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Estimating the genetic value of F1 apple progenies for irregular bearing during first years of production

Jean-Baptiste Durand[1,2], **Baptiste Guitton**[3], **Jean Peyhardi**[2,4], **Yan Holtz**[5], **Yann Guédon**[2], **Catherine Trottier**[4] and **Evelyne Costes**[3]

[1]*Grenoble University, Laboratoire Jean Kuntzmann, BP53, F-38041 Grenoble Cedex 9, France,* [2]*CIRAD/Inria, Virtual Plants Team, UMR AGAP, F-34095 Montpellier, France,* [3]*CIRAD, UMR AGAP, F-34398 Montpellier, France,* [4]*Institut de Mathématiques et de Modélisation de Montpellier, Université Montpellier 2, F-34095 Montpellier, France,* [5]*INRA, AFEF Team, UMR AGAP, F-34398 Montpellier, France*

**correspondence:* jean-baptiste.durand@imag.fr

Highlights: Flowering regularity in apple trees during the beginning of their mature phase was assessed using new descriptors based on annual yields. These descriptors were approximated using subsamples of annual shoot sequences at axis scale to allow genotype evaluation at reasonable sampling costs. The approximation provided a good discrimination between regular and alternate bearing genotypes. QTLs were detected for some descriptors.

Keywords: alternation indices, biennial bearing, breeding, linear mixed model, *Malus x domestica*, QTL detection.

INTRODUCTION

Because irregular bearing generates major agronomic issues in fruit-tree species (Monselise and Goldschmidt, 1982), particularly in apple, the selection of regular cultivars is desirable. Here, we aimed at defining methods allowing an early diagnostic in populations segregating for bearing behaviour.

It was shown by Guitton *et al.* (2012) that biennial bearing is inheritable and segregates in an apple progeny ("Starkrimson"× "Granny Smith"), suggesting that selecting new varieties with intrinsic regular bearing is a possible strategy. However, breeding programs for fruit-tree species do not consider this trait yet, because it requires flowering observations over several years before its value for a given genotype can be assessed (and the first flowering occurs two to four years after grafting). Development of methods for a faster diagnostic of the bearing tendency of a genotype during its first years of production is thus highly desirable.

The Biennial Bearing Index (BBI) has been widely used to quantify biennial bearing at different scales (Wilcox, 1944): whole areas, individual trees or branches - on apple and other fruit trees. Huff (2001) highlighted that the distribution of BBI strongly depends on the mean and variance of yields, under the hypothesis that they are a random sample. Therefore, the accepted interpretation of BBI as a measure of the magnitude of irregular bearing is questionable. Moreover, it has been shown by Pearce and Dobersek-Urbane (1967) that using BBI on trended series may lead to confound alternation and trend. The observation that yield is subject to a progressive increase in the first years of tree production, motivated our research for new descriptors of alternation. With the aim to dissociate yield increase from bearing pattern, we investigated a new modelling approach incorporating a trend term for yearly yields, and terms representing dependencies and amplitudes of successive deviations from the trend. Our expectation was to distinguish the genotype bearing behaviour applying clustering methods on these new descriptors. To avoid measuring yearly numbers of flowers at tree scale, we also investigated the possibility of early discrimination between genotypes, based on the same descriptors, using samples of successive annual shoots (AS) at axis scale. Finally, from the analysis of correlations between descriptors at both tree and AS scales we explored how fruiting behaviour at tree scale may be obtained from that at axis scale.

MATERIALS AND METHODS

A segregating population obtained from a cross between 'Starkrimson' and 'Granny Smith' (Guitton *et al.*, 2012), was used. One or two tree replicates were available for each of the 120 genotypes composing the population. Flowering recurrence was measured at two scales: whole tree and AS scales. The total number of inflorescences per year and tree was observed from the 2nd to the 7th year after grafting. At AS scale, the

succession of vegetative v. floral AS over the same consecutive years were observed along different types of axes: trunk, long and short axillary shoots. Long axes were scaffolds chosen as similar as possible along the trunks. The data consisted of 2- to 6-year sequences of AS, with 4 to 45 sequences per genotype.

Let $T_{g,r}$ denote the number of years of growth of tree replicate r of genotype g and $Y_{g,r,t}$ its number of inflorescences at year t. A Gaussian linear mixed regression model with first-order autoregressive errors (to model the serial correlations between successive residuals) was used

$$Y_{g,r,t} = \beta + \beta_g + (\alpha + \alpha_g + \xi_{g,r})t + \varepsilon_{g,r,t} \quad (1), \quad \varepsilon_{g,r,t} = (\gamma_g + \gamma_{g,r})\varepsilon_{g,r,t-1} + u_{g,r,t} \quad (2).$$

Here, (1) is a trend sub-model, and the first-order autoregressive process (2) on the deviations $\varepsilon_{g,r,t}$ between $Y_{g,r,t}$ and the trend (Fig. 1) quantifies the alternation through the dependencies between successive residuals (measured by γ_g). Their amplitudes were quantified using a BBI-like index on $\varepsilon_{g,r,t}$, normalized by mean yields, defined as

$$\text{BBI_res_norm} = \frac{\left(\sum_r \sum_{t=2}^{T_{g,r}} \left|\hat{\varepsilon}_{g,r,t} - \hat{\varepsilon}_{g,r,t-1}\right|\right) / \sum_r (T_{g,r} - 1)}{\left(\sum_r \sum_{t=1}^{T_{g,r}} Y_{g,r,t}\right) / \sum_r T_{g,r}}.$$

A clustering of the genotypes based on BBI_res_norm and γ_g was obtained using a Gaussian mixture model and the Bayesian information criterion to select the number of clusters (Bishop 2006, Chap. 4 and 9). The ability to retrieve the genotype bearing behaviour (or *class*) from the subsample of AS sequences was assessed by approximating BBI_res_norm and γ_g by their values in the subsamples (leading to two indices referred to as BBI_res_norm_loc and γ_{loc}, respectively). Two other kinds of descriptors computed at AS scale were also used to predict the bearing behaviour: an index of synchronism in flowering based on entropy (Bishop, Chap. 1) and a 2nd-order Markov chain with memory × genotype and memory × year interactions.

Five descriptors, namely BBI_res_norm and γ_g at tree scale, and BBI_res_norm_loc, γ_{loc} and entropy at AS scale, were used for QTL detection which was performed using the STK×GS consensus genetic map (Guitton *et al.*, 2012) and MapQTL® 5.0. (Van Ooijen, 2004), with 4.0 as LOD score threshold for all traits.

RESULTS AND DISCUSSION

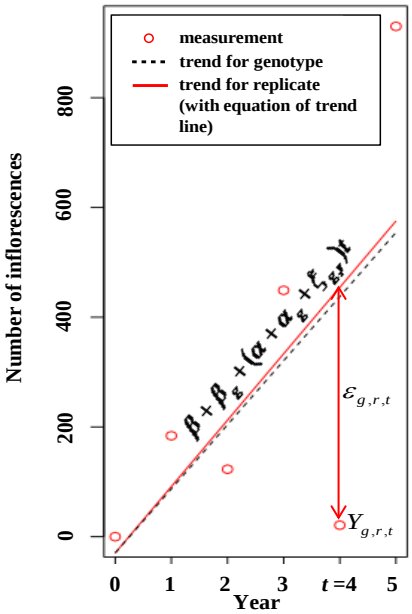


Fig. 1. Data, trend model and residuals for total yields at tree scale for a biennial bearing genotype (γ_g = -0.88, BBI_res_norm = 1.21)

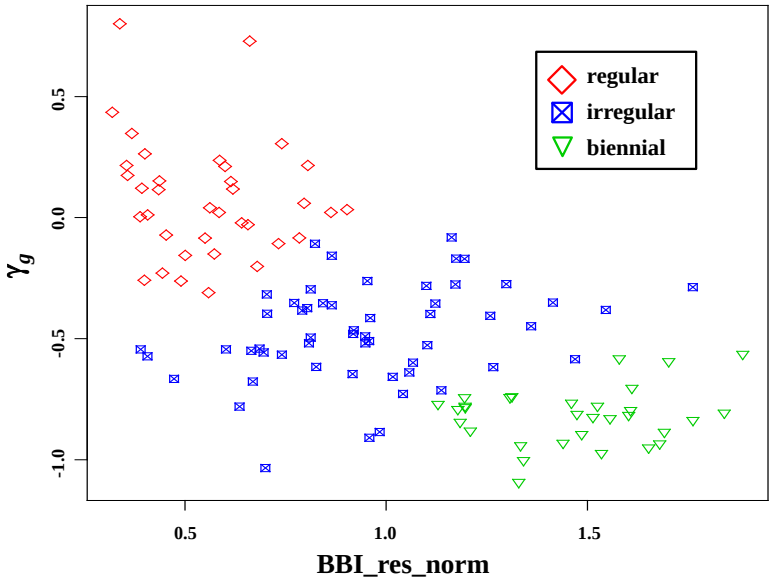


Fig. 2. Clustering obtained using a 3-component Gaussian mixture using BBI_res_norm (x-axis) and γ_g (y-axis). Cluster 1 can be interpreted as regular bearing genotypes, cluster 2 as biennial bearing genotypes and cluster 3 as irregular bearing genotypes.

The clustering obtained using the descriptors at tree scale BBI_res_norm and γ_g highlighted three clusters (Fig. 2). Cluster 1 is characterized by a low BBI_res_norm (low dispersion of yields around trend) and unstructured residuals ($\gamma_g \approx 0$ in (2)); thus, it is interpreted as regular genotypes. Cluster 2 is characterized by a high BBI_res_norm (high dispersion of yields around trend) and residuals with alternate signs (γ_g close to -1), and is interpreted as biennial bearing genotypes. The genotypes in cluster 3 have intermediate values and are interpreted as irregular.

The genotypes have the following behaviours at AS scale, depending on their cluster: genotypes in cluster 1 have high entropies (0.38 on average) (i.e. high uncertainty), which corresponds to asynchronous and irregular flowering at AS scale. The transition probabilities of the Markov chain highlight a higher probability of these genotypes to flower in year *t* after flowering in year $t-1$, and a higher probability to flower in 2009, which is an "off" year for the majority of biennial bearing genotypes (even years being "on" years, on the contrary). Genotypes in cluster 2 have low entropies (0.23 on average), which corresponds to synchronous and well-predictable flowering at AS scale. An AS preceded by a flowering AS in year $t-1$ and a vegetative AS in year $t-2$ has a lower probability to flower in year *t*, and any AS has a lower probability to flower in 2009. Genotypes in cluster 3 have high entropies (0.38 on average), and intermediate probabilities of AS to bear flowers during successive years or in 2009. Comparison of the genotype behaviours at AS and whole tree scales highlights that in the available progeny, regularity comes from the combination of irregular axes and asynchronism, whereas alternation comes from the combination of alternate axes and synchronism.

A clustering was also performed using the descriptors at AS scale, to assess whether the clusters approximate those obtained from descriptors at tree scale. Two confusions occurred between regular and alternate bearing genotypes, and 44 confusions occurred between irregular and both other clusters of genotypes. The other 69 genotypes were correctly classified. As a consequence, regular and biennial bearing genotypes are well discriminated from their behaviour at AS scale, whereas irregular genotypes are poorly discriminated. Thus, we can propose that breeders (i) progressively suppress biennial or irregular genotypes after the first observation of a large decrease in flowering during the beginning of the mature phase (ii) confirm the regular fruiting behaviour of the pre-selected genotypes during the stable mature phase.

Five QTLs altogether were identified in four separated genomic regions, and explained from 13.5 to 22.5% of the genetic variability. At tree scale, two QTLs were found for BBI_res_norm on LG1 and LG8 (LOD 6.69 and 5.82, respectively) and no significant QTL was detected for genotype AR coefficient γ_g. At AS scale, one QTL was mapped for BBI_res_norm_loc on LG8 in the same region (LOD 5.74) than the QTL mapped for BBI_res_norm at tree scale. Two QTL were also detected for γ_{loc} on LG11 and LG14 (LOD 7.24 and 4.55, respectively). By contrast, no QTL was detected for the entropy.

QTLs mapped on LG1 and LG8 corroborate zones that have been identified in a previous study (Guitton *et al.*, 2012). The QTL cluster on LG1 seems to be linked to the antagonist relationship between fruit production and inflorescence initiation in a same year, as reported by Bangerth (2009). The two QTL revealed on LG11 and LG14 for γ_{loc} are located on zones that were not previously associated to flowering or bearing traits in this progeny. Further exploration of these genomic regions is required to interpret precisely which mechanism could underlie these associations. The absence of QTL detection for other descriptors, especially γ_g at tree scale and entropy at AS scale, may be due to the population size. Indeed, 120 individuals can be limiting to detect QTL with small effects (Bernardo, 2004) and only major QTLs (explaining more than 13% of the trait variance) were confirmed in the present study. However, it may be noticed that the QTLs detected in the present study do not depend on year effects but rather are associated to genotype bearing behaviour over years.

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