuous treatments for fruiting regulation. Without better understanding of the molecular control of bud differentiation, our ability to overcome alternate bearing in varying climates is usually temporary and incomplete. On the other hand, in well adopted stable climates alternate bearing can be reasonably well avoided or continuously minimized. Still, an unexpected incident might lead to synchronized alternate bearing also in usually favorable climatic conditions. Various methods have been developed and horticultural techniques modified to reduce or overcome alternate bearing.

Pruning is a one of the oldest and basic methods to control production in olive orchards. Pruning has a wide range of effects on the olive tree and olive orchards in general. It is instrumental in shaping tree form, controlling vegetative vigor, enhancing light penetration for regrowth and flower bud differentiation, adaptation to spray and harvest mechanization, etc. Although the olive is a sectorial tree with each scaffold performing rather individually, some overall effect on fruiting can be achieved by balancing the amount of fruiting wood in relation to the expected production. Opening the trees for effective light penetration into the canopy will increase the fruiting potential by enhancing flower bud differentiation. At the same time, the amount of available fruiting wood can be controlled. Applying a more severe pruning before the 'on' year will result in reducing the number of fruits by limiting the amount of fruiting wood. It will also cause initiation of new vegetative growth at the stamps of the pruned branches. This new vegetative growth could develop into fruiting wood for the following season if enough of the currently yielding wood had been removed. Towards the expected 'off' year pruning is than directed only to enhance light penetration, where the new developed canopy is too dense. In regions with a stable inductive climate, alternate bearing could be pretty much controlled by pruning. In regions with less stable climate and with slow growing cultivars not responding enough to pruning, additional methods, such as fruit thinning, will be needed.

Fruit thinning has an important impact on both fruit quality during the 'on' year itself and the fruiting potential for the following one. The amount of developing fruit on each tree and even scaffold is directly correlated with its size. Thus, excess production results in small fruit, which are of inferior value for table olives (Hartmann, 1952; Martin *et al.*, 1980), and, as shown presently by Dag *et al. (unpubl.),* the amount of oil per fruit is reduced. This reduction is due to the smaller flesh/stone ratio in the small (within each cultivar) induced by excess fruiting (Lavee & Wodner, 2004). As by reducing fruit number their size and amount of mesocarp containing the oil is increased, even a significant removal of fruit in the 'on' year has only a moderate effect on reducing the final fruit and oil yields. The currently developing seeds were shown to have a negative effect on flower bud differentiation (Stutte & Martin, 1986b; Lavee, 1989) Reduction in fruit number on the trees reduces the number of seeds and minimizes their inhibiting effect on the fruiting in the following season. Fruit thinning is foremost a tool to improve yield quality during the 'on' year when it is performed (Hartmann, 1952). Severe thinning is at the same time a useful tool to reduce alternate bearing particularly in regions with unstable production. Thinning is performed by spray application of naphthaleneacetic acid (NAA) usually 10–20 days after full bloom once the degree of fruit-set has been established (Lavee & Spiegel, 1958, 1967; Martin *et al.*, 1980). Late summer application of gibberellic acid (GA_3) was shown to reduce flower bud differentiation and could be used to reduce the flowering towards the 'on' years (Fernandez-Escobar *et al.*, 1992; Lavee & Haskal, 1993). The drawback of this method is its early application before the winter induction of flower bud differentiation and the climatic conditions for fruit-set during flowering. In northern Italy, a substituted vitamin based NAA ("66F") was reported to increase fruit-set when applied at the beginning of flowering (Bartolini *et al.*, 1993). This might be an interesting approach for increasing fruit production in the 'off' year. Enhanced fruit-set was also achieved by late winter application of gibberellin inhibitors of the triazol group, such as paclobutrazol, dichlorobutrazol etc., in addition to their effect on reduction or temporary reduction of vegetative growth (Prolingis & Voyiatzis, 1986; Lavee & Haskal, 1993; Rugini & Pannelli, 1993; Iannotta *et al.*, 1999; Palliotti, 1999). The use of Pacloburazol or similar substances is presently studied both for growth and fruiting regulation in the new dense hedge-row developing orchards and in regular intensive orchards before the 'off' year. Harvest time should be considered in relation to alternate bearing. During the early stage of fruit maturation, harvest time has only a very slight effect on alternate bearing. However, late harvest at advanced or full fruit maturation has a significant negative affect on the conditions leading to the consecutive uniform crop development. Harvesting the fruit as early as maturation allows is of particular importance in the 'on' years to prevent amplifying the crop reduction in the 'off' ones. Avoidance of late harvest in the 'on' year is critical both for oil and table olives, shifting in 'on' years the product of the later toward early harvested fruit for green pickles.

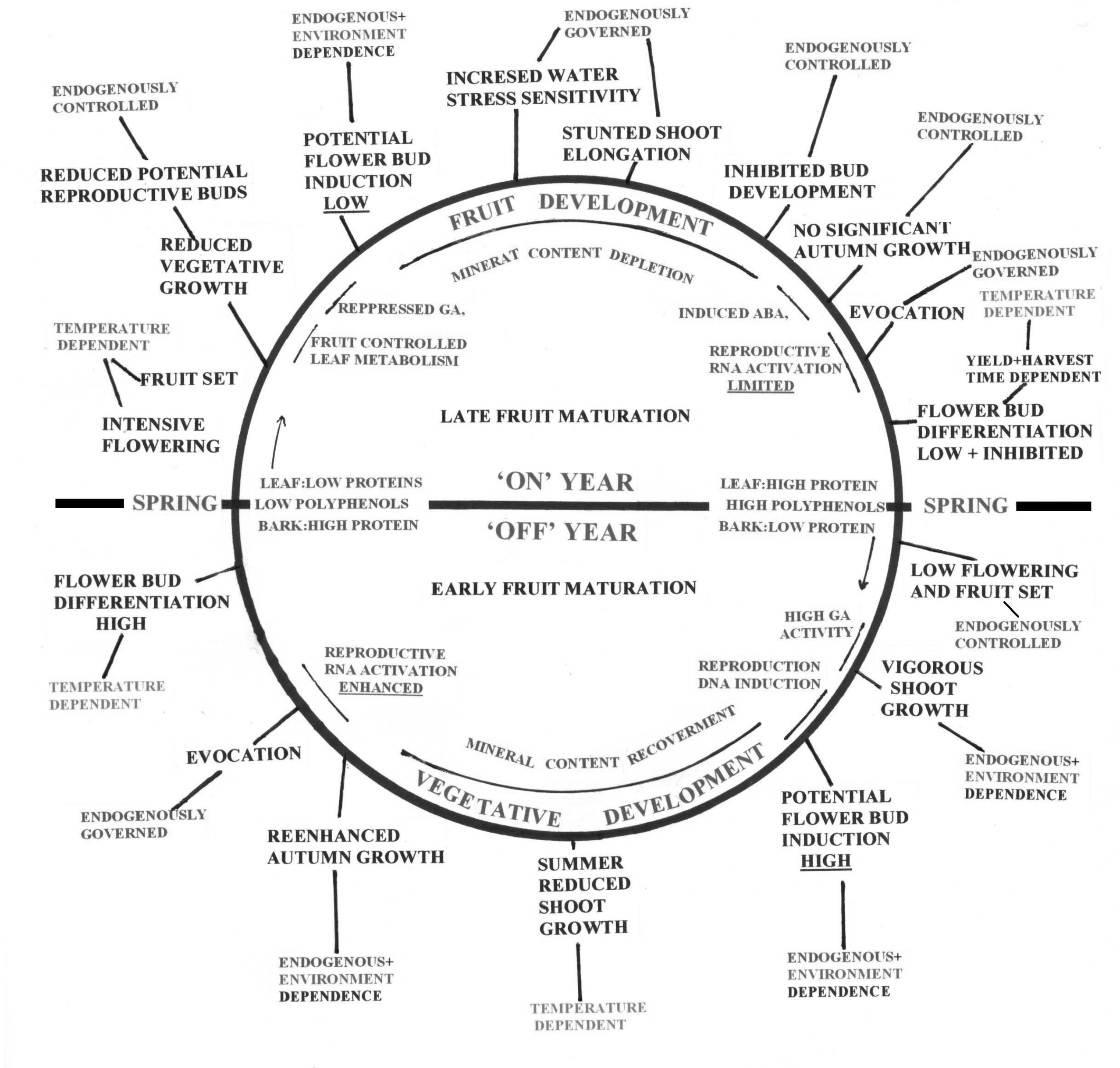

Fig. 3: A general scheme of the alternate bearing events, involvement of endogenous processes and interaction with the environment during an 'on' followed by an 'off' year (in black are the developmental stages, in red endogenous processes and in green environmental involvement).
Fig. 3: Splošna shema dogodkov alternativne rodnosti, vpliv notranjih dejavnikov in interakcija z okoljem v rodnem in nerodnem letu (s črno barvo so označenena razvojna obdobja, z rdečo notranji procesi in z zeleno vpliv okolja).

Girdling was found an efficient and feasible method for the reduction of alternate bearing in intensively cultivated table olive orchards. Girdling increased fruit set (Hartmann, 1950) and in some regions, mainly with warm winters, increased also the number of inflorescences when executed prior to the 'off' year (Lavee *et al.*, 1983). Girdling increased significantly the number of perfect flowers on the girdled scaffolds, widening the ratio between perfect and male flowers (Levin & Lavee, 2005). To reduce alternate bearing, winter girdling is applied to half the scaffolds in one year and to the second half in the next. Thus, each scaffold of the tree is girdled every second year. This procedure has only a slight and some times no effect on the combined yield of the two years, but is efficient in reducing alternate bearing in the long run (Ben-Tal & Lavee, 1984). This method is particularly useful for intensive irrigated orchards grown in regions with uniform weather conditions even when they were somewhat deficient in winter chilling. Continuous use of the alternate girdling method has no negative effect on the long term performance of the trees once applied to vigorous intensively grown ones. Girdling might cause scaffold decline when applied to weak and slow growing trees under extensive cultivation without irrigation in stress prone regions.

Finally, the possible involvement of nutrition, irrigation and fertigation in controlling alternate bearing has to be considered. Under normal balanced growing conditions, all aspects of intensification have very little influence on alternate bearing. Intensive olive cultivation increases production but does not significantly affect the alternate fruiting habit of the trees. Nutritional deficiencies and/or water stress might enhance alternate bearing. In such cases, nutritional or irrigation intervention would affect the level of biannual bearing as well. The use of these factors cannot be considered a significant mean to reduce alternate bearing. Spot-wise use of nutritional and water application are useful to avoid or correct alternate bearing in specific cases, when it was induced by an acute nutritional deficiency or water stress particularly during the early induction period.

CONCLUSIONS

Alternate bearing is a built-in character of olive trees. It is over all controlled by an interaction between vegetative growth and fruit load. The expression of alternate bearing involves a wide range of changes in activation and repression of endogenous metabolic pathways. Environmental conditions are the main trigger to induce the metabolic changes leading to alternate bearing expression. A wide range of climatic events at different stages during the annual development of the olive tree might activate an array of metabolic pathways related to alternate bearing development. A continuous and complex interaction between the ambient temperatures, humidity and other environmental factors are involved in both the vegetative and reproductive development of olive buds. The information about the endogenous pathways and the genes involved in vegetative and reproductive bud differentiation and transformation is extremely limited. The nature of the signal transduction to initiate balanced or unbalanced vegetative/reproductive tree development is not yet known. Horticultural intervention via pruning, thinning, girdling and other cultural and nutritional means can reduce and even eliminate alternate bearing in regions with favorable and stable climatic conditions. Under more marginal and unstable environmental conditions, alternate bearing is most difficult to control and horticultural, often even drastic, means have to be reinitiated anew after each of the various extreme climatic events. For better understanding and controlling of alternate bearing, wide scale studies at the molecular level of the genes involved in olive flower bud initiation and development, and also the signals required for initiating the relevant metabolic pathways are urgently needed.

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POVZETEK

Alternativna rodnost je zelo razširjen pojav pri številnih sadnih vrstah, ki povzroča veliko težav pri gojenju, trženju in ekonomičnosti proizvodnje. Pojav alternativne rodnosti je močno opazen tudi pri gojeni oljki (Olea europaea). *Izražanje izmenične rodnosti pri oljkah vključuje številne spremembe v aktivaciji in zaviranju endogenih metabolnih poti. Stopnja izmenične rodnosti je močno odvisna od dejavnikov okolja in se lahko spreminja glede na klimatske okoliščine posameznega pridelovalnega območja. V delu so predstavljeni pomembnejši endogeni in okoljski dejavniki ter njihove interakcije, ki privedejo do alternativne rodnosti, in postopki, s katerimi lahko pojav zmanjšamo.*

Ključne besede: *Olea europaea*, oljke, indukcija cvetnih brstov, izmenična rodnost, zmanjševanje izmenične rodnosti

REFERENCES

Badr, S. A., H. T. Hartmann & G. C. Martin (1970): Endogenous gibberellins and inhibitors in relation to flower induction and inflorescence development in olive. Plant Physiol., 46, 674–679.

Baktir, I., S. Ulger & D. G. Himelrick (2004): Relationship of seasonal changes in endogenous plant hormones and alternate bearing of olive trees. HortScience, 39, 987–990.

Bartolini, S., R. Viti & C. Vitagliano (1993): Effects of different growth regulators on fruit-set in olive. Acta Hortic., 329, 246–248.

Ben-Tal, Y. & S. Lavee (1984): Girdling of olive trees, a partial solution to biennial bearing. II. Influence of consecutive mechanical girdling on flowering and yield. Riv. Ortoflorofrutti. Ital., 68, 441–451.

Ben-Tal, Y. & M. Wodner (1993): Involvement of different gibberellins on flowering of biennial bearing fruit trees. Bard Proj. U.S 1587/88 Report, p. 1–37.

Cuevas, J., L. Rallo & H. F. Rapaport (1994): Crop load effects on floral quality in olive. Scientia Hortic., 59, 123–130.

De la Rosa, R., L. Rallo & H. F. Rapaport (2000): Olive floral bud growth and starch content during winter rest and spring budbreak. HortScience, 35, 1223–1227.

Fabri, A. & L. Alerci (1999): Anatomical aspects of flower and leaf bud differentiation in *Olea europaea* L. Acta Hortic., 474, 245–249.

Fernandez-Escobar, R., M. Benlloch, D. Navarro & G. C. Martin (1992): The time of floral induction in the olive. J. Am. Soc. Hort. Sci., 117, 304–307.

Fernandez-Escobar, R., R. Moreno & M. Garcia-Creus (1999): Seasonal changes of mineral nutrients in olive leaves during the alternate-bearing cycle. Scientia Hortic., 82, 25–45.

Fernandez-Escobar, R., R. Moreno & M. A. Sanchez-Zamora (2004): Nitrogen dynamics in the olive bearing shoot. HortScience, 39, 1406–1411.

Goldschmidt, E. E. (2005): Regulatory aspects of alternate bearing in fruit trees. Italus Hortus, 12, 11–17.

Hackett, W. P. & H. T. Hartmann (1967): The influence of temperature on floral initiation in the olive. Physiol. Plant., 20, 430–436.

Hartmann, H. T. (1951): Time of floral differentiation of the olive in California. Bot. Gaz., 112, 323–327.

Hartmann, H. T. (1950): The effect of girdling on flower type, fruit set and yield on the olive. Proc. Amer. Soc. Hort. Sci., 56, 217–226.

Hartmann, H. T. (1952): Spray thinning of olives with naphthalene-acetic acid. Proc. Amer. Soc. Hort. Sci., 59, 187–195.

Hartmann, H. T. & I. Prolingis (1957): Effect of different amounts of winter-chilling on fruitfulness of several olive varieties. Bot. Gaz., 119, 102–104.

Hartmann, H. T. & J. E. Whisler (1975): Flower production in olive as influenced by various chilling temperature regimes. J. Amer. Soc. Hort. Sci., 100, 670–674.

Iannotta, N., L. Perri, F. Zaffina & V. Priore (1999): The influence of different types of treatment on fruit set in the Carolea cultivar *(Olea europaea* L.). Acta Hort., 474, 305–307.

Kitsaki, C. K., J. B. Drossopoulos & S. Trezis (1995): Endogenous free abscisic-acid in floral, bark and leaf tissues of olive during anthesis and early fruit development. Scientia Hortic., 64, 95–102.

Lavee, S. (1989): Involvement of plant growth regulators and endogenous growth substances in the control of alternate bearing. Acta Hortic., 239, 311–322.

Lavee, S. (1996): Biology and physiology of the olive. In: World olive Encyclopaedia. International Olive Oil Council, Madrid, p. 59–106.

Lavee, S. & N. Avidan (1981): Possible involvement of chlorogenic acid in controlling alternate fruiting of the olive. Proc. 13th Int. Bot. Conf. Sydney, p. 62.

Lavee, S. & N. Avidan (1994): Protein content and composition of leaves and shoot bark in relation to alternate bearing of olive trees *(Olea europaea* L.). Acta Hortic., 356, 143–147.

Lavee, S. & A. Haskal (1993): Partial fruiting regulation of olive trees *(Olea europaea* L.) with Paclobutrazol and Gibberellic acid in the orchard. Adv. Hort. Sci., 7, 83–86.

Lavee, S. & P. Spiegel (1958): Spray thinning of olives with growth regulators. Ktavim, 9, 129–138.

Lavee, S. & P. Spiegel-Roy (1967): The effect of time of application of two growth substances on the thinning of olive fruit. Proc. Amer. Soc. Hort. Sci., 91, 180–185.

Lavee, S. & M. Wodner (2004): The effect of yield, harvest time and fruit size on the oil content in fruit of irrigated olive trees *(Olea europaea),* cvs. Barnea and Manzanillo. Scientia Hortic., 99, 267–277.

Lavee, S., H. Harshemesh & N. Avidan (1986): Phenolic acids – possible involvement in regulating growth and alternate fruiting in olive trees. Acta Hortic., 179, 317–328.

Lavee, S., A. Haskal & Y. Ben-Tal (1983): Girdling olive trees, a partial solution to biennial bearing. I. Methods, timing and direct tree response. J. Amer. Soc. Hort. Sci., 58, 209–218.

Levin, A. G. & S. Lavee (2005): The influence of girdling on flower type, number, inflorescence density, fruit set and yield in three different olive cultivars (Barnea, Picual and Souri). Aust. J. Agric. Res., 56, 827–831.

Martin, G. C., S. Lavee, G. S. Sibbett, C. Nishijima & S. P. Carlson (1980): A new approach to thinning olives. Calif. Agric., 34(8–9), 7–8.

Monselise, P. S. & E. E. Goldschmidt (1982): Alternate bearing in fruit trees. Hortic. Rev., 4, 128–173.

Morettini, A. (1950): Olivicoltura. 1st Ed. Ramo Editoriale degli Agricoltori, Rome.

Navaro, C. (1990): Flower bud induction in Manzanillo olive. Acta Hortic., 286, 195–198.

Palliotti, A. (1999): Effect of training system on tree growth, yield and oil characteristics in different cultivars. Acta Hortic., 474, 189–192.

Prolingis, I. C. & D. G. Voyiatzis (1986): Influence of paclobutrazol plant growth regulator on vegetative and reproductive growth of olives *(Olea europaea* L.). Acta Hortic., 170, 587–588.

Pritsa, T. S. & D. G. Voyiatzis (2004): Seasonal changes in poly amine content of vegetative and reproductive olive organs In relation to floral initiation, anthesis, and fruit development. Aust. J. Agric. Res., 55, 1039–1046.

Rallo, L. & G. C. Martin (1991): The role of chilling in releasing olive floral buds from dormancy. J. Amer. Soc. Hort. Sci., 116, 1058–1062.

Rallo, L., P. Torreno, A. Vargas & J. Alvarado (1994): Dormancy and alternate bearing in olive. Acta Hortic., 356, 127–136.

Rugini, E. & G. Pannelli (1993): Preliminary results on increasing fruit set in olives *(Olea europaea* L.) by chemical and mechanical treatments. Acta Hortic., 329, 209–210.

Ryan, D., P. D. Prenzler, S. Lavee, M. Antolovch & K. Robards (2003): Quantitative changes in phenolic content during physiological development of the olive *(Olea europaea)* cultivar Hardy's Mammoth. Int. J. Food Chem., 51, 2532–2538.

Seyyednejad, M., H. Ebrahimzadeh & A. Talaie (2001): Carbohydrate content in olive Zard c.v. and alternate bearing pattern. Int. Sugar J., 103, 84–87.

Stutte, G. & G. C. Martin (1986a): Effect of light intensity and carbohydrate reserves on flowering in olive. J. Amer. Soc. Hort. Sci., 111, 27–31.

Stutte, G. & G. C. Martin (1986b): Effect of killing seeds on return bloom of olive. Scientia Hortic., 29, 107–113.

Troncoso, A., J. L. Garcia & S. Lavee (2006): Evaluation of the present information on the mechanisms leading to flower bud induction, evocation and differentiation. 5^{th} Int. Congress on olive growing. Turkey. Acta Hortic. *(In press)*