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The Olive tree from juvenility to maturity

Insight on the developmental changes over years and the genetic basis of vegetative and reproductive traits

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Why Study The Architecture of Fruit trees ?

Trees internal organization and volume on orchard influence their light interception efficiency, fruit quality and yield regularity (Lauri et al. 1997; Maguylo et al. 2004)

Several studies on the genetic determinism of fruit tree growth traits on 1 year old seedlings (de Wit 2004; Hammami et al. 2011) and grafted trees over consecutive years (Segura et al. 2008)

On perennial species, the traits of agronomic interest occur after several years
Structural complexity of the trees increases over years
Traits changes depending on the year due to ontogeny

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Efficient phenotyping strategy is needed
Decomposition of trees structure in quantitative variables related to the tree topology and geometry

Objectives and strategy

Understand and identify the genetic determinants involved in the olive tree architecture

Vegetative development: Primary growth and Branching
changes in growth depending on tree age
The distribution of axillary shoots within the tree

Reproductive development: Flowering and Fruiting
The distribution of inflorescences on annual shoots and their laterals
Fruit set percentage and Production regularity

Olive tree represents an interesting model of evergreen Mediterranean species on which this strategy could be tested

Genetic Material

F1 full-sib 'Olivière' x 'Arbéquina' progeny

X

Arbequina: is a very productive Spanish cultivar, self compatible with low vigor, adapted for high density, and a small fruit

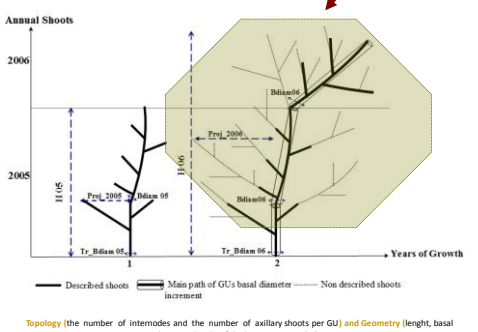
Olivière: is a male sterile vigorous French cultivar with a fast growth rate, a large fruit and a rapid entrance in production

The 160 hybrids and the 2 parents originated from cuttings were randomly planted at INRA experimental station near Montpellier (as 6 repetitions/ genotype)

Phenotyping strategy

324 trees (2 repetitions/genotype) during the first 5 years of growth.

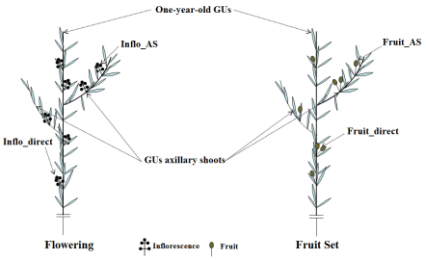
Flowering GUs sampling at Crown Periphery



Topology (the number of internodes and the number of axillary shoots per GU) and Geometry (lenght, basal diameter, lenght of the longest internode)

Phenotyping strategy

Two one-year-old GUs (long or medium) were selected at the tree periphery



At the Tree scale: Fruits were harvested and weighed over four consecutive years **2008-2011**

Data Analysis

The data collected at the GU level was **unbalanced** : GUs developed at a given year of growth were located at different branching orders.

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Inability to test both year and branching order factors and their interaction jointly

A model selection was performed minimizing the Akaike and Bayes Schwarz information criteria

For all variables

$$P_{ij} = \mu + G_i + Y_j + (GxY)_{ij} + \varepsilon_{ijl}$$

P_{ij} phenotypic value of genotype *i*
μ overall mean of the progeny
G_i effect of genotype i,
Y_j effect of the year of growth
$(GxY)_{ij}$ their interaction
ε_{ijl} residual error effect for the *l* measured trees or GUs.

To account for variance heterogeneity or covariance between consecutive years a variance function and/or a correlation structure of residuals were included

The broad-sense heritability was estimated as the ratio between the genotypic and the phenotypic variances: $h_b^2 = \sigma^2_G / \sigma^2_P = \sigma^2_G / [\sigma^2_G + (\sigma^2_\varepsilon/n)]$

Olive Tree Ontogeny: Tree Scale

Significant effect of the year of growth for all overall tree form traits

Trees: constant gain in height, volume and trunks basis diameter over years of growth
The variances increased over years and were thus heterogeneous

For traits related to whole tree form : High correlations between consecutive years
The correlation value decreased when the lag between years increased

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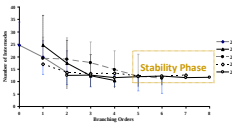
Tree form is progressively built with a "**memory**" which intensity decreases with years

Ben Sadok et al. (2012)

Olive Tree Ontogeny: GU Scale

Significant effect of the year of growth for all traits

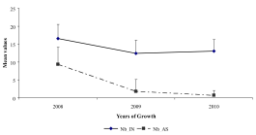
Vegetative GUs



Decrease in average in the third year of growth and until the fifth year

Stable phase from **order 5** in the **third year of growth** and at all observed orders in the **forth and fifth year of growth**

Flowering GUs

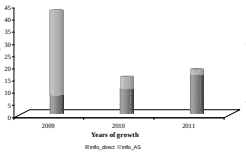


At crown periphery: sylleptic branching decrease

The number of internodes decreased slightly

Ben Sadok et al. (2012); Ben Sadok et al. (submitted)

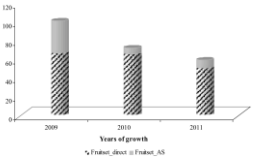
Olive Tree Ontogeny: GU Scale



After high flowering and fruiting in 2009, **the total number of inflorescences and fruits decreased**

This decrease is due to that of sylleptic branching

Negative correlation between Inflo_direct and Nb_AS **antagonism in the development of axillary meristem (vegetative lateral or inflorescences)**



Fruit set was **greater on direct inflorescences** than on inflorescences born on sylleptic laterals **whatever the year**

Ben Sadok et al. (2012)

Genetic Effect: Vegetative growth

Considering traits at all orders during the first five years of growth

Significant Genetic Effect
Local and stable variables (internode length) or **global variables (overall tree form)** cumulated over years.

Intermediate scales such as **growth units** and **annual shoots** appeared **less appropriate to capture genetic effects**, at least during the exclusively vegetative phase of trees.
(only Nb_AS and Nb_S was under significant genetic control)

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The young olive trees were in constant adaptation to environmental conditions
The multiplication method: cuttings with heterogeneous root growth

Considering traits at high order during growth stability phase

Significant G effect was found for primary growth and branching traits

Ben Sadok et al. (2012)

Genetic Effect: Reproductive growth

Variables	Factors			Variance Function[a]	Covariance structure[b]	Variance estimates			H²
Tree scale	G	Y	GxY			σ^2_G	σ^2_{GxY}	σ^2_ε	
Yield	**	**	**	-	-	239.58	242.66	476.78	0.60
GUs scale									
Inflo_tot	-	**	*	-	-	0.04	0.13	0.30	0.30
Inflo_direct	*	**	**			0.22	0.23	0.81	0.52
Inflo_AS	NS	**	**			-	1.18	2.93	NS
Inflo_L	NS	*	*	-	-	-	0.07	0.93	NS
Inflo_M	*	**	**	-	-	0.09	0.57	2.43	0.32
Inflo_S		**	**			0.03	0.47	1.65	0.36
Fruit_tot	**	**	NS	varExp	corExp	0.79	-	0.50	0.75
Fruit_direct	**	**	NS	varPower	corExp	0.67	-	1.00	0.57
Fruit_AS	NS	*	**	-	-	-	0.79	1.48	NS
Total_Fruitset	**	**	NS	varPower	corExp	6.81	-	2.28	0.85
Fruitset_direct	**	*	NS	varExp	corExp	6.50	-	5.57	0.70
Fruitset_AS	*	*	NS	varExp	-	0.49	-	3.27	0.23

Significant G effect

Significant GxY effect

Significant G effect

The highest heritability values were estimated for variables related to flowering and fruiting behaviour

Ben Sadok et al. (submitted)

Linkage map construction with new microsatellites

94 new **Olive microsatellites** were developed: 54 Genomic and 40 EST (Essalouh et al. submitted)

SSRs were integrated into an existing genetic map of 'Olivière' x 'Arbequina' progeny (Khadari et al. 2010)

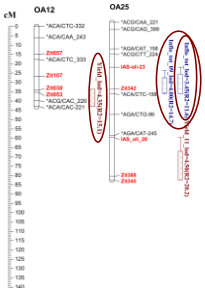
Maps	LG (no.)	Mapped Markers (no.)	SSRs (no.)	Mean LG size (cM)	Map Length (cM)	Average marker spacing (cM)	Maximum Gap	Observed genome coverage (%)
'Olivière'	25 (*34*)	212 (*197*)	68 (*34*)	69.81 (*61.3*)	1745.3 (*2210.2*)	8,23 (*11.2*)	32,5 (*48,5*)	77,9
'Arbequina'	21 (*31*)	252 (*191*)	75 (*30*)	76.07 (*63.4*)	1597.6 (*1966.2*)	6,34 (*10,3*)	30,8 (*40.4*)	83,8
Integrated	26 (42)	450 (436)	103(26)	82.63 (*91.0*)	2148.4 (*3823.2*)	4,77 (8,7)	30,5 (*81*)	86,9

'Olivière' x 'Arbequina' integrated map is the most saturated olive map developed so far with the largest proportion of mapped SSRs markers

Ben Sadok et al. (submitted)

QTL Mapping of flowering and fruiting traits

QTLs detected for **BLUP of genotypic effect** for either **yield or flowering and fruiting variables at GU scale** were mainly under allelic effects from '**Arbequina**' parent



2 QTLs were found for BLUP of genotype effect on Yield and Inflo_tot

Co-localisation: Inflo_tot and Inflo_tot_09
Significant correlation and high variance for Inflo_tot observed in 2009

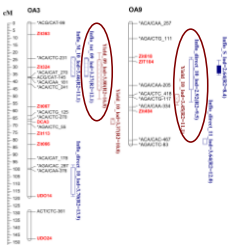
Ben Sadok et al. (submitted)

QTL Mapping of flowering and fruiting traits

Numerous QTLS were detected for all variables in a specific year

Co-localisation: **Yield** and **Fruit set** in the **two first production years**
+
Significant correlation between BLUP of genotype effect on **tree Yield** and **Number of fruits and Fruit set at GU scale**

A common genetic control between Fruit set and Yield



Co-localisation: **Yield** and **Flowering**

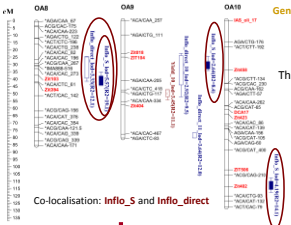
In 2010: the co-localisation concerns Inflo_direct

Vegetative growth could have **higher impact on yield** when tree is ageing and its branching decreases

Ben Sadok et al. (submitted)

QTL Mapping of flowering and fruiting traits

QTLS were detected for variables born on a specific position along GUs



Genotypic BLUP of number of inflorescences in specific positions

Three non-epistatic QTLs were mapped for Inflo_S

Co-localisation: **Inflo_S** and **Inflo_direct**

This suggests a common genetic control of flowering at local scale, probably at meristem scale.

Ben Sadok et al. (submitted)

Conclusion and perspective

Defining a phenotyping strategy
when during the olive tree ontogeny and at which observation scale, growth and branching traits are under genetic influence

Heritability values were high for architectural traits measured on **crown periphery during the 'stability phase'** of olive trees.

Account for the **morphogenetic factors** including **branching orders** and **years of growth** factors in a quantitative genetics approach during the **juvenile phase**

The maximal internode length could be interesting for selecting new cultivars with compact crown

A strong genetic control was highlighted for most flowering and fruiting traits
The reproductive development has a multigenic control

QTLs for Yield co-localized with QTLs detected for flowering and fruiting at GUs **when the number of lateral flowering GUs was the highest**
Young tree production for a giving year rely more on branching
(The number of flowering GUs rather than the number of inflorescences per GU)

Progenies showing interesting superiority in comparison to their parents with an increasing and regular production over years
Genetic progress can be performed in future selection programs
Additional years need to be investigated for bearing behaviour study
Trait combination between vegetative development, fruiting precocity and regularity
Validate their stability over time

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