Influence of the genetic variation of branching during early growth on light interception efficiency of apple trees: a modelling study with MAppleT

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Highlights: Light interception is a key parameter to optimise fruit tree production. Assuming that genetic variability of branching along trunks impacts tree development, total leaf area and light interception in the consecutive years, we estimated STAR values on 1 to 5 years old simulated apple trees. We analyse the relative impact of proleptic and sylleptic shoots, and depending on their length category on STAR variance.

Keywords: STAR, Modeling, Leaf Area, Branching, Sensitivity analysis, *Malus x domestica*

INTRODUCTION

The architecture of a tree has an impact on light interception, water transport and transpiration as well as carbon acquisition and allocation. Therefore, the optimisation of tree architectures is desirable in fruit tree culture to improve fruit production in quantity, regularity and quality. For apple tree, most architectural traits vary genetically, particularly during the first years of tree life (Segura *et al.*, 2008). However, it remains difficult to integrate these traits in breeding programs, because their values change during tree development (Laurens *et al*., 2000). Considering the complexity of apple tree architecture over years of growth and the large number of trees required for quantitative genetics studies, it is not convenient to grow and measure phenotypes in the field especially at fine scales. For that reason, we rely on modelling strategies (DeJong *et al*., 2011) as well as environmental simulation tools to perform computer-based virtual experiments.

Our strategy makes use of MAppleT, i.e. Markov Apple Tree, a FSPM which simulate apple tree topology and geometry for Fuji cultivar (Costes *et al*., 2008). The light interception of the simulated trees was estimated using MµSLIM, namely Multi-Scale Light Interception Model, included in OpenAlea (Da Silva *et al*., 2008). This research aims at demonstrating that a sensitivity analysis could be used to investigate the impact of the known genetically variable architectural traits on light interception efficiency. In a previous study, we analysed the impact and interactions of a limited number of geometrical traits on the whole tree light interception (Han *et al*., 2012). The contribution of the stochastic part of Markov models to the total variance of the output was also examined and was particularly low. Here, we complemented our approach by considering the variation in the trunk first annual shoot branching of the same apple hybrids, and examining the variability induced on light interception, when 5 years old (yo).

MATERIALS AND METHODS

The tree simulations were initiated with trunks sequences previously observed within a segregating population of apple hybrids (Segura *et al.*, 2008). Different axillary shoots types were considered: in the first year of growth, each axillary bud could develop immediately into a sylleptic shoot or remain latent until next budbreak when they could develop into proleptic shoots, or still remain latent. Both sylleptic and proleptic shoots could be short, medium or long. A sample of initial (1yo) and resulting final (5yo) simulated tree architectures are shown in Fig.1. The number of sylleptic and proleptic shoots in each category along the 1yo trunks was considered and divided by the corresponding annual trunk length, in order to express a branching density. All the other parameters of the model were kept with default values (Costes *et al*., 2008). In particular, the Markov models estimated for Fuji cultivar were used to simulate the type of growth unit and axillary shoots developed from each bud, either terminal or axillary, in the consecutive years. The simulated trees thus differed only because of the different initial branching sequences.

For light interception efficiency evaluation, the Silhouette to Total Area Ratio (STAR) (Oker-Blom and Smolander, 1988), was used. The STAR of a whole tree, for one direction, is the ratio of its Projected Leaf Area (PLA) to its Total Leaf Area (TLA) . For the light environment simulation, the diffuse mode available in MµSLIM was used to simulate the radiance of an overcast sky. The integrated STAR value was obtained by averaging the STAR from 46 directions with weighting coefficients derived from the standard overcast sky radiance (Moon and Spencer, 1942). The virtual experiments covered five years growth of a set of 111 trees and the whole tree STAR was calculated on June 30 of each year.

For investigation of our model response, we preferred a metamodelling approach (or response surface modelling) rather than sensitivity analysis methods based on eFAST or Sobol (Slatelli *et al.*, 2000), because

$$STAR_i = \sum_k f_k(X_{k,i}) + \varepsilon_i$$

the latter options require much higher number of simulations. Among metamodelling approaches, a Generalized Additive Model (GAM) (Wood, 2006) was used, by which STAR was viewed as an additive sum of nonparametric functions of each input parameter:
where *k* is the number of parameters *X* for tree *i* and ε is its residual error term.
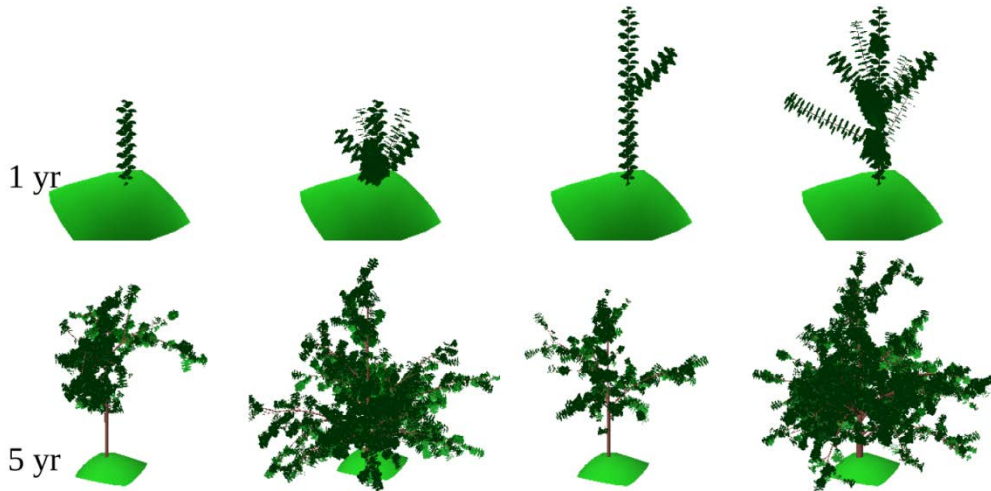

Fig. 1. Visualization of simulated apple tree architectures. These sample architectures were produced by MAppleT with different branching sequences for the trunk first annual shoots.

RESULTS AND DISCUSSION

The TLA of the simulated trees increased rapidly in both mean and variance, from the first to the fifth year of growth (Fig. 2.), with a stabilization of variance in the fifth year. By contrast, the STAR values decreased, and then stabilized in both mean value and variance in the fourth and fifth years, with a variance notably smaller than that observed in TLA.
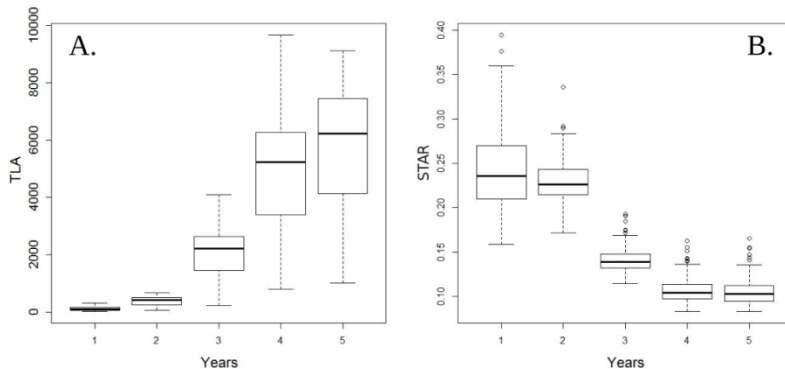

Fig. 2. Mean values and variation of simulated TLA and STAR values for 111 apple trees from 1 year to 5 years.

The prediction of STAR values with GAM model was performed for two specific combinations of input parameter values. First, the number of proleptic and sylleptic laterals per unit length was considered. The approximate effects on STAR revealed significant influences of proleptic shoots in the second year of growth, whereas the effect of sylleptic shoots was the highest in the first year of growth and remained significant until the fifth year (Table 2. left). The estimated GAM explained 76.14% to 22% (adjusted R²) of the total variation of STAR values. Fluctuations in shape of the output variable responses are revealed by the value of estimated degree of freedom (edf). Second, the number of each type of sylleptic (long, medium and short) per unit length was considered. All showed significant effects in the first year, long and medium sylleptics continued their significance in the second year, and only long sylleptics remained significant in the consecutive years (Table 2. Right). The estimated GAM explained 78.2% of the total variation of STAR values in the first year of growth and then decreased to approximately 30%. The function of STAR responses to long sylleptic shoots had the highest edf value, indicating a higher number of fluctuations.

Thus, branching along the first annual shoot of the trunks enhances the variability in tree architecture and

TLA. However, when reaching year 4 or 5, the STAR values show small variance despite of the high variance of TLA which is the STAR normalizing term. This suggests a light interception optimization within trees showing lower TLA and a threshold of efficiency that is not overcome by the sole increase of leaf area. In terms of carbon capture efficiency, even though the gross photosynthesis increases with TLA, it is actually more related to PLA and therefore the photosynthesis per unit leaf area is more likely to follow STAR pattern.

Table 2. Approximate effects of the input parameters on STAR values with a GAM. Input variables were the number of sylleptic (s) and proleptic (p) shoots per unit length $(.l^{-1})$, for the left table and the three types of sylleptic shoots, long (sl), medium (sm) and short (ss) per unit length $(.l^{-1})$, for the right table.

Years		edf	F	p-value		R²	Years		edf	F	p-value		R²
1	$s.l^{-1}$	4.41	59.36	<2e-16	***	76.1	1	$sl.l^{-1}$	5.52	22.38	<2e-16	***	78.2
	$p.l^{-1}$	2.70	1.61	0.18				$sm.l^{-1}$	1.00	18.52	3.89e-05	***	
								$ss.l^{-1}$	2.54	3.67	0.0129	*	
2	$s.l^{-1}$	1.52	23.26	7.77e-09	***	32.3	2	$sl.l^{-1}$	2.01	5.97	0.00167	**	33.0
	$p.l^{-1}$	1.00	6.90	0.009	**			$sm.l^{-1}$	1.00	10.12	0.00192	**	
								$ss.l^{-1}$	1.00	0.34	0.55609		
3	$s.l^{-1}$	1.12	17.90	1.19e-05	***	17.1	3	$sl.l^{-1}$	2.12	6.83	0.000529	***	24.5
	$p.l^{-1}$	1.00	0.47	0.49				$sm.l^{-1}$	1.00	0.80	0.370685		
								$ss.l^{-1}$	1.00	1.01	0.315264		
4	$s.l^{-1}$	1.88	12.28	4.25e-06	***	22.6	4	$sl.l^{-1}$	2.37	10.04	7.89e-06	***	32.6
	$p.l^{-1}$	1.00	0.09	0.76				$sm.l^{-1}$	1.00	0.51	0.475		
								$ss.l^{-1}$	1.00	1.55	0.216		
5	$s.l^{-1}$	1.89	12.33	3.84e-06	***	22.6	5	$sl.l^{-1}$	2.49	10.72	2.42e-06	***	34.3
	$p.l^{-1}$	1.00	0.05	0.82				$sm.l^{-1}$	1.00	0.43	0.510		

Here, the GAM approach was selected because of its robustness with correlated variables, like the different types of sylleptic shoots. However it does not take into account the interactions between variables, and further study using variable selection (Wood, 2006) would certainly allow a more refined analysis. Comparing the present results with those obtained in Han *et al*. (2012) highlights a higher impact on STAR when varying organ geometry than early branching. This may be due to the repeated occurrence of individual organs over the years whereas the topology has a declining effect linked to tree ontogeny. Even though the improvement of light penetration within tree canopies has been a constant objective of fruit tree architecture manipulation through the setting up of training systems (Willaume *et al.*, 2004), breeding and genetic selection could open new avenue for light interception optimization, and could be more efficient for saving time, labour and resources than yearly topology manipulation through pruning.

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