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DOES OLIVE CULTIVAR ORIGIN AFFECT FLOWERING DATE?

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Abstract
Olive cultivars flower with a quite stable spring-warming heat sum and some of them are clearly non synchronous. We computed the correlation of flowering date with Euclidean distances of origin. This analysis was done on several cultivars in four common-garden experiments. Mantel test found association with geographical position of cultivar origin.

Keywords: *Olea europaea*, phenology, flowering time, adaptation.

Introduction

In *Olea europaea* L. (olive) flowering time is driven by winter chilling for removing dormancy and spring-warming for expression. The day of flowering (DOF) decreases as spring temperature increases (Alcala and Barranco, 1992). Several models, relying on pollen concentration, flower maturity and temperature records, have been developed to predict timing of flowering, based on temperature data series (Chuine *et al*., 1998, 1999; De Melo-Abreu *et al.*, 2004). Common garden experiments, for selecting suitable pollinators in partly self-sterile andromonoecious cultivars (CVs), have revealed a genetic variation of DOF, pointing out early- and late-flowering CVs. This variation seems mainly due to differences in chilling requirement among early or late CVs, whereas spring warming requirements were found less variable (De Melo-Abreu *et al.*, 2004). Flowering data recorded on the same CVs and site in different years allow testing the stability of DOF and the genetic or environmental effect on flowering time. Here we test the relative DOF in different environments and experiments by using datasets of CV collections from the literature. The objectives of this study were: i) to test the stability of DOF in different CVs; ii) to assess the genetic control of flowering time; iii) to test the relationship between DOF ranking and purported origin of CVs.

Materials and Methods

Meta-analysis of time series of DOF was conducted on datasets from four common garden experiments, which compared DOF of olive CVs in two or more years. The following dataset were used. FE: 20 CVs recorded in years 2000 and 2001. (Ferrara *et al*. 2002). FA: Six CVs in years 1999, 2000 and 2001 (Farinelli *et al*., 2002). BG: 18 CVs in years 1991, 1992, 1993 and 1994 (Bongi *et al*., 2002). AF: 54 CVs in years 1975 and 1978. As most datasets report starting and ending of flowering, the middle of this range was calculated and used as DOF. Calendar dates were transformed in day of the year (DOY).

In order to test the stability of flowering behaviour of olive CVs (early or late flowering) a mixed-effect model analysis (Bates *et al.*, 2011) was performed between DOF recorded in different years on the same set of CVs. In each comparison the colder year (later average DOF) was regressed against the warmer year (earlier average DOF). Meta-analysis was conducted using the R-project package lme4 (object type lmer) (Bates *et al*., 2011). A mixed-effect model was applied with a categorical variable, the experiments, and two years of observation on CVs as covariates. In order to test the influence of CV origin on flowering, Mantel test was conducted, using the R-project package ADE4 (Thioulouse *et al*., 1997), between the matrix of Euclidean distances among CVs based on DOF and other distance matrices based on geographic and ecological variables of the CV site of origin: geographical coordinates, bio-climatic range (Rivas-Martinez *et al*., 2004), elevation and distance from the sea.

Results and Discussion

Under the hypothesis of a strong genetic control of DOF, it is expected that early and late CVs behave in the same way across different years, with a temporal shift due to the difference in chilling and heat-sum between warm and cool years. In Fig. 1 such temporal shift is measured by the line intercept, whereas the line slope indicates a change in DOF range. The internal coherence of single experiments, as measured by regression, was not significant, especially for

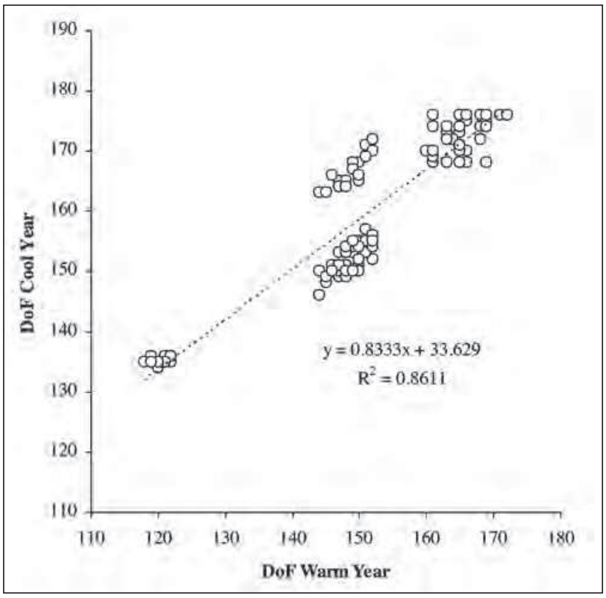

Fig 1 - Correlation between flowering date (DoF) of olive CVs in two different years. Pooled dataset from five experiments (see methods).

Tab. 1. General linear regression between flowering time of olive CVs recorded in different years from four common garden experiments.
*Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

Coefficient	Estimate	Std. Error	t value	P value
Intercept	61.45	9.37	6.56	***
slope	0.634	0.062	10.24	***

Tab. 2 - Mantel test with Monte Carlo sample between matrix of distance based on flowering time of olive CVs and other matrices of distance based on CV origin.

Variable	p null hypothesis	R^2 Mantel random
Coordinates	0.001 ***	0.123934
Bio-climate	0.014 *	0.03136143
Elevation	0.362	0.008427723
Distance from sea	0.716	-0.01636136

the experiments at the ends of DOF range. Middle clusters showed internal coherence, but resulted from serial observations. When data from several experiments were analysed together (fixed-effect model), the correlation between years was high (R^2 0.86) and highly significant (Fig. 1). Therefore, flowering time of olive CVs can be considered a stable trait under strong genetic control, provided that serial tagged sampling is applied. The experiments with high significance were done observing a labelled shoot repeatedly. The regression slope <1 (Tab. 1) suggests that the DOF range in cool years is shorter than in warm ones, contrary to common sense, but in agreement with evidence reported by Barranco *et al.,* (1994). Thus, a delay in flowering results in a shortened fertility period. This confirms the validity of a general flowering model based on cold induction and thermal sum, with parameters specific to each genotype.

Given the relatively stable flowering behaviour of olive CVs, we searched for possible ecological factors that could have contributed to the evolution of this phenology trait. Mantel test (Tab. 2) revealed a positive and highly significant correlation between flowering time difference and geographical distances. Correlation with difference in bio-climatic range was also significant, although the R^2 value was low. No significant correlation was found with elevation and distance from the sea.

Non symmetric correspondence analysis would eventually identify critical locations but these results (Tab. 2) demonstrates that DOF differences are minimal between CVs that are originated nearby. Flowering time directly affects cross fertilization among different olive CVs and appears non correlated to kinship but it is probably the result of human selection.

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