Genotypic Differences in the Leaf Emergence Rate of Young Peach Trees

Jocelyne Kervella¹, Loïc Pagès², and Michel Génard²

Institut National de la Recherche Agronomique, Domaine Saint-Paul, F-84143 Montfavet cedex, France

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Abstract. Leaf emergence was studied on main and first-order shoots of peach and nectarine [*Prunus persica* (L.) Batsch.] trees belonging to nine standard cultivars, during their first growing season. The number of emerged leaves was recorded on main shoots (originating from the grafted buds) and on first-order shoots (inserted directly on main shoots). Similarly shaped leaf emergence curves were observed on main and first-order shoots for all the cultivars. Leaf emergence rate decreased gradually as the number of leaves increased. The number of emerged leaves could be modeled as a monomolecular function of accumulated thermal units. Significant differences were found between cultivars in a multiple analysis of variance of the model parameters, for main and first-order shoots. The ranking of the cultivars was similar for both types of shoots. Leaf emergence rate was lower on first-order shoots than on main shoots. Differentiating between shoot types is necessary for a reliable comparison of genotypes.

Leaf emergence observation is useful to quantify growth and development. Leaf emergence is a component of the dynamics of leaf area and therefore of plant growth. The number of leaves is also an indirect count of the number of metamers (set of node, internode, leaf, and axillary bud, as defined by White, 1979). As such, it may be used to characterize development stages (Snyder and Bunce, 1983). For example, leaf number on the main shoot at a given date may be related to potential tillering at that date in wheat and barley (Baker et al., 1986; Kirby et al., 1985b; Klepper et al., 1982) or to first flower appearance in soybean (Yourstone and Wallace, 1990a). For these reasons, leaf emergence has been studied by many workers on annual crops such as wheat, barley, maize, soybean, and bean. A better knowledge of tree leaf emergence would also be of interest in many fields such as tree growth, fruit quality or pathology, as underlined by Eisensmith et al. (1980). However, studies on trees in general, and on fruit trees in particular are much fewer.

The influence of environmental conditions on leaf emergence rate is well documented on annual crops. Temperature appears to be the main environmental factor determining leaf emergence rate. Response of leaf emergence rate is curvilinear when studied over a wide range of temperatures (Cao and Moss, 1989a; Warrington and Kanemasu, 1983). However, leaf emergence rate is often approximated as null below a base temperature (T_b), linearly dependent on temperature between T_b and an optimal temperature (T_{opt}), and constant above T_{opt} (Baker et al., 1986; Bauer et al., 1990; Cao and Moss, 1989a; Hodges and Evans, 1992), since the decrease of leaf emergence rate is weak except for very high temperatures (Warrington and Kanemasu, 1983). Accumulated thermal units are computed using this approximation.

Daylength also influences leaf emergence rate, but to a lesser extent than temperature (Cao and Moss, 1989b). Leaf emergence rate increases with increasing daylength (Volk and Bugbee, 1991; Yourstone and Wallace, 1990b). Response to daylength increase is curvilinear and is generally greater for low initial daylength.

Water, nitrogen supply, or CO₂ concentration may alter leaf emergence, but these are also minor effects compared to those of temperature, except in case of severe water stress, very low nitrogen supply (Bauer et al., 1984; Longnecker et al., 1993; Snyder and Bunce, 1983), or CO₂ concentrations much higher than usual (Baker et al., 1989).

Leaf emergence rate expressed vs. thermal time is generally considered as constant in constant environmental conditions, but changes have sometimes been reported. Some have been correlated with developmental changes such as double ridge formation for wheat (Baker et al., 1986; Cao and Moss, 1991), flowering (Hoogenboom et al., 1987), or pod set (Sinclair, 1984a) for soybean. A steady decrease of leaf emergence rate with thermal time has been reported by Wilson (1976) for *Panicum maximum*, Pagès et al. (1993) for peach tree, and Schultz (1992) for grapevine, whereas Yourstone and Wallace (1990a) observed an increase of leaf emergence rate for soybeans.

Shoot type may affect leaf emergence rate. Higher leaf emergence rates have been observed on main shoots than on tillers for wheat and barley (Kirby et al., 1985b). These differences are not constant (Klepper et al., 1982). They might be greater in limiting environments (Longnecker et al., 1993).

Genotypic differences for leaf emergence rate have been evidenced in several studies [Ceulemans et al., 1988 (*Populus*); Baker et al., 1986 (wheat); Hodges and Evans, 1992 (maize); Yourstone and Wallace, 1990b (soybean)], but they do not affect greatly T_b and T_{opt} , which may be considered as constant within a given species. Cao and Moss (1989a) found slight genotypic differences for optimal temperatures which ranged respectively from 21.3 to 24.3°C in wheat and from 20.1 to 21.8°C in barley genotypes. Volk and Bugbee (1991) showed that a model assuming the same optimal temperature for all cultivars and differences in response to temperature variations would fit reasonably well their data. Base temperatures could also be approximated as constant for all cultivars in wheat (Kirby et al., 1985a) and soybean (Sinclair, 1984b).

Our objective is to describe genotypic differences of growth and development characteristics among standard peach and nectarine cultivars (Kervella et al., 1994) for breeding purposes. In this study, we investigated genotypic differences for leaf emergence rate. We compared cultivars grown outdoors, in well irrigated and fertilized conditions, where water stress or nutrient deficiency were not likely to affect leaf emergence. To compare genotypes, we studied leaf emergence on two types of shoots: main shoots

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¹Station de Recherches Fruitières Méditerranéennes.

²Unité de Recherches en Ecophysiologie et Horticulture.

issuing from the grafted buds, and first-order shoots directly inserted on main shoots. We modeled the number of emerged leaves on individual shoots as a function of accumulated thermal units. We could then rank cultivars according to their leaf emergence patterns and study the relation between those patterns and final characteristics of shoots.

Material and Methods

Four peach ('Flavorcrest', 'Redwing', 'Royal Glory', and 'M 1339') and five nectarine ('Armking', 'Silver Gem', 'Flavortop', 'Snowqueen', and 'Fairlane') cultivars were studied (Table 1).

All cultivars were chip-budded in March 1992 on 1-year-old seedlings of peach rootstock 'GF 305' and potted in 50-liter containers in a 3 peat : 1 sand mixture.

They were grown outdoors in Avignon in a wind-protected area, fertigated with a 12N-9P-34K nutrient solution and left unpruned. Plant diseases and pests were controlled chemically when necessary and resulted in minor damage. Damaged shoots were discarded from observation.

Leaves at the unfolded stage (two parts of the blade unstuck) were counted twice a week from 30 Apr. to 4 Aug. and then once a week till leaf emergence had stopped on all shoots, on 29 Sept. This integer counting of emerged leaves is less accurate than plastochron index or Haun's scale, but it avoids handling of young leaves which might damage them and alter their growth. In addition, because of great variations in final leaf length (2 to 20 cm) during the growing season, a developmental reference stage seemed more adequate than a length-based reference stage.

The number of emerged leaves was counted on main shoots and on all the first-order shoots of a subsample of three to nine trees (Table 1). Among first-order shoots, short shoots, with very few leaves and internodes that do not elongate, could be clearly distinguished as in Pages et al. (1993). These short shoots were not taken into account in the analysis. The final length of main shoots was also recorded.

Hourly air temperatures were recorded by the Bioclimatology station of the INRA Research Center of Avignon-Montfavet, located about 200 m from the experimental area.

To approximate the curvilinear response of leaf emergence rate to temperature variations, daily thermal units (*tu*) were calculated from hourly air temperatures (Th_i) as $tu = \sum_{i=1}^{24} (Th_i - T_b)/24$, where Th_i is replaced by T_{opt} if it is higher than T_{opt} .

Thermal units were computed for a range of T_b (between -2 and

4C) and T_{opt} (between 20 and 30C) values. The coefficient of correlation between leaf number increase and thermal unit accumulation at successive observation dates varied little over those ranges of T_b and T_{opt} values.

The values 0C for T_b and 26C for T_{opt} , which corresponded to the highest value of the coefficient of correlation, were retained for further analysis. Daily thermal units were summed from budding date to compute the accumulated thermal units (*Tu*) at each observation date.

As detailed in the Results, the number of leaves did not increase linearly with accumulated thermal units. A nonlinear function was chosen to model the number of emerged leaves. The nonlinear regression model was fitted separately for each main shoot, using least-square estimators.

The patterns of leaf number curves for all the first-order shoots of one tree, were related. A model taking into account those relations was fitted globally for all the first-order shoots of each tree, again using least-square estimators.

Because of the lack of independence between successive measurements on the same shoot, traditional statistical analysis is not appropriate to compare growth curves. Direct comparison of parameters may also be misleading because of correlations between the estimators of the parameter values: curves with close parameter values may differ notably and parameter values for close curves may be quite different.

To compare genotypes, we applied the method proposed by Yourstone and Wallace (1990b). The parameters of the fitted models were analyzed as dependent variables in a multiple analysis of variance (MANOVA), which takes into account the correlations between parameters.

Canonical variates (i.e., linear combinations of the initial variates for which between-cultivar differences are maximal compared to within-cultivar differences) were then computed for each tree. These canonical variates were used to compare the results for main and first-order shoots and to study the relation between final number of leaves, final length, and leaf emergence rate of cultivars.

Results

In the growing conditions of our experiment, grafted buds developed into vigorous shoots, that branched profusely.

The increase of the emerged leaves number with accumulated thermal units was curvilinear on main shoots, as illustrated for cultivars 'Armking' and 'Silver Gem' (Fig. 1). Leaf emergence

Table 1. List of peach and nectarine cultivars studied.

Cultivar	Abbreviation ²	Ripening date	No. of main shoots studied	No. of first-order shoots studied
<i>Peach</i>				
Royal Glory	R _y	17 July	3	88 (3) ³
Redwing	Rw	20 July	3	107 (3)
Flavorcrest	Fc	21 July	23	273 (8)
M 1339	M 9	11 Aug.	4	122 (4)
<i>Nectarine</i>				
Armking	A k	25 June	23	343 (9)
Snowqueen	Sq	4 July	5	146 (5)
Silver Gem	Sg	25 July	24	232 (8)
Flavortop	Ft	30 July	3	124 (5)
Fairlane	F1	29 Aug.	4	134 (5)

²Abbreviation of cultivar name used in Fig. 3.

³Number of trees on which first-order shoots were studied.

Fig. 1. Leaf emergence curves of individual main shoots from 'Armking' and 'Silver Gem'.

Fig. 2. Leaf emergence curves for sample of first-order shoots from one 'Armking' and one 'Silver Gem' trees

rate decreased steadily from the beginning to the end of the growing season. Within each cultivar, variations were found between trees. In most cases leaf emergence rate decreased more slowly for trees with low initial leaf emergence rate. Such compensations resulted in very similar numbers of emerged leaves for all the trees of a given cultivar by the end of the growing season.

To represent the decrease of leaf emergence rate and the compensations observed, the number of emerged leaves N may be modeled as a monomolecular function of accumulated thermal units:

$$N(Tu) = A[1 - e^{-R_0(Tu - T_0)/A}] \quad [1]$$

where A is the asymptotic values of the number of leaves, R_0 is the initial leaf emergence rate, T_0 is the date (expressed in accumulated thermal units) at which development starts.

Leaf emergence rate, which is obtained by deriving Eq. [1], is therefore $dN/dTu = R_0 e^{-R_0(Tu - T_0)/A}$.

Thus, when Tu increases, leaf emergence rate decreases, and for a given A it decreases more slowly if R_0 is low.

This model fitted the data very well, and coefficients of determination R^2 of number emerged leaves vs. accumulated thermal units for individual trees ranged from 0.993 to 0.999.

Curves of first-order shoots were similar in shape to those of main shoots (Fig. 2). On first-year peach trees, first-order shoots appear at dates widespread over the entire growing season. On a given tree, curves of the number of emerged leaves plotted vs. accumulated thermal units for late first-order shoots could be derived from curves for earlier shoots by a downward translation (Fig. 2). Leaf emergence rates of all first-order shoots of one tree were almost equal at any given date. Therefore, the number of emerged leaves N_j of first-order shoot j grown on tree k could be modeled as $N_j(Tu) = A_k [1 - e^{-R_{0k}(Tu - T_{0k})/A_k}] + C_j$ where C_j is a constant specific to shoot j , such that $N_j(T_{0j}) = 0$, if T_{0j} is the date at which shoot j starts growing, A_k , R_{0k} are parameters similar to those of main shoots for an hypothetical first-order shoot appearing at T_{0k} accumulated thermal units on tree k .

It follows that for any shoot j belonging to tree k ,

$$N_j(Tu) = A_k e^{R_{0k}(T_{0j} - T_{0k})/A_k} [1 - e^{-R_{0k}(Tu - T_{0j})/A_k}] \quad [2]$$

T_{0j} was derived from observation. From Eq. [2], a three-parameter (A_k , R_{0k} , T_{0k}) model was fitted globally for all the first-order shoots of each tree using least-square estimators.

Again, this model fitted the data very well. R^2 exceeded 0.900 for 94% of the 1569 axes studied.

Cultivar differences were highly significant for main shoots (Table 2). There was a close correlation between first canonical variates for both branching orders (Fig. 3), indicating related patterns of leaf emergence for both types of shoots (Fig. 4). Leaf emergence rates were consistently lower for first-order shoots than for main shoots.

First canonical variates were highly correlated ($R = 0.929$, $P = 0.00003$) with final number of emerged leaves on main shoots. They were also correlated with final main shoot length ($R = 0.874$, $P = 0.005$). However, some discrepancies were found in the rankings of genotypes according to final length of main shoots and leaf emergence curves. Thus 'Silver Gem' and 'MI339' exhibited similar intermediate leaf emergence curves, but 'Silver Gem' main shoots, averaging 1.10m of final length, were not much longer than those of 'Fairlane' (1.04 m), which had the lowest leaf emergence rate, whereas 'MI339' main shoots were nearly as long (1.36 m) as those of 'Armking' (1.40 m), which had the highest leaf emergence rate.

Table 2. Multivariate analysis of variance for the parameters models on main and first order shoots.

	df		SSCP ^z		WILKS criterion
<i>Main shoots</i>					
Genotype	8	41.6522	20.1784 13.5387	36.5875 14.9143 45.3027	0.112***
Residual	84	47.2833	5.10583 67.7611	0.97407 -45.6851 42.5703	
<i>First-order shoots</i>					
Genotype	8	12.28255	-14.9669 20.4498	4.42783 -5.28023 3.95848	0.467*
Residual	42	36.7174	-27.1081 28.5502	14.5765 -12.1490 45.0415	

^zSum of squares and cross product matrix.*,***Significant at $P = 0.05$ or 0.001 , respectively. Fig. 3. Relationship between genotype averages of first canonical variates (CV₁) for main and first-order shoots. Abbreviations of cultivar names are given in Table 1.

Discussion

Shapes of leaf emergence curves were similar for all the cultivars tested, as confirmed by the good fitting of the non-linear models for most shoots. These shapes are characterized by a steady decrease of leaf emergence rate with thermal time. This decrease is not explained by daylength decrease, since daylength increased from the first to the 16th observation (at 1115 accumulated thermal units) and decreased only thereafter.

With the function used to model the number of emerged leaves

as a function of accumulated thermal units, leaf emergence rate can be expressed as $dN/dTu = R_0(1 - N/A)$.

Therefore with this model, the predicted leaf emergence rate decreases linearly with the number of emerged leaves. A negative relation between leaf emergence rate and the number of leaves already produced has been reported by Wilson (1976) in grass. This relation would be consistent with other experimental results which show that, in given environmental conditions, leaf emergence rate is higher for plants having produced fewer leaves, either because they have been sown later (Kirby et al., 1985a) or because they have been grown in shorter daylength (Cao and Moss, 1989b). Genotype could determine the regulatory effect of the number of emerged leaves on leaf emergence rate in given environmental conditions.

This does not mean that the number of leaves produced at the end of the growing season is only cultivar-dependant. Experimental results on the final number of shoots for various sowing dates (Kirby et al., 1985a) or levels of nitrogen supply (Longnecker et al., 1993) show that environmental conditions may also influence the final number of leaves.

Quantitative differences in the dynamics of leaf emergence were found among the cultivars studied, although they were all of standard habit and probably closely related (Scorza et al., 1985).

These genotypic differences for leaf emergence are not the determinant of shoot length or of shoot leaf area but they may have important practical consequences. Despite highly significant differences in leaf emergence curves, the final number of emerged leaves did not differ greatly among cultivars. 'Fairlane', with the lowest final number of leaves produced only 30% fewer leaves than 'Armking'. Genotypic differences in average internode length can counterbalance these differences in leaf emergence, so that identical shoot length may be reached either with many short internodes or with fewer long internodes. The number of possible sites for flowering or branching will not be the same in both cases. Spatial distribution of leaves will also be altered, with possible consequences on the microclimate, and especially on light distribution, within the tree crown. Great differences in light distribution have been related to bud density by Scorza (1984) comparing dwarf and standard genotypes.

Compensatory effects may also be expected between average single leaf area and leaf emergence rate, as observed by Ceulemans et al. (1988) on poplar, so that increased emergence rate will not

Fig. 4. Predicted leaf emergence curves for main (solid lines) and hypothetical first-order shoots appearing at 500 accumulated thermal units (dotted lines). Thick lines are the curves for each genotype. The simulated average over all genotypes (thin curves) are given as references for comparison.

necessarily result in higher tree leaf area. Again, the canopy structure would be altered, however.

The procedure applied to characterize genotypes in this study is too time-consuming for breeding purpose. Our results may be used to define alleviate procedures. A similar ranking of cultivars was obtained for main and first-order shoots. If this is a general rule, one can study only either main or first-order shoots to characterize genotypes.

Although the ranking of cultivars was the same for both types of shoots, it must be underlined that differences between main and first-order shoots were important. Leaf emergence rates were always lower for first-order shoots than for main shoots at a given date. The branching order is one component of the morphogenetical gradient. To compare genotypes, one must ensure that the dynamics of leaf emergence is studied on similar shoots on all the genotypes. The distinction between main and first-order shoots is easy on first-year trees. On older trees, the characterization of shoots might be more difficult and render comparison between genotypes less accurate.

Genotypic differences were found in leaf emergence rate among standard cultivars. Crossing standard cultivars with diverse leaf emergence patterns, differing average internode length and average leaf area should provide standard hybrids with contrasting architectural characteristics.

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