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Genetic determinism of the vegetative and reproductive traits in an F1 olive tree progeny

Evidence of tree ontogeny effect

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Abstract The agronomic performance of fruit trees is significantly influenced by tree internal organization. Introducing architectural traits in breeding programs could thus lead to select new varieties with a regular bearing and lower input demand in order to reduce training and environmental costs. However, an interaction between tree ontogeny and genetic factors is expected. In this study, we investigated the genetic determinism of architectural traits in the olive tree, accounting for tree development over 5 years until first flowering occurrence. We studied an F1 progeny issued from a cross between two contrasted genotypes, 'Olivière'

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and 'Arbequina'. Tree architecture was decomposed in quantitative traits, related to (1) growth and branching, (2) first flowering and fruiting. Models, including the year of growth, branching order and genotype effects, were built with variance function and covariance structure when necessary. After a model selection, broad sense heritabilities were calculated. During the first 3 years, both the mean values of vegetative traits and genetic factor significance depended on the shoot within-tree position. Dependencies between consecutive years were revealed for traits related to whole tree form. Whole tree form variables showed medium to high broad sense heritability values, whereas reproductive traits were highly heritable. This study demonstrates the existence of ontogenic trends in the olive tree, which result in traits heritable only at the tree periphery. A phenotyping strategy adapted to its architectural characteristics and a list of relevant traits, such as maximal internode length, is proposed. Transgressive effects suggest that genetic progress could be performed in future selection programs.

Introduction

Plant architecture is of major importance in cultivation management and productivity enhancement. This is particularly true in fruit trees species, for which productivity is closely linked to tree development over years (Costes et al. 2006). Trees internal organization and volume in orchard have been shown to influence their light interception efficiency, fruit quality and yield regularity (Jackson 1980; Lauri et al. 1997; Maguylo and Lauri 2004). The integration of architectural traits in breeding programs is thus a promising way to improve

the control of vegetative development and bearing regularity (Laurens et al. 2000; Costes et al. 2004). Several studies have been performed on the genetic determinism of fruit tree growth traits on young seedlings (de Wit et al. 2004; Hammami et al. 2011). However, on perennial species, the traits of agronomic interest occur after several years, usually at the end of the juvenile period (Hackett 1985), when the trees have reached a high level of structural complexity. Due to the high number of individuals that must be described for studying trait heritability and performing quantitative trait loci (QTL) analysis, an efficient phenotyping strategy is required to perform quantitative genetic studies on such species. A first strategy has been proposed in apple tree (Segura et al. 2006, 2007), in which plant architectural analysis, as initially defined by Hallé et al. (1978) and further developed in a range of forest and fruit tree species — oak (Heuret et al. 2003), peach (Fournier et al. 1998), apple (Lauri et al. 1997; Costes et al. 2003; Renton et al. 2006), walnut (Sabatier and Barthélémy 2001) — provided the conceptual framework. The proposed strategy was to dissect tree architecture in a number of quantitative variables related either to the tree constituent's organization (i.e., the plant topology) or to the dimensions and spatial location of organs (i.e., the plant geometry; Godin 2000). Variables were classified in growth and branching traits, including reproductive organs organization, and were collected on different shoot types that resulted from different growth and elongation characteristics leading to axes polymorphism often observed in fruit trees (Champagnat 1965; Zimmerman and Brown 1971). More generally, different shoot types can be considered with respect to lengths, differentiation states, i.e., vegetative and floriferous and branching which can be terminal or lateral, monopodial or sympodial depending on the species (McManus and Veit 2002; Barthélémy and Caraglio 2007).

Studying the genetic determinism in a perennial crop requires the estimation of the different effects that interact during tree architectural development. Indeed, plant architecture results from a balance between endogenous growth processes and environmental constraints (Hallé et al. 1978), and architectural traits change over time due to tree ontogeny (Barthélémy and Caraglio 2007). In fact, the structure of axes depends on their topological and ontogenetic position within the tree structure: annual shoots having a same differentiation stage can be observed at different tree ages and the most differentiated ones are usually located at the highest rank and branching order at the whole tree level (Nicolini 1998; Heuret et al. 2006). In the apple tree, Segura et al. (2008) have proposed to distinguish ontogenetic, climatic and genetic effects in a mixed linear model for repeated data applied after a staggered start experimental design. Nevertheless, the application of a similar strategy based on (1) architectural analysis for identifying shoot types

and differentiation stages, (2) decomposition of tree architecture in quantitative variables at different scales and observed over years, and (3) mixed linear modelling for estimating the genetic effects, to other species with different architectural pattern is still challenging. The olive tree (Olea europaea L. subsp. europaea) constitutes an interesting case study in this prospect. The olive tree is an evergreen perennial species, mainly present around the Mediterranean Basin, where it is one of the oldest and most important fruit trees (Doveri et al. 2008). Its growth is rhythmic in temperate climate, but without winter buds. Its phyllotaxy is opposite decussate. Branching is most often sympodial after terminal growth cessation. Olive flowers either staminate (male) or perfect (hermaphrodite) are born on inflorescences called panicle mostly developed at leaf axils. Their proportion is variable among different inflorescences, branches, cultivars and years of growth (Fabbri et al. 2004; Martin and Sibbett 2005). Moreover, olive trees are predominantly allogamous (Dìaz et al. 2006) and have a high genetic variability with more than 2,600 cultivars described (Rugini and Lavee 1992). The lack of genetic knowledge, the natural long juvenile phase (up to 15 years), the difficulties in tree manipulation and the genetic complexity ($2n=46$) for a genome size of about 3,120 Mbp (Loureiro et al. 2007; Khadari et al. 2010), makes olive breeding difficult (Omrani-Sabbaghi et al. 2007).

We assumed that, even though olive tree exhibits additional difficulties than those previously mentioned for the apple tree, in particular the absence of morphological markers to detect the growth cessation, it represents an interesting model on which the previously described strategy could be tested. In the present study, we investigated the genetic determinism of architectural traits in an F1 olive tree progeny derived from a cross between two olive cultivars with contrasted architectural traits. Because the two parents are highly polymorphic and the number of progenies is high, the observed phenotypic variability in this population is assumed to represent a large range of the species phenotypic plasticity. The knowledge acquired on this phenotypic plasticity should help olive cultivation as clonal varieties are the traditional types for olive products (Loussert and Brousse 1978). Giving an overview of olive tree development during the first years of growth, and until first flowering, we investigated major factors impacting tree architecture and the relations between inflorescences localization on shoots and fruit set. This led us to define a strategy based on architectural analysis which takes into account the degree of differentiation of growth units during tree ontogeny. Finally, we carried out a heritability estimation which highlights the most promising traits for further genetic analysis, and provides the foundation for QTL detection in this progeny.

Materials and methods

Genetic material

The progeny under study derived from 'Olivière' × 'Arbequina' cross and counts 160 genotypes. 'Olivière' is a vigorous French cultivar with a fast growth rate, a large fruit and a rapid entrance in production (Moutier et al. 2004b, 2008). 'Arbequina' is a very productive Spanish cultivar with low vigor, adapted for high density, and a small fruit (Rallo et al. 2004). After having optimized the conditions for cutting success in a range of cultivars, i.e., considering the period in the year, the shoot type to be sampled, the cutting method including soil type and humidification techniques (Garcia et al. 2005), a cutting campaign was performed on the whole population and the two parents, in order to obtain at least six replications per genotype. In 2005, six cuttings were chosen as homogeneous as possible for each genotype and the two parents. Progenies and parents were planted at INRA-Montpellier experimental station, according to a six complete block design, where the genotypes were randomly distributed in each block (6×2 m; N/S rows orientation). After plantation, trunks were cut back to 50 cm to homogenize the plantation and trees were not pruned afterwards. Standard irrigation and phytosanitary treatments were carried out all over the experiment.

Architectural description

Phenotyping strategy

Tree description was performed on the first two blocks of the experimental plot because of high phenotyping costs. On a total of 324 trees (two replicates/genotype), tree topology was formalized in a multiscale tree graph (MTG) according to the methodology defined by Godin et al. (1999). The data base contained four different scales: tree, sympode, growth unit (GU) and internode. In the first year of growth (2005), all GUs, whatever the branching order, were observed. Branching orders were incremented from axes developed after cutting, which were considered as order 0. GUs were classified into three types according to their length: long (≥20 cm); medium (5 cm≤20 cm) and short (<5 cm). Topological traits such as the number of internodes (Nb_IN) and the number of sylleptic axillary shoots per GU (i.e., shoots developed immediately without bud resting period, Nb_AS$_s$) were measured for long and medium GUs. Two geometrical variables were linked to each GU, their length (L) and basal diameter (Bdiam), whereas the length of the longest internode (IN_Max) was noted for each annual shoot. The mean internodes length was deduced from the GU length and number of internodes (Mean IN_L = L/Nb_IN). At the whole tree scale,

trunk height (H) and projection of the longest branch on the tree (Proj) were used to calculate tree basis area (B_area = Π Proj^2) and volume (V=1/3 * B_area * H).

In the following 2 years (2006 and 2007), a subsample corresponding to the main path of GUs in the tree and along the longest lateral branch was selected within each tree. The same observations than in the first year, i.e., including topology and geometry, were performed on the GUs belonging to the path and at whole tree scale (Fig. 1a). In the fifth year (2009), a last description of the trees was done, collecting at once data on 2008 and 2009 GUs, following the main path of GUs in the tree. Branching records included both sylleptic and proleptic axillary shoots (i.e., developed immediately or after a resting period, respectively). These sylleptic and proleptic axillary shoots were classified depending on their length (Nb_L$_s$, Nb_M$_s$, Nb_S$_s$ and Nb_L$_p$, Nb_M$_p$, Nb_S$_p$, respectively). It must be noticed that incremental variables such as basal diameters were not available for 2008 year of growth.

In 2009, the trees had entered into their reproductive period allowing us to initiate the study of their flowering and fruiting behaviour. For this, two 1-year-old GUs (long or medium) were selected at the tree periphery. Each GU was described at both flowering and fruit set periods (Fig. 1b). The number of inflorescences and fruits born along these GUs or along their sylleptic laterals were noted Inflo (or Fruit)_direct and Inflo (or Fruit)_AS$_s$, respectively. These axillary GUs were classified, as previously, depending on their length (Nb_L$_{sF}$, Nb_M$_{sF}$, Nb_S$_{sF}$), and their total number of internodes was noted. The total number of axillary GUs (Nb_AS$_{sF}$) and the percentage of fruiting (% Fruiting, % Fruitset_direct, % Fruitset_AS$_s$) were calculated afterwards. The basal diameter of each floral GU (Bdiam_GU$_F$) was recorded.

All data extraction from MTG files was performed using VPlants software (http://openalea.gforge.inria.fr). Both measured and derived variables (Table 1) were classified according to the observation scale: whole tree and growth units.

Data analysis

First, changes in primary growth and branching variables during tree ontogeny were examined. Two main factors were considered, the year of growth and the branching order. Since the studied variables were measured on the same trees, their values on consecutive years of growth or branching orders may be not independent. Moreover, diameters were measured repeatedly at the basis of trunks or GUs and consisted in an incremental variable. Thus, variances homogeneity and covariance between consecutive years or orders were considered. Due to the lack of the basal diameter measurements for 2008, genetic analysis of trunk basal diameter measurements did not consider this year. However, the analysis was possible at GU scale, using the basal diameter

Fig. 1 Schematic representation of a 2-year-old phenotyped olive tree: **a** architectural traits (whole tree form, primary growth and sylleptic vs. proleptic branching traits) collected along the trunk and main path of growth units (GUs) over 5 years; **b** flowering and fruiting traits collected on 1-year-old GUs at flowering and fruit set periods; the number of inflorescences and fruits born along the floral GUs (Inflo (Fruit)_direct) or along a sylleptic lateral (Inflo(Fruit)_AS$_s$) were counted
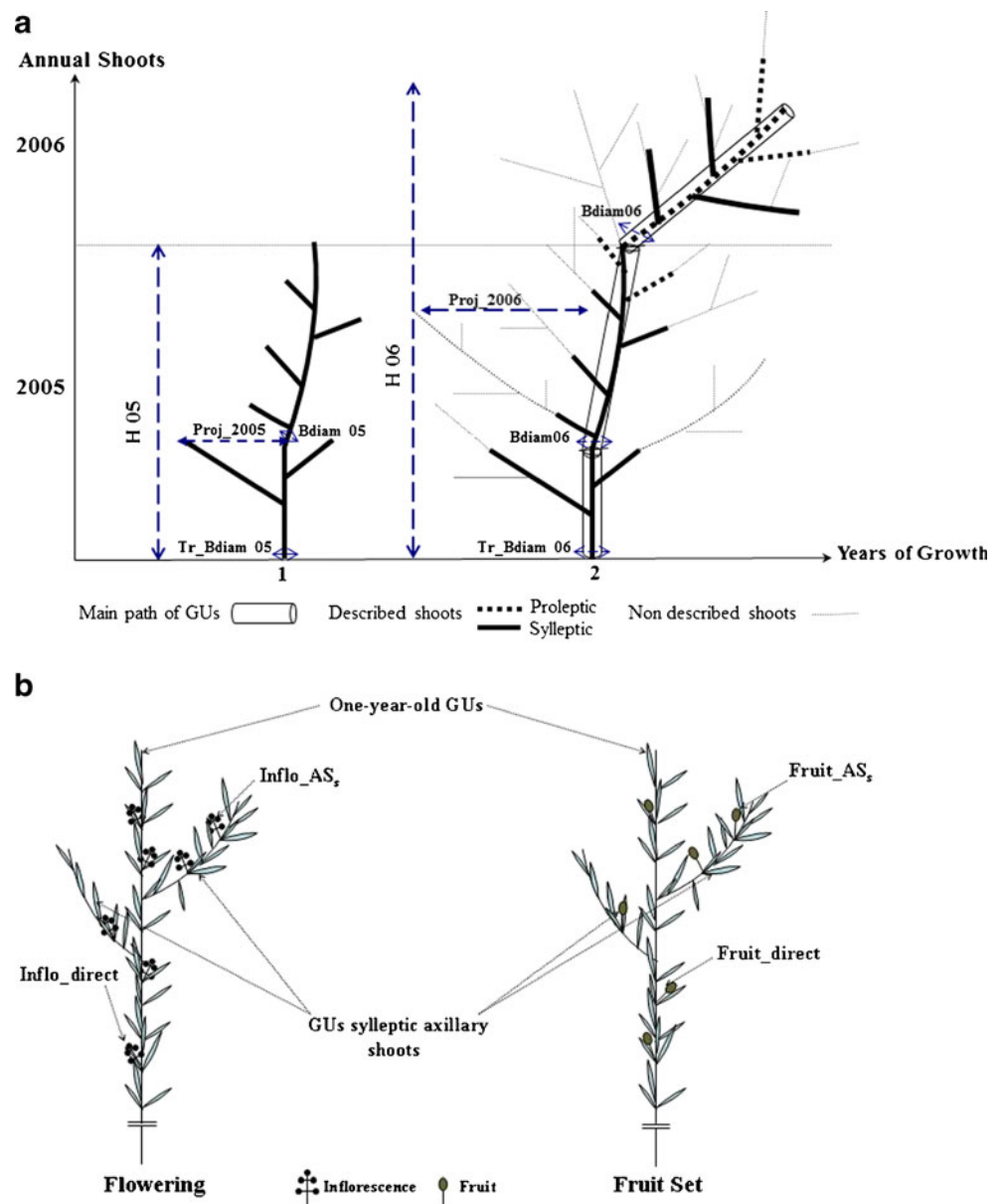
of 1-year-old floral 2008 GUs measurements. In addition, due to the high number of variables under study and their possible redundancy, correlations between variables were also considered. Non parametric Kendall's tau correlation coefficient was used because it is more convenient for not normally distributed variables (Becker et al. 1988).

Second, we analyzed the genetic effect on each studied variable. Depending on the variable and the experimental unit considered in the tree, different mixed linear models were built. The normality of each variable distribution was checked. When not verified, the corresponding variable was transformed with a square root transformation (distinguished by the index sqrt).

For 1-year-old GUs considered to characterize the flowering and fruiting behaviour in a single year, the following mixed linear model was used:

$$P_{il} = \mu + G_i + \varepsilon_{il} \qquad \text{(model1)}$$

where P_{il} is the phenotypic value of genotype i on the l measured GUs, μ is the overall mean of the progeny, G_i is the random effect of the genotype i, and ε_{il} is the random residual error effect for the l measured growth units.

Flowering and fruiting variables were not normally distributed and were thus transformed for the analysis.

For variables collected at the whole tree level over consecutive years, the effect of genotype and year of growth,

Table 1 List of quantitative variables collected on olive tree topology, geometry, flowering and fruiting traits with detailed formula for calculated variables

Observation scale	Measured and derived Variables	Abbreviations	Formula
Whole tree	Height (m)	H	
	Projection (m)	Proj	
	Basis area (m²)	B_area	$\Pi(Proj)^2$
	Tree Volume (m3)	V	$1/3 \times B\_area \times H$
	Trunk basal diameter (mm)	Tr_Bdiam	
Growth units	Topology		
	Nb of internode	Nb_IN	
	Nb of sylleptic axillary shoots (from 2005 to 2009)	Nb_AS_s	
	Nb of long, medium, short sylleptic axillary shoots/GU	Nb_L_s; Nb_M_s; Nb_S_s	
	Nb of proleptic axillary shoots (in 2008)	Nb_AS_p	
	Nb of long, medium, short proleptic axillary shoots/GU	Nb_L_p; Nb_M_p; Nb_S_p	
	Geometry		
	Length (cm)	L	
	Mean Internode length (cm)	Mean IN_L	L/Nb_IN
	Length of the longest internode (cm)	IN_Max	
	Basal diameter (mm)	Bdiam	
One-year-old floral growth units	Topology		
	Nb of internodes	Nb_IN_F	
	Nb of sylleptic axillary shoots	Nb_AS_{sF}	
	Nb of long, medium, short sylleptic axillary shoots	Nb_L_{sF}; Nb_M_{sF}; Nb_S_{sF}	
	Flowering and Fruiting		
	Nb of inflorescences (or Fruit)	Inflo (or Fruit) _tot	Inflo(or Fruit) _direct + Inflo(or Fruit) $\_AS_s$
	Nb of direct inflorescences (or Fruit)	Inflo(or Fruit) _direct	
	Nb of inflorescences(or Fruit) on sylleptic axillary shoots	Inflo(or Fruit) $\_AS_s$	
	id. on long, medium, short sylleptic axillary shoots	$Inflo\_L_s$; $Inflo\_M_s$ $Inflo\_S_s$	
	Percentage of fruiting	% Fruiting	Fruit_tot/Inflo_tot
	Percentage of direct fruit set	% Fruitset_direct	Fruit direct/Inflo_direct
	Percentage of laterals fruit set	% $Fruitset\_AS_s$	$Fruit\_AS_s/Inflo\_AS_s$

The index (sqrt) refers to root square transformation of the corresponding flowering and fruiting variables

and their interactions were estimated according to the following model:

$$P_{ijl} = \mu + G_i + Y_j + (G \times Y)_{ij} + \varepsilon_{ijl} \qquad \text{(model2)}$$

where P_{ij} is the phenotypic value of genotype i, at the year of growth j, μ is the overall mean of the progeny, G_i is the random effect of genotype i, Y_j is the fixed effect of the year of growth, $(G \times Y)_{ij}$ is their random interaction and ε_{ijl} is the random residual error effect for the l measured trees.

For architectural variables collected at the GU level over several years, the dataset was unbalanced, because the GUs developed at a given year of growth were located at different branching orders and the number of GUs developed per year and order depended on each tree. Thus, we were not able to test both year and branching order factors and their interaction jointly. As a consequence, different models were considered, including either the year or the branching order effect and their interaction with the genotype. These models

were compared on the basis of Bayes Schwarz information criteria (BIC). Because all selected models included a year effect, only model 2 is presented in the following results.

Variance homogeneity between levels was examined for all studied traits. For traits showing heterogeneous variances, a function of variance was introduced into the model. Different variances functions, as described by Pinheiro and Bates (2000), were compared: varIdent, with different variances per level of the fixed factor; varPower, with variance increasing as a power function; varExp, with variance increasing as an exponential function; varConstPower, combines a constant value with a power function. In the three latter cases, the function parameters were estimated during model fitting. Moreover, because correlations between consecutive years or orders may exist, a covariance structure was taken into account in the residual term of the corresponding mixed linear model. Different covariance structures were tested, i.e., compound symmetry (corComSymm), autoregressive of order 1 (corAR1) and exponential (corExp). For each variable, a model selection was performed on the basis of BIC minimization, which allowed us to select the significant factors, the variance function and the covariance structure to be considered. After this model selection step, the normality of residual distribution was checked.

An additional analysis of the genetic effect was performed at the GU level for the number of internodes, and the length gathering measurements on high branching orders at the tree periphery: from order 5 to order 7 recorded from 2007 until 2009 years of growth. The model used included the year of growth and genotype effects.

Broad-sense heritability of branching, flowering and fruiting traits was estimated as the ratio between the genotypic and the phenotypic variances: $h_b^2 = \sigma_G^2/\sigma_P^2$. Because no significant interaction between the genotype and the year factor was selected whatever the variable, heritability calculation was: $h_b^2 = \sigma_G^2/[\sigma_G^2 + (\sigma_\varepsilon^2/n)]$, where σ_G^2 is the genotypic variance, σ_ε^2 is the residual error variance estimated from the selected model, and n is the number of replicates per genotype (Gallais 1989; Knapp et al. 1985). All statistical analyses were performed using R software v.2.9.2, with REML estimation method, under lme4 and nlme packages (R Development Core Team, 2009).

Lastly, a first evaluation of the population performance was performed in comparison to the average values of the two parents (mid-parent) and the best parent (high-parent). Transgressive effects were estimated for all studied traits using the following equations, respectively (Fehr 1987; Barbosa-Neto et al. 1996).

$$\mathrm{Mid-parent\ heterosis}(\%) = (\mathrm{F1} - \mathrm{MP})/\mathrm{MP} \times 100 \quad (1)$$

$$\mathrm{High-parent\ heterosis}(\%) = (\mathrm{F1} - \mathrm{HP})/\mathrm{HP} \times 100 \quad (2)$$

where F1 is the average trait value in the population, MP is the average trait value for the parents and HP is the average trait value for the best parent. In the following, 'Arbequina' was considered as the best parent because of its high productivity combined to a low vigour.

Results

From juvenility to maturity: tree ontogeny analysis

Vegetative development

Every year after plantation, the olive trees showed a constant gain in height and volume and the trunks increased in basis diameter over years of growth (Tr_Bdiam) with mean values ranging from 0.83 cm in the first year of growth to 7.72 cm in the fifth (Table 2). For all these whole tree traits, Kendall's tau (τ) coefficients between consecutive years were significant. The highest correlation values were identified between 2 consecutive years and decreased when the lag between years increased, e.g., for the trunk basal diameter (τ=0.12 (2005–2006); τ=0.07 (2005–2009); τ=0.28 (2006–2007). Similar correlation tendency was found for the tree volume, basal area (B_area), trunk height (H) and projection (Proj; data not shown). The variances of all these variables increased over years and were thus heterogeneous (data not shown).

The average length of GUs (L), positively correlated to their number of internodes (Nb_IN), was maximal at orders 0 and 1, whereas lower values were observed at order 2 during the first and second year of growth (Fig. 2). Subsequently, the number of internodes (Nb_IN) and GU length (L) decreased in average in the third year of growth and until the fifth year. The mean number of internodes ranged from 19.4 in the first year of growth (in 2005) to 13.4 in the fifth year of growth (in

Table 2 Mean values and standard deviations of whole tree variables as a function of years (2005–2009) in 'Olivière' × 'Arbequina' progeny: Trunk Basal diameter (Tr_Bdiam), tree height (H), Projection (Proj), Basis area (B_area) and volume (V)

	2005	2006	2007	2009
Tr_Bdiam (cm)	0.83 (0.19)	2.24 (0.52)	4.50 (0.93)	7.72 (1.15)
H (m)		1.25 (0.25)	1.69 (0.29)	2.58 (0.30)
Proj (m)		0.60 (0.16)	1.00 (0.15)	1.45 (0.22)
B_area (m^2)		1.25 (0.64)	3.22 (0.99)	6.83 (1.93)
V (m^3)		0.53 (0.33)	1.85 (0.7)	5.96 (2.07)

Fig. 2 Mean values and standard deviations of the number of nodes and length (cm) per growth unit (*GU*) as a function of years and branching orders in 'Olivière' × 'Arbequina' progeny: illustration of the ontogenic trend and occurrence of a stable phase from order 5 in the third year of growth
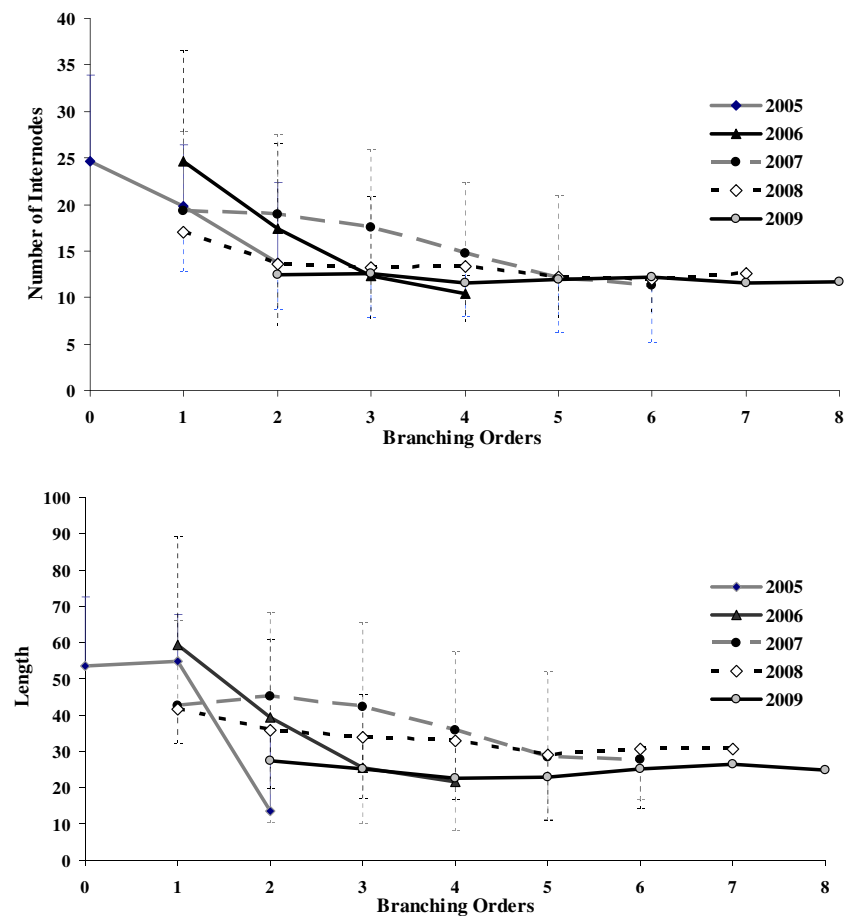
2009). A stable phase was reached from order 5 in the third year of growth (2007: Nb_IN=12 and L=28 cm; Fig. 2) and at all observed orders in the fourth and fifth year of growth (2008: Nb_IN=12 and L=30 cm; 2009: Nb_IN=12 and L=25 cm; Fig. 2). Neither the GU length nor the number of internodes was significantly correlated over consecutive years with τ values not significantly different from zero (τ=0.07 is the highest coefficient value). Similarly, these traits were not correlated between successive branching orders of the GUs (data not shown).

The mean number of sylleptic lateral GUs per parent GU decreased with years and branching orders, in a similar way to that observed for GU length and number of nodes (data not shown). The three types of GUs (long, medium and short) were observed as sylleptic laterals whatever the year and branching order (Fig. 3). However, sylleptic lateral GU types changed depending on the parent GU age: the older the parent GU the higher the proportion of long GUs (Fig. 3). The percentage of long GUs decreased during the first 3 years whereas short GUs increased from the third year of growth becoming the majority in the fifth year of growth. The proportion of GUs of medium length was almost stable during the first 5 years of growth. No significant correlations were found for the number of sylleptic axillary shoots per GU neither

between consecutive years nor between branching orders (data not shown). On 2008 GUs, proleptic laterals were also observed. The mean number of sylleptic and proleptic laterals per parent GU was of 4.9 and 3.15, respectively. As observed for the sylleptic axillary shoots, the three types of GUs (long, medium and short) were observed as proleptic laterals along 2008 GUs (Table 3). At that developmental stage, medium and short sylleptic lateral GUs were prevalent whereas the number of long, medium and short proleptic lateral GUs were almost equal in average (Table 3).

Reproductive development

The number of inflorescences born on the 1-year-old floral GUs was 39 in average. Among them, a large proportion (75 %) was born on sylleptic axillary shoots (Inflo_AS) whereas a lower proportion was born directly along the GU (Inflo_direct; Fig. 4a). Likewise, inflorescences on sylleptic laterals were mainly born on short and medium types (Fig. 4b). The fruit set observed in 2009 on all flower locations, was of 53 % in average. Fruit set on direct inflorescences (Fruit_direct) was greater than that on inflorescences born on laterals (Fruit_AS; 62 % and 35 %, respectively).
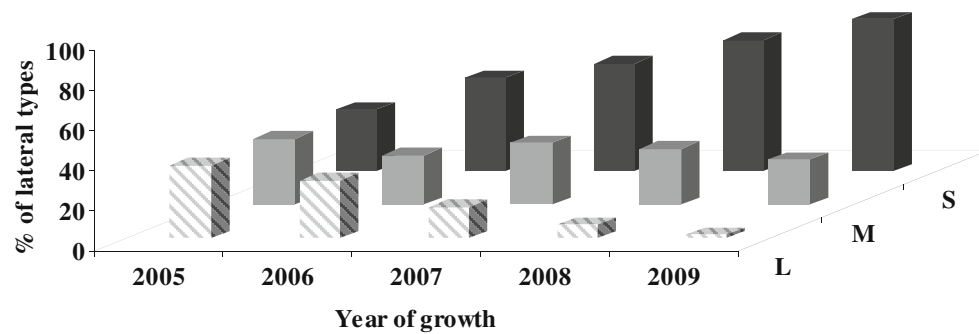
Fig. 3 Percentage of sylleptic lateral growth units (*GUs*) types (long, medium or short) depending on parent GU age in 'Olivière' × 'Arbequina' progeny

Correlation between variables

Phenotypic correlations were investigated between variables measured at a same scale through bi-plot examination (Fig. 5). Whole-tree form traits were highly correlated: for instance, tree projection and height were positively correlated to trunk basal diameter with a Kendall's τ coefficient of 0.62 and 0.66, respectively (Fig. 5a1, a2). At GUs level, the number of internodes was highly correlated to the GU length (τ=0.78; Fig. 5b). Significant correlation was observed between traits related to internodes lengthening at local scale, i.e., between IN_Max and Mean_IN_L (τ=0.55; Fig. 5c), even though the relationships is not perfectly linear but tends to be logarithmic. High correlation coefficients were found between most flowering and fruiting traits. The total number of inflorescences or fruits, Inflo (or Fruits)_tot, was highly correlated to the number of inflorescences born on axillary shoots, Inflo (or Fruits)_AS, (τ=0.82; Fig. 5d) and mostly to those born on medium laterals, $Inflo\_M_s$, (τ=0.59 to be compared with 0.27 and 0.40 for $Inflo\_L_s$ and $Inflo\_S_s$, respectively, data not shown). It is noticeable that a negative correlation was found between the number of direct inflorescences (or Fruits) and the number of the floral GU laterals, Nb_AS_{sF} per node, (τ=−0.30; Fig. 5e), even though a large dispersion of values was observed.

Genetic analysis

Since significant correlations were identified for the variables related to overall tree form measured over years, covariance structures were taken into account into the modelling approach (model 2, Table 4). The model selected according to the BIC criteria included an auto-regressive structure (corAR1) for all tree form traits except for the basal diameter of the trunk (Tr_Bdiam) where the compound symmetry (corCompSymm) structure was the most suitable. Heterogeneous variances were found for the tree basis area (B_area) and volume (*V*) as well as the basal diameter of the trunk (Tr_Bdiam). Thus, a variance function, power or constant power of covariate, was selected in the

selected models (Table 4). Significant effect of both factors genotype and year of growth was found for all studied variables except trunk basal diameter where the genotype effect was not significant. The interaction effect ($G \times Y$) was not significant for all tree form traits (Table 4).

For traits related to primary and secondary growth measured on growth units, no significant correlation was observed over consecutive years or branching orders. However, because heterogeneous variances were found, the models included a variance function. The genotype effect was significant for two topological variables only (Nb_AS_s and Nb_S_s). For all the other variables, the genotype had no significant effect whereas the year of growth had a highly significant effect. For all variables, the interaction $G \times Y$ was not significant (Table 4).

For geometrical traits, the models selected according to BIC criteria also included the genotype and year effects. Because variances were heterogeneous for the GU length and internode maximal length, a power of covariate variance function was selected in the corresponding model (*L*; IN_Max, Table 4). The effect of the year of growth was highly significant for all variables without significant interaction with the genotype effect. Genotype effect was significant for variables measured on internodes (IN_Max; Mean IN_L), whereas no significant effect was found on GU length (*L*; Table 4).

When GUs at high branching orders only were considered during growth stability phase (2007 to 2009 year of growth), significant genotype effect was found for both topological and geometrical traits (Nb_IN and L,

Table 3 Mean values and standard deviations of the number of sylleptic and proleptic lateral growth units (GUs) depending on their types (long, medium or short) in 'Olivière' × 'Arbequina' progeny observed along 2008 GUs, at the tree periphery: whatever the type, the mean number of proleptic axillary GUs was almost stable

Laterals	*L*	*M*	*S*
Proleptic	1.13 (2.10)	1.08 (1.88)	0.93 (1.78)
Sylleptic	0.33 (1.05)	1.71 (3.01)	2.86 (3.63)

Fig. 4 Percentage of inflorescences along floral growth units (*GUs*) observed at the tree periphery in 'Olivière' × 'Arbequina' progeny: **a** direct inflorescences; **b** inflorescences born on laterals and per lateral types (long, medium or short)
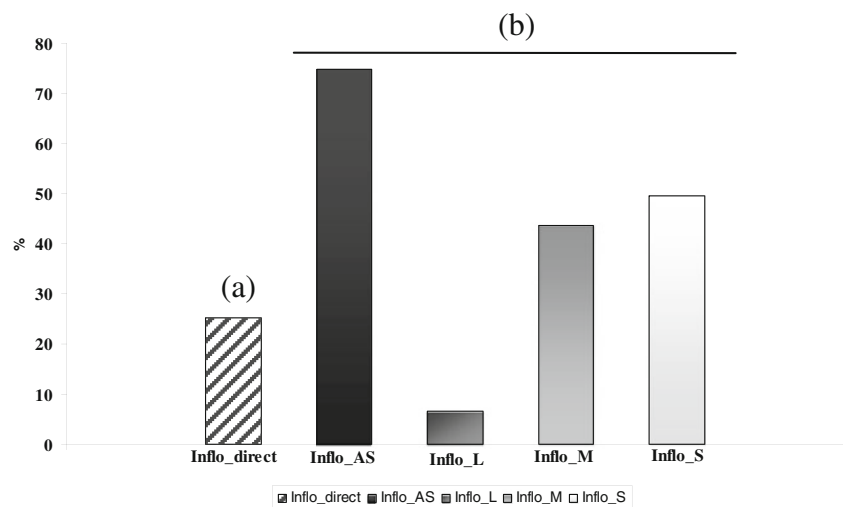

Table 4). For all variables, the branching order effect was not significant whereas the effect of the year of growth was still significant, even though less markedly than in the previous years.

Looking for the number of sylleptic and proleptic axillary GUs, the selected model included genotype effect only, since the branching order effect was not significant for all the variables. Genotype effect was highly significant for the proleptic axillary shoots (Nb_AS$_p$), whereas it was barely significant for the sylleptic axillary shoots (Nb_AS$_s$, Table 5).

All traits related to flowering and fruiting measured on 1-year-old GUs at the tree periphery displayed highly significant genotypic effects (Table 4). Similarly, genotypic effect was significant for the basal diameter of these floral GUs.

Broad-sense heritability

Consistently with the genetic analysis results, traits related to tree form showed moderate to high heritability values ranging from 0.45 and 0.47 for the tree longest branch projection (Proj) and tree volume (*V*) to 0.58 for tree height (*H*) and 0.68 tree basis area (B_area, Table 4).

Among traits related to tree topology, moderate heritability values were found for two sylleptic branching traits: Nb_AS$_s$ (h_b^2=0.25), Nb_S$_s$ (h_b^2=0.45). Moderate heritability values were also estimated for the number of proleptic axillary shoots along 2008 GUs: Nb_AS$_p$ (h_b^2=0.26), as well as for all the three types of proleptic axillary shoots: Nb_L$_p$ (h_b^2=0.29), Nb_M$_p$ (h_b^2=0.23), Nb_S$_p$ (h_b^2=0.37). Summing long sylleptic and proleptic GUs, the total number of long axillary GUs became heritable: Nb_L (h_b^2=0.41, data not shown).

Considering geometrical traits, low to high heritability values were estimated for variables related to internodes lengthening: Mean IN_L (h_b^2=0.20), IN_Max (h_b^2=

0.56), whereas the basal diameter of floral 2008 GUs, showed a moderate h_b^2 value of 0.29. Most traits related to their flowering and fruiting behaviour had high heritability values (Table 4), especially Inflo_tot$_{(sqrt)}$ (h_b^2=0.55) and Fruit_tot$_{(sqrt)}$ (h_b^2=0.69).

Heterosis

All traits related to tree vegetative and reproductive development showed high variation among progenies with values exceeding the best parental form (Fig. 6). Negative transgressive effects were observed for trunk basal diameter and tree height when compared to both mid-parent and best parental form, whereas the tree volume showed a similar transgressive effect only when compared to the mid-parent. This indicates that some progenies were less vigorous than the low vigor parent 'Arbequina' (Table 6). Consistently, the number of internodes, the length of GUs and their total number of axillary shoots also showed negative transgressive effects. More local variables, such as the mean and maximal internode length, exhibited negative transgressive effects only when compared to the mid-parent but did not transgress the best parental form (Mean IN_L and IN_Max, Table 6).

Most of the variables measured on the floral GUs had a negative transgressive effect when compared to either the mid or the best parental form. However, positive transgressive effect was observed for the number of direct inflorescences (Inflo_direct, Table 6).

Discussion

The present study aimed at decomposing the variance of architectural traits observed within an olive segregating population into morphogenetic factors, i.e., genetic,
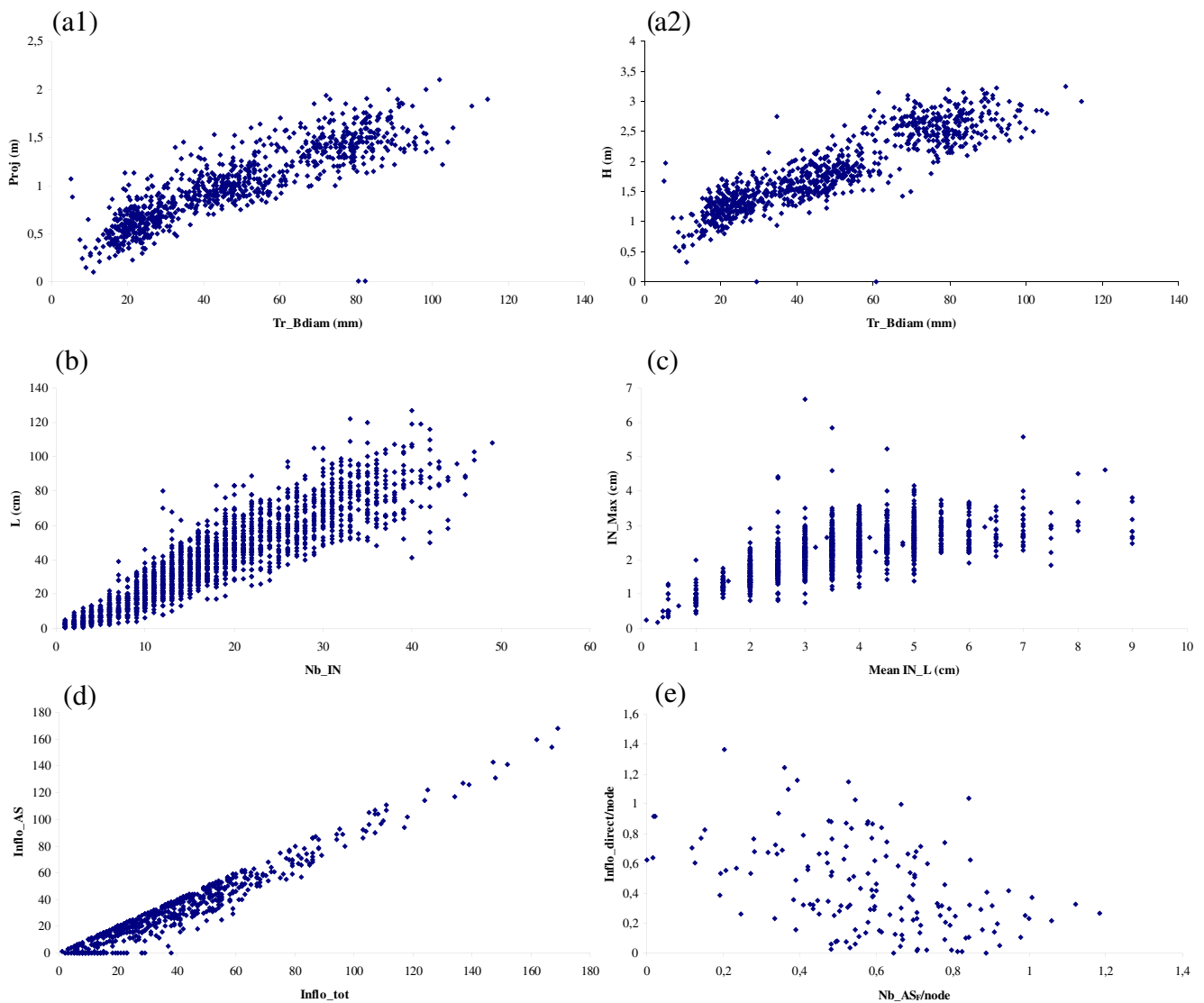
Fig. 5 Biplot between phenotypic values of architectural traits in 'Olivière' × 'Arbequina' progeny: **a1** whole tree variables: Trunk basal diameter (Tr_Bdiam) and tree longest branch projection (Proj); **a2** Trunk basal diameter (Tr_Bdiam) and Tree height (*H*); **b** topological and geometrical variables measured on GUs: Number of internodes (Nb_IN). and GU length (*L*); **c** internodes lengthening variables: mean internode length (Mean_IN_L) and maximal internode length (IN_Max); **d** flowering and fruiting variables measured on 1-year-old floral GUs: total number of inflorescences (Inflo_tot) and number of axillary inflorescences (Inflo_AS); **e** flowering and branching variables measured on 1-year-old floral GUs: mean number of direct inflorescences per node (Inflo_direct/node) and mean number of axillary floral short GU per node (Nb_AS$_F$/node). See text for the corresponding Kendall's tau (*τ*) correlation coefficients

branching order and year of growth. Since the experiment was performed in field, environmental conditions may have generated uncontrolled effects due to micro environmental and climatic year variability (Alía et al. 1997; Li and Wu 1997). However, low variability in the minimum, maximum and mean temperatures was observed between the 5 consecutive years of observation (Fig. S1). Moreover, as trees were irrigated, their growth was not limited by water demand for transpiration. We can thus hypothesize that tree ontogeny and genetic factors were the main sources of variations between years, without being able to formally separate climatic effects from true ontogenetic effects, as previously

proposed by Segura et al. (2006). As another source of variation may result from spatial heterogeneity within the orchard, a first spatial analysis was performed that showed not significant effect of tree rows and blocks (data not shown).

Another source of heterogeneity may result from the multiplication method, since the trees originated from cuttings which are likely to generate more heterogeneous root growth than after grafting on a single rootstock genotype (in addition, rootstocks are usually chosen as homogeneous as possible before grafting). The heterogeneity may also concern the scion growth due to the uncertainty of the cutting technique success. For the 'Olivière' × 'Arbequina' progenies, the

Table 4 Models selected according to Bayes Schwarz information criterion (BIC) for architectural traits related to whole tree form, growth units (GUs) and 1-year-old floral GUs in 'Olivière' × 'Arbequina' progeny

Variables	Modelling factors			Variance function	Covariance structure	Variance estimates		H^2
	G	Y	$G \times Y$			V_G	V_P	
Whole tree								
H	**	**	NS	–	corAR1	0.03	0.06	0.58
Proj	**	**	NS	–	corAR1	0.01	0.02	0.45
B_area	**	**	NS	varPower	corAR1	0.16	0.23	0.68
V	**	**	NS	varConstPower	corAR1	0.04	0.08	0.47
Tr_Bdiam	NS	**	NS	varPower	corCompSymm	8.51×10^{-8}	0.08	NS
Growth Units								
Geometry								
L	NS	**	NS	varPower	–	24.31	320.03	0.07
L (07 to 09)	*	*	NS	–	–	34.14	151.29	0.23
Mean IN_L	*	**	NS	–	–	2.78×10^3	1.36×10^4	0.20
IN_Max	**	**	NS	varPower	–	1.50	2.65	0.56
Topology								
Nb_IN	NS	**	NS	varPower	–	1.27×10^{-5}	2.76×10^{-3}	NS
Nb_IN (07 to 09)	*	*	NS	varConstPower	–	1.38×10^{-11}	8.87×10^{-10}	0.16
Nb_AS$_s$	**	**	NS	varExp	–	2.03	12.25	0.25
Nb_L$_s$	NS	**	NS	varExp	–	3.15×10^{-8}	0.65	NS
Nb_M$_s$	NS	**	NS	varPower	–	5.29×10^{-11}	4.91	NS
Nb_S$_s$	**	**	NS	varConstPower	–	0.09	2.15	0.45
One-year-old floral GU								
Geometry								
Bdiam_GU$_F$	**	–	–	–	–	0.57	1.91	0.29
Flowering and Fruiting								
Inflo_tot$_{(sqrt)}$	**	–	–	–	–	1.75	3.15	0.55
Inflo_direct$_{(sqrt)}$	**	–	–	–	–	0.77	1.49	0.52
Inflo_AS$_{s\,(sqrt)}$	**	–	–	–	–	2.39	4.61	0.52
Inflo_M$_{s\,(sqrt)}$	**	–	–	–	–	1.05	3.46	0.30
Inflo_S$_{s\,(sqrt)}$	**	–	–	–	–	0.97	2.16	0.44
Fruit_tot$_{(sqrt)}$	**	–	–	–	–	3.00	4.29	0.69
Fruit_direct$_{(sqrt)}$	**	–	–	–	–	0.85	1.82	0.46
Fruit_AS$_{s(sqrt)}$	**	–	–	–	–	2.30	3.88	0.59

Variance function and correlation structure when selected are indicated. Broad sense heritability (H^2) was calculated as the ratio between genotypic and phenotypic variances estimates

Significance of effects: *NS* not significant; *significant ($0.01 < p \leq 0.05$); **highly significant ($p \leq 0.01$)

initial percentage of success — corresponding to root growth resumption — was about 40 % and depended on cutting periods, i.e., autumn or spring (G. Garcia, personal communication). However, after optimization of cutting technique (Garcia et al. 2005), no bias was introduced in the population and cuttings were obtained for each genotype before transplantation.

A main limitation for estimating the genetic effects also results from the low number of replicates per genotype since only two trees per genotype were observed. However, it would have been difficult to phenotype a larger number of trees due to the complexity of tree architecture (we presently phenotyped 324 trees in total). Therefore, we attempted to found a balance between a large number of genotypes necessary to increase the power of QTL detection (Bernardo 2004) and the number of replicates per genotype which improves the estimation of the genotypic effect.

Table 5 Models selected according to Bayes Schwarz information criterion (BIC) for sylleptic and proleptic branching traits along 2008 growth units (GUs) in 'Olivière' × 'Arbequina' progeny

	Variables	Factor	Variance function[a]	Variance estimates		H^2
		G		V_G	V_P	
2008 Growth Units	Sylleptic branching					
	Nb_AS$_s$	*	–	4.22×10^{-13}	17.61	NS
	Nb_L$_s$	*	varExp	5.37×10^{-9}	0.09	NS
	Nb_M$_s$	*	–	0.41	4.74	0.09
	Nb_S$_s$	*	–	1.48×10^{-13}	6.59	NS
	Proleptic branching					
	Nb_AS$_p$	**	–	2.52	9.66	0.26
	Nb_L$_p$	**	–	0.75	2.60	0.29
	Nb_M$_p$	**	–	0.46	2.02	0.23
	Nb_S$_p$	**	–	0.72	1.96	0.37

Variance function when selected is indicated. Broad-sense heritability (H^2) is calculated from genotypic and phenotypic variances estimates

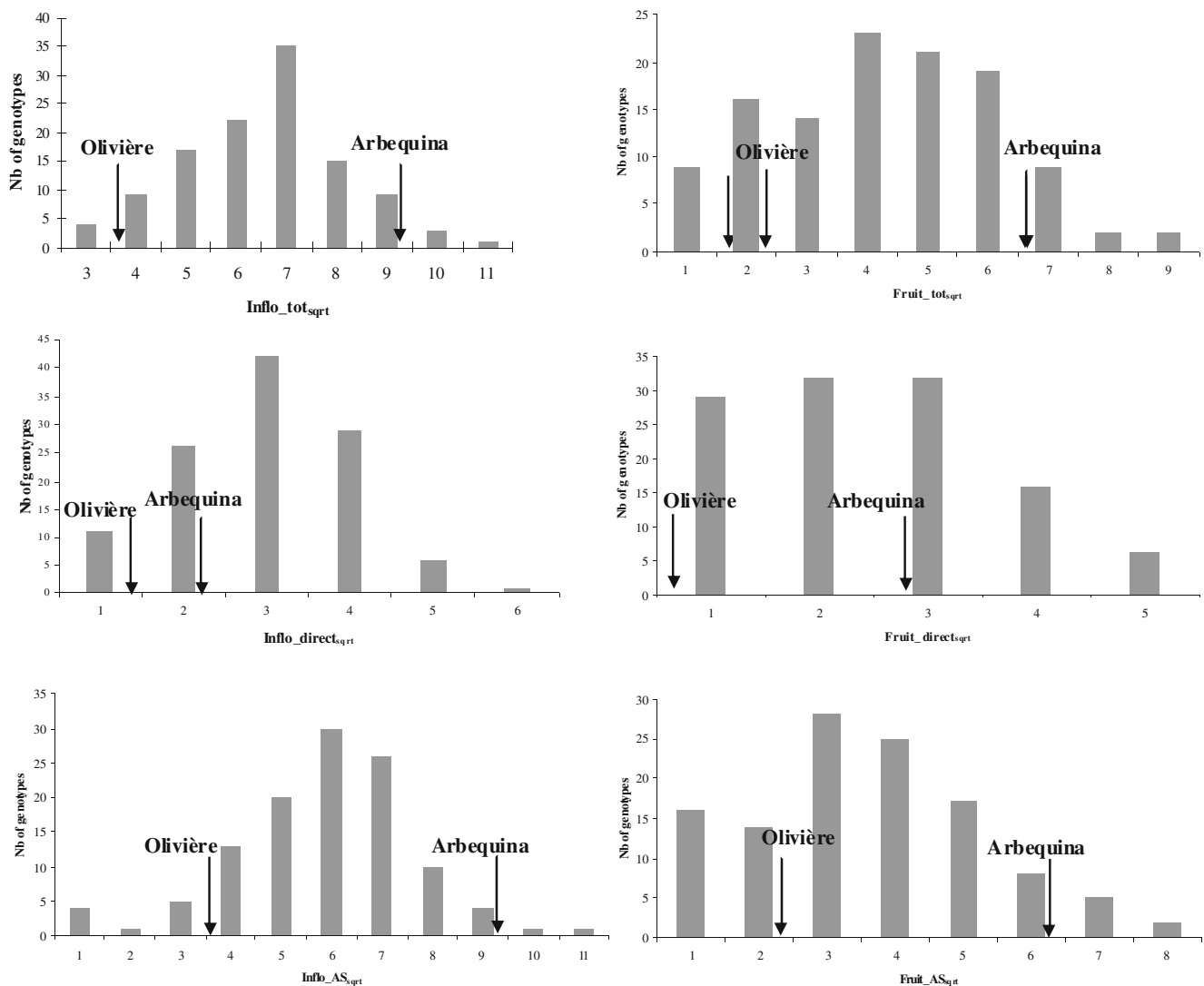Significance of effects: *NS* not significant; *significant ($0.01 < p \leq 0.05$); **highly significant ($p \leq 0.01$)

Fig. 6 Histograms of flowering and fruiting traits, measured at the tree periphery on 1-year-old floral growth units (GUs) in 'Olivière' × 'Arbequine' progeny based on genotypic means. Mean values of the parents are indicated by arrows. Transgressive effects were observed among the progeny, with some progenies values more extreme than parental values. A root square transformation was applied for all variables. See Table 2 for variable abbreviations

Table 6 Estimation of progenies performance for the variables related to vegetative and reproductive development

Variables	'O × A'	'A'(HP)	'O'	MP Heterosis (%)	HP Heterosis (%)
Whole tree					
Tr_Bdiam (cm)	47.25	49.90	53.12	**−8.27**	**-5.31**
H (m)	1.87	2.00	2.27	**−12.51**	**−6.50**
B_area (m^2)	3.78	3.40	3.95	2.77	11.17
V (m^3)	2.92	2.64	3.64	**−7.10**	10.60
GUs					
Nb_IN	16.97	18.07	17.10	**−3.49**	**−6.08**
IN_Max (cm)	3.55	3.33	4.03	**−3.53**	6.60
Mean IN_L (cm)	2.15	2.12	2.62	**−9.28**	1.41
L (cm)	38.27	39.81	45.62	**−10.40**	**−3.86**
Nb_AS$_s$	11.58	15.53	10.26	**−10.19**	**−25.43**
Nb_L$_s$	3.44	6.76	4.10	**−36.64**	**−49.11**
Nb_M$_s$	3.26	3.38	1.73	27.59	−3.55
Nb_S$_s$	4.92	5.23	4.42	1.968	−5.92
Flowering GU					
Inflo_tot	39.39	86.75	14.5	−22.19	−54.59
Inflo_direct	7.12	4.75	2.00	**110.96**	**49.89**
Inflo_AS$_s$	32.26	82.00	12.5	−31.72	−60.65
Fruit_tot	16.89	45.50	5.50	−33.76	−62.86
Fruit_direct	4.96	8.50	0.25	**13.37**	−41.53
Fruit_AS$_s$	11.92	37.00	5.25	−43.57	−67.75

Trait mean values were presented for the parents 'Arbequina' ('A', male parent) and 'Olivière' ('O', female parent) and the progeny 'O × A'. The heterosis was expressed as percentage of F1 progeny trait mean value over the best parental form, here Arbequina (High-Parent, HP) and over the average of both parental forms (Mid-Parent, MP). Values showing transgressive effect and corresponding to a potential improvement of tree shape and flowering are indicated in bold

Olive tree ontogeny

Architectural traits of the studied olive progenies showed major changes during the first years of growth, which can be interpreted with respect to tree ontogeny. Primary growth and branching decreased during the first 3 years, consistently with studies previously carried out on several, either fruit or forest, perennial species (Costes et al. 2003; Sabatier and Barthélémy 2001; Solar et al. 2006; Suzuki 2002). For most topological traits measured on GUs, the observed variance was not explained by the genetic factor and the measurements on consecutive years of growth and branching orders were independent. These results are unlike those found on the same characters observed on apple over the first 3 years of growth (Segura et al. 2008). By contrast, significant effect of the year of growth was found on all primary growth and branching variables during the same period. The relative low genetic control in this progeny found for topological traits of GUs during the first years of tree development, suggests that the young olive trees were in constant adaptation to environmental conditions. This may result from the multiplication method and interactions with climatic conditions (see above). Among topological traits observed over the first 5 years of growth, only the total number of sylleptic axillary shoots and those of short length were under significant genetic control.

Regarding geometrical traits, such as GU length and diameter, similar changes over years were found, with

similar conclusions with respect to absence of genetic control. The absence of significant interaction ($G \times Y$) effect whatever the variable considered shows that the ontogenetic gradient is common to all the genotypes. However, the variables which represented shoot geometry more locally, such as the maximal internode length, remained stable over the years of growth, and showed a significant genetic effect. This suggests that internode lengthening is under genetic control whereas metamer appearance is a process sensitive to the environment leading to architectural plasticity. A similar finding was proposed on apple tree by Segura et al. (2006). Significant genetic effect was also found on other geometrical traits that were related to whole tree form, cumulated over years, and h^2 estimations for tree volume and trunk height are in the same range as those found in previous studies on apple (Watkins and Spangelo 1970; Durel et al. 1998; Liebhard et al. 2003). Moreover, high correlations between consecutive years were found with an auto-regressive structure. This indicates that the tree form is progressively built with a 'memory', which intensity decreases with years. It may be noticed that no significant genetic factor was found on the same variables, e.g., for trunk height, when less years were cumulated: not significant after the second year of growth (2006), the genetic effects became significant from the third year (2007). Similarly, genetic effect was not significant on branching angles that correspond to a more local tree form descriptor (data not shown).

The decrease in growth and sylleptic branching with increasing tree age reaches constant values in the fourth and fifth years of growth (2008 and 2009), at all described orders. These observations on olive trees are consistent with previous studies on several fruit and forest species such as apple, peach, birch and alder (Crabbé 1987; Génard et al. 1995; Lauri and Costes 1994; Champagnat 1954). However, syllepsis did not entirely disappear along olive tree GUs when tree age increased. On the contrary, GUs observed at the tree periphery at adult stage bear both sylleptic and proleptic shoots. Such mixture of sylleptic and proleptic laterals along shoots has been reported on species grown in tropical environment (Bell 1991). In the population, the stable phase coincided with the transition to adult state, since progenies have started to produce inflorescences and fruits in 2008. Along floral GUs, the presence of sylleptic laterals is likely to increase the tree production potential since these laterals bear inflorescences which largely contribute to the total shoot flowering potential. However, because sylleptic laterals may also compete with the inflorescences born directly along the GUs, branching organization and its relationship with fruiting behaviour must be further investigated.

The present study confirms that ontogeny, climatic years and observation scales must be taken into account for studying the genetic determinism of architectural traits in trees. These finding allow us to define when during the olive tree ontogeny and at which observation scale, growth and branching traits are under genetic influence. Unlike previous results on apple trees (Segura et al. 2007, 2008), the crown periphery is a suitable observation area for studying genetic determinism of olive tree architectural traits. Local and stable variables such as internode length and global variables collected at the whole tree scale were revealed appropriate to capture genetic effects contrary to intermediate scales such as growth units, at least during the exclusively vegetative phase of the trees. This allows us to propose a short list of the most relevant traits: whole tree form (tree height and longest branch projection), internode lengthening (IN_Max), and a detailed description focused on floral GUs at the crown periphery giving access to both branching and flowering–fruiting variables.

Reproductive growth

The 'Olivière' × 'Arbequina' progenies entered into flowering in 2008, which corresponds to the fourth year of growth. The majority of trees (74 % of genotypes) started to produce fruits on 3-year-old shoots. This indicates a precocious entering into the adult stage, in a perennial known for having a slow entrance into production, up to 6 years for cv. Santa Caterina (Tous et al. 2005). This earliness is more likely to be inherited by 'Arbequina',

which was characterized as precocious being reported to reach production stage on the second year after plantation in Catalonia (Tous et al. 2005).

In 2009, all progenies reached maturity and produced 39 inflorescences per GUs on average which is on the range of values observed in cultivars considered as highly flowering, e.g., Manzanillo and Barnea: 34 to 40 inflorescences originated from 17 to 21 nodes (Lavee et al. 1999). Inflorescences were mainly located on lateral axes born along medium and short shoots (75 % of the total number of inflorescences observed in our study). Since 'Arbequina' has been described as the cultivar producing the most abundant axillary inflorescences among a range of French and Spanish olive cultivars (Moutier et al. 2004a), the high percentage of inflorescences in axillary position observed in the progeny may be inherited from that parent (male).

Total fruit set calculated on the basis of number of inflorescences was high (e.g., 52 % of inflorescences had at least one fruit) in comparison to low values usually reported for olive tree (Hartmann 1950). For instance, the fruit set percentage based on inflorescences number observed for Kadesh, Manzanillo, Maelia and Barnea cultivars was of 22.4 %, 28.9 %, 38.8 % and 44.8 %, respectively (Lavee et al. 1996). Generally, among 500,000 flowers that a mature olive tree can produce, only 1–2 % develop into a fruit able to reach maturity (Rallo and Fernandez-Escobar 1985; Martin 1990; Lavee et al. 1996, 1999). For 'Arbequina', only 4 % fruit reaches maturity from 60 % of hermaphrodite (perfect) flowers (Cuevas et al. 1995). The reasons of the low final fruit set on olive include genetic mechanisms as well as environmental and agronomic conditions. Firstly, the flower and drupes abscission may be caused by nitrogen deficiency, a lack of soil moisture and olive fly early damage (Pansiot and Rebour 1960). Secondly, low fruit set may result from dysfunctions during the development of reproductive organs leading for instance to pistil abortion. Lastly, both male sterility and incompatibility between cultivars is likely to hamper ovule fertilization (Cuevas et al. 1999). In olive, non-fertilized perfect flowers start to abscise through 3 weeks after anthesis while well fertilized ones abscises partially through 6 weeks after anthesis (Ateyyeh et al. 2000). In our studied progeny, 'Olivière' parent is a male sterile (Bellini et al. 2003), self-incompatible cultivar, whereas 'Arbequine' is self-compatible (Moutier et al. 2004b). The high fruit set observed in the population suggests that enough quantity of pollen were delivered and parental genotypes were compatible. Because male sterility has been shown to be encoded by mitochondrial variants and maternally transmitted (Besnard et al. 2000), we suspect that the success of fruit set in the progeny may be due to open pollination conditions and to the presence of a diversity of genotypes surrounding our progeny, i.e., a collection of about twenty French and foreign olive cultivars. However, compatibility between cultivars has been shown to be under a

complex genetic control which involves numerous alleles (Mookerjee et al. 2005; Saumitou-Laprade et al. 2010). Further studies are thus required to decipher which alleles are present in the 'Olivière' × 'Arbequina' progeny and to distinguish between self and cross pollinations.

In 'Olivière' × 'Arbequina' progeny, the higher number of inflorescences leading to a lower fruit set on lateral GUs than on direct inflorescences suggests higher competition for nutrients on lateral GUs than in direct positions. Competition between developing buds may also drive the axillary bud fate, as we observed negative correlation between the number of sylleptic axillary shoots and the number of inflorescences at a given node. This is consistent with the results of Rugini and Pannelli (1993), who found that vegetative shoot removal or growth regulators applications at bloom reduce the competition between vegetative and reproductive activities at the shoot scale. Moreover, competition for nutrients among fruitlets and between fruitlets and flowers has been shown to be a major factor for post-anthesis flower and fruit abscission (Rallo and Fernandez-Escobar 1985; Rapoport and Rallo 1991; Lavee et al. 1996, 1999). These authors reported that an artificial reduction in the number of flowers increases proportionally the fruit set, and have suggested that higher distance between inflorescences and fruits is likely to increase fruit set (Uriu 1959; Lavee et al. 1999). The relationship between inflorescences or fruit positions along the shoots and fruit set has also been shown to differ depending on the cultivar. In particular, flowering density differs between the two parents, with very dense flowering on 'Arbequina' shoots in comparison to 'Olivière' (Moutier et al. 2004a).

Conclusion

Our study confirms the importance of taking into account the morphogenetic factors in a quantitative genetics approach since results found in a fruit species may be partially transferable to another species. Our finding led us to propose an efficient phenotyping method for a quantitative genetics approach in olive tree, focusing on particular developmental stages and on particular variables such as the maximal internode length that may be interesting for selecting new cultivars with compact crown. The presence within the F1 full-sib population of genotypes showing interesting superiority in comparison to their parents, suggests that genetic progress can be performed in future selection programs. This heterosis probably results from the high level of heterozygosis of the species and allele recombination within the population we studied. In particular, progenies exhibiting higher values than their parents for flowering and fruiting traits, or less vigorous than 'Arbequina', could constitute sources of transgressive forms for innovative material. A step forward in this direction will be performed in the next future, by performing QTL detection on the traits investigated in the present study. This step will be possible, thanks to the high level of polymorphism found within the progeny that allowed us to develop a genetic map mainly based on simple sequence repeat markers (Khadari et al. 2010). Trait combination between vegetative development, fruiting precocity and regularity must be further investigated since irregular bearing is often observed in olive trees and constitute a major agronomic limitation (Martin and Sibbett 2005).

References

Alía R, Moro J, Denis JB (1997) Performance of *Pinus pinaster* provenances in Spain: interpretation of the genotype by environment interaction. Can J For Res 27:1548–1559

Ateyyeh FA, Stösser R, Qrunfleh M (2000) Reproductive biology of the olive (*Olea europaea* L.) cultivar 'Nabali Baladi'. J App Bot 74:255–270

Barbosa-Neto JF, Sorrells ME, Cisar G (1996) Prediction of heterosis in wheat using coefficient of parentage and RFLP-based estimates of genetic relationship. Genome 39:1142–1149

Barthelemy D, Caraglio Y (2007) Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. Ann Bot 99:375–407

Becker RA, Chambers JM, Wilks AR (1988) The new S language. Wadsworth and Brooks/Cole

Bell AD (1991) Plant form: an illustrated guide to flowering plant morphology. Oxford University Press, Oxford, pp 262–263

Bellini E, Giordani E, Rosati A (2003) Genetic improvement of olive from clonal selection to cross-breeding programs. Adv Hortic Sci 22(2):73–86

Bernardo R (2004) What proportion of declared QTL in plants are false? Theor Appl Genet 109:419–424

Besnard G, Khadari B, Villemur P, Bervillé A (2000) Cytoplasmic male sterility in the olive (*Olea europaea* L.). Theor Appl Genet 100:1018–1024

Champagnat P (1954) Recherches sur 'les rameaux anticipés' des végétaux ligneux. Rev Cytol Biol Vég 15:1–51

Champagnat P (1965) Physiologie de la croissance et de l'inhibition des bourgeons: Dominance apicale et phénomènes analogues. Rameaux courts et rameaux longs: problèmes physiologiques. Encycl Plant Physiol 15:1106–1171

Costes E, Sinoquet H, Kelner JJ, Godin C (2003) Exploring within-tree architectural development of two apple tree cultivars over 6 years. Ann Bot 91:91–104

Costes E, Lauri PE, Laurens F, Moutier N, Belouin A, Delort F, Legave JM, Regnard JL (2004) Morphological and architectural traits on fruit trees which could be relevant for genetic studies: a review. Acta Horticult 663:349–356

Costes E, Lauri PE, Regnard JL (2006) Analysing fruit tree architecture: consequences for tree management and fruit production. Hortic Rev 32:1–61

Crabbé J (1987) Aspects particuliers de la morphogenèse caulinaire des végétaux ligneux et introduction à leur étude quantitative. IRSIA, Bruxelles

Cuevas J, Rapoport HF, Rallo L (1995) Relationship among reproductive processes and fruitlet abscission in 'Arbequina' olive. Adv Hortic Sci 9:92–96

Cuevas J, Pinney K, Polito VS (1999) Flower differentiation, pistil development and pistil abortion in olive (Olea europaea L. 'Manzanillo'). Acta Horticult 474:293–296

De Wit I, Cook NC, Keulemans J (2004) Characterization of tree architecture in two-year-old apple seedling populations of different progenies with a common columnar gene parent. Acta Horticult 663:363–368

Dìaz A, Martin A, Rallo P, Barranco D, De la Rosa R (2006) Self incompatibility of 'Arbequina' and 'Picual' olive assessed by SSR markers. J Am Soc Hortic Sci 131:250–255

Doveri S, Sabino Gil F, Dìaz A, Reale S, Busconi M, Da Câmara MA, Martìn A, Fogher C, Donini P, Lee D (2008) Standardization of a set of microsatellite markers for use in cultivar identification studies in olive (Olea europaea L.). Sci Hortic 116:367–373

Durel CE, Laurens F, Fouillet A, Lespinasse Y (1998) Utilization of pedigree information to estimate genetic parameters from large unbalanced data sets in apple. Theor Appl Genet 96:1077–1085

Fabbri A, Bartolini G, Lambardi M, Kailis S (2004) Olive propagation manual. Landlinks Press, Collingwood, Australia 160 pp

Fehr WR (1987) Principles of cultivar development, Volume 1: Theory and technique. McGraw-Hill, New York

Fournier D, Guédon Y, Costes E (1998) A comparison of different fruiting shoots of peach trees. Acta Horticult 465:557–565

Gallais A (1989) Théorie de la sélection en amélioration des plantes. Masson, Paris

Garcia G, Moutier N, Feral S, Salles JC (2005) Amélioration du bouturage de 20 variétés françaises d'olivier. Le Nouvel Olivier 43:4–8

Génard M, Pagès L, Kervella J (1995) Modélisation de la ramification sylleptique chez le pêcher. Architecture des arbres fruitiers et forestiers. Ed. INRA: 81–89

Godin C (2000) Representing and encoding plant architecture: a review. Ann For Sci 57:413–438

Godin C, Costes E, Sinoquet H (1999) A method for describing plant architecture which integrates topology and geometry. Ann Bot 84:343–357

Hackett WP (1985) Juvenility, maturation and rejuvenation in woody plants. Hortic Rev 7:109–115

Hallé F, Oldman RA, Tomlinson PB (1978) Tropical trees and forests: an architectural analysis. Springer, Berlin

Hammami SBM, León L, Rapoport HF, De la Rosa R (2011) Early growth habit and vigour parameters in olive seedlings. Sci Hortic, in press

Hartmann HT (1950) The effect of girdling on flower type, fruit set, and yields in the olive. Proc Am Soc Hortic Sci 56:217–226

Heuret P, Guédon Y, Guérard N, Barthélémy D (2003) Branching pattern modeling in young red oak (Quercus rubra L., Fagaceae) trees in plantation. Ann Bot 91:479–492

Heuret P, Meredieu C, Coudurier T, Courdier F, Barthélémy D (2006) Ontogenetic trends in the morphological features of main stem annual shoots of Pinus pinaster Ait. (Pinaceae). Am J Bot 93 (11):1577–1587

Jackson JE (1980) Light interception and utilization by orchard systems. Hortic Rev 2:208–267

Khadari B, El Aabidine A, Grout C, Ben Sadok I, Doligez A, Moutier N, Santoni S, Costes E (2010) A genetic linkage map of olive based on amplified fragment length polymorphism, intersimple sequence repeat and simple sequence repeat markers. J Am Soc Hortic Sci 135(6):548–555

Knapp SJ, Stroup WW, Roos WM (1985) Exact confidence intervals for heritability on a progeny mean basis. Crop Sci 25:192–194

Laurens F, Audergon JM, Claverie J, Duval H, Germain E, Kervella J, Lelezec M, Lauri PE, Lespinasse JM (2000) Integration of architectural types in French programmes of ligneous fruit species genetic improvement. Fruits 55:141–152

Lauri PE, Costes E (1994) Processus de croissance et ramification anticipée chez le Pêcher (Prunus persica (L.) Batsch.). Architecture des arbres fruitiers et forestiers. Ed. INRA: 61–67

Lauri PE, Térouanne E, Lespinasse JM (1997) Relationship between the early development of apple fruiting branches and the regularity of bearing — an approach to the strategies of various cultivars. J Hortic Sci 72:519–530

Lavee S, Rallo L, Rapoport HF, Troncoso A (1996) The floral biology of the olive I. Effect of flower number, type and distribution on fruit set. Sci Hortic 66:149–158

Lavee S, Rallo L, Rapoport HF, Troncoso A (1999) The floral biology of the olive II. The effect of inflorescence load and distribution per shoot on fruit set. Sci Hortic 82:181–192

Li B, Wu R (1997) Heterosis and genotype × environment interactions of juvenile aspens in two contrasting sites. Can J For Res 27:1525–1537

Liebhard R, Kellerhals M, Pfammatter W, Jertmini M, Gessler C (2003) Mapping quantitative physiological traits in apple (Malus × domestica Borkh.). Plant Mol Biol 52:511–526

Loureiro J, Rodriguez E, Costa A, Santos C (2007) Nuclear DNA content estimations in wild olive (Olea europaea L.ssp. europaea var. sylvestris) and Portuguese cultivars of O. europaea using flow cytometry. Genet Res Crop Evol 54:21–25

Loussert R, Brousse G (1978) L'olivier: techniques agricoles et productions méditerranéennes. Maisonneuve et Larose, Paris

Maguylo K, Lauri PE (2004) Growth and fruiting characteristics of eight apple genotypes assessed as unpruned trees On 'M.9' Rootstock and as own-rooted trees in Southern France. Acta Horticult 732:93–99

Martin GC (1990) Olive flower and fruit production dynamics. Acta Horticult 286:141–153

Martin GC, Sibbett GS (2005) Botany of the olive. In: Sibbett GS, Ferguson L, Coviello JL, Lindstrand M (eds) Olive production manual. University of California, Agriculture and Natural Resources, OaklandCA, pp 15–19

McManus MT, Veit BE (2002) Meristematic tissues in plant growth and development. Sheffield biological series. Academic Press, Sheffield

Mookerjee S, Guerin J, Collins G, Ford C, Sedgley M (2005) Paternity analysis using microsatellite markers to identify pollen donors in an olive grove. Theor Appl Genet 111:1174–1182

Moutier N, Garcia G, Lauri PE (2004a) Shoot architecture of the olive tree: effect of cultivar on the number and distribution of vegetative and reproductive organs on branches. Acta Horticult 636:689–694

Moutier N, Pinatel C, Martre A, Roger JP et al (2004b) Identification et caractérisation des variétés d'olivier cultivées en France. Tome 1, Naturalia Pub, Turriers, p 248

Moutier N, Garcia G, Lauri PE (2008) Natural vegetative development and fruit production of olive trees. Acta Horticult 791:351–356

Nicolini E (1998) Architecture et gradients morphogénétiques chez de jeunes hêtres (Fagus sylvatica L. Fagaceae) en milieu forestier. Can J Bot 76:1232–1244

Omrani-Sabbaghi A, Shahriari M, Falahati-Anbaran M, Mohammadi SA, Nankali A, Mardi M, Ghareyazie B (2007) Microsatellite markers based assessment of genetic diversity in Iranian olive (Olea europaea L.) collections. Sci Horticult 112(4):439–447

Pansiot FP, Rebour H (1960) Amélioration de la culture de l'olivier. Etudes agricoles de la FAO 50:17–21

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-Plus. Springler-Verlag, New York

R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Rallo L, Fernandez-Escobar R (1985) Influence of cultivar and flower thinning within the inflorescences on competition among olive fruits. J Am Soc Hortic Sci 110:303–308

Rallo L, Barranco D, Caballero JM, Del Río C, Martín,A, Tous J, Trujillo I (2004) Variedades de olivo en España. Ed. Munidi-Prensa, pp 84–85

Rapoport HF, Rallo L (1991) Post-anthesis flower and fruit abscission in the olive cultivar 'Manzanillo'. J Am Soc Hortic Sci 116:720–723

Renton M, Guédon Y, Godin C, Costes E (2006) Similarities and gradients in growth unit branching patterns during ontogeny in ' Fuji ' apple trees: a stochastic approach. J Exp Bot 57:3131–3143

Rugini E, Lavee S (1992) Olive. In: Hammerschlag FA, Litz RE (eds) Biotechnology of perennial fruit crops. CAB, Wallingford, pp 371–382

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

Sabatier S, Barthélémy D (2001) Annual shoot morphology and architecture in Persian Walnut, Juglans regia L. (Juglandaceae). Acta Horticult 544:255–264

Saumitou-Laprade P, Vernet P, Vassiliadis C, Hoareau Y, de Magny G, Dommée B, Lepart J (2010) A self-incompatibility system explains high male frequencies in an androdioecious plant. Science 327:1648–1650

Segura V, Cilas C, Laurens F, Costes E (2006) Phenotyping progenies for complex architectural traits: a strategy for 1-year-old apple trees (Malus × domestica Borkh.). Tree. Genet. Genome 2:140–151

Segura V, Denancé C, Durel CE, Costes E (2007) Wide range QTL analysis for complex architectural traits in a 1-year-old apple progeny. Genome 50:159–171

Segura V, Cilas C, Costes E (2008) Dissecting apple tree architecture into genetic, ontogenetic and environmental factors: mixed linear modelling of repeated spatial and temporal measures. New Phytol 178:302–314

Solar A, Solar M, Stampar F (2006) Stability of the annual shoot diameter in Persian walnut: a case study of different morphotypes and years. Trees 20:449–459

Suzuki A (2002) Influence of shoot architectural position on shoot growth and branching patterns in Cleyera japonica. Tree Physiol 22:885–890

Tous J, Romero A, Plana J (2005) In: Rallo L, Barranco D, Caballero JM, Del Río C, Martín A, Tous J, Trujillo I (eds) Vigor—Chapter 2: Variedades de olivo en España (Libro II: Variabilidad y selección). Junta de Andalucía, MAPA y Ediciones Mundi-Prensa, Madrid

Uriu K (1959) Periods of pistil abortion in the development of the olive flower. Proc Am Soc Hortic Sci 73:194–202

Watkins R, Spangelo LPS (1970) Components of genetic variance for plant survival and vigour of apple trees. Theor Appl Genet 40:195–203

Zimmerman MH, Brown CL (1971) Trees, structure and function. Springer Verlag, New York