Genotype of Apple Trees Affects Growth and Fruiting Responses to Shoot Bending at Various Times of Year

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ABSTRACT. Growing shoots of two apple [*Malus sylvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf.] genotypes differing in shoot architecture, the preselection X.3318 and the cultivar 'Chantecler', were bent on three dates during the summer and one in the winter to evaluate the interactive effects of shoot architecture and bending date on lateral shoot development and growth over 3 years. Bending X.3318, with a high proportion of vegetative lateral shoots on 1-year-old wood, on different dates did not change the percentage of lateral budbreak (62% to 65%). However, bending in June or July increased lateral growth on 1- and 2-year-old wood in a mesotonic position, whereas bending in winter reduced lateral growth and redistributed the shoots more basitonically. Both number and weight of fruits were reduced by bending. In 'Chantecler', which forms many flower buds on 1-year-old wood, bending during flower bud formation (June–July) increased the percentage of lateral budbreak (60% vs. 45% for the control) and the number of flower buds. After 3 years of development, early summer treatments reduced the abortion of laterals as compared to the control. As a consequence, bending increased the number, as well as the weight of fruit. These results show that the effects of bending on the development and growth patterns of lateral shoots vary with genotype.

Horticultural use of branch reorientation away from the vertical position, referred to hereafter as bending, is a long-established practice for reducing vegetative growth and increasing flowering and fruiting of apple (*Malus sylvestris* var. *domestica*) (Luckwill, 1970). Bending has been proposed as an alternative to pruning for promoting early fruit production and controlling tree size (Lauri and Lespinasse, 1999; Lespinasse, 1996). It has been integrated into various training systems, such as the slender- and super-spindle systems (Weber, 2000; Wertheim, 1980), and the solaxe training system (Lespinasse, 1996).

Several studies provide experimental evidence for the effects of bending on both vegetative growth and flowering, referred to as gravimorphic reactions by Wareing and Nasr (1961). Bending resulted in short shoots, mainly by reducing the number of nodes (Kato and Ito, 1962) and the length of internodes (Wareing, 1970). Bending also promotes lateral shoot development on the upper part of the arched shoot (Mullins, 1965a), while reducing the growth of acrotonic (i.e., the most distal) lateral shoots (Lakhoua and Crabbé, 1975b). The effects of bending on flowering and fruiting remain controversial both in terms of the whole, generally young, tree and of the individual branch (Forshey and Elfving, 1989). Depending on the experiment, entire trees or individual branches oriented horizontally or downward either increase (Tromp, 1970; Wareing, 1970) or do not have a consis-

tent effect (Longman et al., 1965; Mullins, 1965b) on flower bud formation and fruiting.

When interpreting such discrepancies, different conditions should be taken into account. It has been shown in apple that cumulative lateral branch length and the distribution of such branches along the parent shoot depend on at least three factors: 1) the orientation to which the shoot is trained (Lakhoua and Crabbé, 1975a); 2) the time of bending, i.e., after cessation of growth or at different dates during winter and spring (Lakhoua and Crabbé, 1975b); and 3) the length of time during which the stem is bent before being brought upright again (Lakhoua and Crabbé, 1975c).

Another factor that may play an important role in shoot response to bending, but which has not been studied in depth, is the genotype-specific shoot architecture. The growth and fruiting behavior of each genotype may be characterized by a specific combination of morphological traits (Lauri et al., 1995, 1997). Notably, the proportions of lateral types—vegetative, inflorescence—on 1-year-old wood of the shoot, and their development are important in affecting growth of the fruiting branch during the following years. These genotypic characteristics should therefore be integrated to better analyze the reactions of shoots to horticultural practices, such as spur pruning (Lauri and Térouanne, 1999) or branch orientation (Lauri et al., 1995).

As part of an ongoing research project on apple tree training, the present study was initiated to gather information on the interaction between genotype and bending in two genotypes displaying contrasting shoot architecture and fruiting patterns. The objectives of this study were to 1) describe, over 3 years, the lateral development of shoots left to grow without artificial constraints and 2) analyze the qualitative (type of lateral) and quantitative (growth) responses to bending on various dates during the growing season and the following winter.

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Materials and Methods

PLANT MATERIALS. One advanced selection and one cultivar, with contrasting growth and fruiting habits, were chosen from selections released from the breeding program of the Institut National de la Recherche Agronomique (INRA), France. The preselection X.3318 is a cross between 'Winesap', a scab [*Venturia inaequalis* (Cke.) Wint.] resistant cultivar, and 'Fuji', and is a promising scab-resistant genotype. It has an alternate bearing habit and is characterized by upright growth and a strong tendency to develop water sprouts in response to natural or artificial bending (Fig. 1). The cultivar Belchard Chantecler, hereafter referred to as 'Chantecler', is a cross between 'Golden Delicious' and 'Reinette Clochard'. It has a regular bearing habit and a wider intrinsic branch angle than X.3318, with no substantial branch renewal in response to bending (Fig. 1).

EXPERIMENTAL DESIGN. Forty-five trees of each genotype, grafted onto Malling 9 (M.9) rootstocks, were planted in two adjacent rows, a genotype per row, in Winter 1993 at the INRA station in Bordeaux, France. Tree spacing was 5 m between the rows and 2 m between trees within the row. They were trained as small solaxe trees (Lespinnasse, 1996) to facilitate observations, with the scaffold branches maintained in a horizontal position along a wire, at a height of 2.2 m. This system allowed the fruiting branches to develop freely on each side of the row. Since this trial was situated within a collection of cultivars, pollination was adequate. Fruits were thinned chemically [Rhodofix, 1% naphthaleneacetic acid, 12 g·ha⁻¹ a.i. and Sevin, 85% carbaryl, 510 g·ha⁻¹ a.i.], and supplemented with hand-thinning to leave one fruit per inflorescence.

In Spring 1995, 250 shoots in their first year of growth, on the horizontal scaffolds on both sides of the rows and of approximately the same length and orientation, were selected within each genotype. Bending treatments were performed on three dates in 1995 (23 June, 11 July, and 4 Aug.) as well as 22 Jan. 1996. Fifty shoots were treated on each date. Fifty shoots were left as controls. Bending was carried out by tying down the growing shoots at an angle of 120° from the vertical, using a cord attached two-thirds of the way along the shoots to avoid wounding the distal part of the shoot (Fig. 1B).

DATA COLLECTION AND ANALYSIS. In Summer 1996, the nodes on each 1-year-old shoot were counted and the type of lateral on 1-year-old wood (1YW) was recorded. Laterals were classified into one of the four types: latent (L), vegetative (V), inflorescence (I), and scar (S) (i.e., death of a V or I lateral). Hereafter, unless otherwise specified, the term lateral will refer only to the growing types, i.e., V and I. At harvest, around mid-September 1996 for X.3318 and 5 Oct. 1996 for 'Chantecler', individual fruits were collected and the equatorial diameter measured with an electronic caliper. For each genotype, a regression model of fruit diameter (D) vs. weight (W) was derived from a sample of 50 fruit taken from adjacent non-treated branches: X.3318: $W = 0.0009 \times D^{2.806}$ and 'Chantecler': $W = 0.001 \times D^{2.7871}$.

At the end of the 1996 growing season, the length of each lateral was measured. When the lateral bore an inflorescence, only the bourse-shoot was measured. If more than one bourse-shoot developed, each bourse-shoot was measured separately.

In 1997, each previously described lateral, now on 2-year-old wood (2YW), was reclassified into one of the lateral type categories, based upon the terminal bud of the lateral. All fruit that developed on 1YW of the 1996 laterals were removed when 10–12 mm large. At harvest, individual fruit were collected and their

diameters measured. Fruit weight was estimated from the diameter, as in the previous year. At the end of the season, the length of the annual growth of each lateral was measured.

In Spring 1998, lateral development on 3-year-old wood (3YW) was again recorded and classified into one of the lateral type categories. Statistical analysis was performed using ANOVA-MANOVA procedure from the STATISTICA statistical package (StatSoft, Paris, France, 1984–98).

Results

EFFECTS ON GROWING LATERALS ON 1, 2, AND 3YW. As expected, summer bending resulted in shorter shoots (40 nodes and 90 cm on average vs. 46 nodes and 93 cm on average for the control) in X.3318, but not in 'Chantecler' (35 nodes and 70 cm on average for all treatments) (data not presented). Bending did not influence the percentage of 1YW laterals relative to the total number of nodes on the shoot on X.3318 (62% to 65%; Table 1), whereas for 'Chantecler' bending on 23 June and 11 July increased the percentage of laterals on 1YW, in comparison with winter bending and the control (Table 1).

The number of laterals on 1, 2, and 3YW varied with genotype (Fig. 2). For X.3318, bending had little effect. The number of laterals decreased slightly between 1 and 2YW and then increased between 2 and 3YW. On 3YW, the percentage of growing laterals was significantly higher on control shoots than on other treatments, except 11 July. For 'Chantecler', there was a sharp decrease between 1 and 2YW and a smaller one between 2 and 3YW. Large differences were observed between treatments: on control shoots, only 50% of laterals that developed on 1YW were still growing on 3YW, increasing to 75% for shoots bent in early summer, and intermediate values for the 4 Aug. and 22 Jan. treatments.

These variations were mainly the results of two phenomena: death of laterals (extinction, e; Lauri et al., 1995) and increase in growing points over the previous year due to the development of

Fig. 1. Silhouettes of 3-year-old shoots of genotypes X.3318 and 'Chantecler'. (A) Control shoots and (B) shoots bent in Jan. 1996, 120° from the vertical. Arrows on bent shoots indicate the point of attachment.

Table 1. Effects of bending date on the percentage of laterals on 1-year-old wood relative to the total number of nodes of the parent shoots, for genotypes X.3318 and 'Chantecler'.²

Bending date	Laterals on 1YW (%)	
	X.3318	'Chantecler'
23 June	64.5 a ^y	59.6 a
11 July	64.9 a	58.4 a
4 Aug.	62.0 a	47.1 b
22 Jan.	64.9 a	48.4 b
Control	61.7 a	45.4 b

²Data are means of 50 observations.

^yMean separation within columns by Newman-Keuls multiple range test, $P < 0.05$.

more than one bourse-shoot on the spur (multiple bourse-shoots; μ) (Table 2). X.3318 was characterized by less death of laterals, i.e., lower ϵ values (6% to 18%), and more multiple bourse-shoots, i.e., higher μ values (3% to 34%) than 'Chantecler' (12% to 42% and 5% to 8%, respectively). For X.3318 the higher m values were between 2 and 3YW, whereas for 'Chantecler' the higher ϵ values were between 1 and 2YW. The extreme ϵ values for 'Chantecler' (42% between 1 and 2YW) and μ values for X.3318 (34% between 2 and 3YW) were found in control shoots.

EFFECTS ON LATERAL DEVELOPMENT. Generally speaking, the V and I development patterns differed between the two genotypes (Table 3). X.3318 presented a typical alternating pattern, although the difference was small in 3YW. 'Chantecler' had a high number of I on 1YW, which decreased on 2 and 3YW. Bending affected these patterns in diverse ways. For X.3318, the decrease in the total number of nodes on the parent shoot brought about by summer treatments decreased the number of V on 1YW without consistently affecting I, and reduced the number of I on 2YW without affecting V. On 3YW, summer treatments reduced V and there was a better balance between V and I than in the control. The effect of winter treatment was intermediate between those of the control and summer treatments. On 'Chantecler', 23 June and 11 July treatments increased the number of I on 1, 2, and 3YW without a consistent effect on V.

Considering the length of the laterals, vegetative laterals were longer than bourse-shoots (data not presented). For both cultivars, lateral shoots were in large part growing from the upper side of the bent parent shoot (data not presented) and were in upright position (Fig. 1B). The mean length of laterals varied with position along the shoot, as well as with genotype and bending date (Fig. 3). On both 1YW and 2YW of the control shoots of X.3318 (Fig. 3A and B) and 'Chantecler' (Fig. 3C and D), laterals were longer in the distal zone of the shoots - a typical acrotonic tendency. On 1YW of X.3318 (Fig. 3A), bending on 23 June, 11 July, and, to a lesser extent, 4 Aug. was characterized by the persistence of this distal zone, similar to the control, and by the development of branches in the middle position (position 0.5) which were a little smaller than the distal ones. The 22 Jan. treatment shifted this tendency from the mesotonic (Bell, 1991) towards a more basitonic zone (position 0.3) with a decrease of the acrotonic zone. On 2YW (Fig. 3B), the acrotonic zone was much smaller for all the treatments, with the persistence of a mesotonic or a basitonic zone for the summer and winter treatments, respectively. On 1YW of 'Chantecler' (Fig. 3C), although acrotony remained predominant in all the treatments, summer bending tended to reduce the length of the laterals in the distal zone whereas winter bending did not. On 2YW (Fig. 3D) acrotony

remained strong on control shoots but there was a loss of acrotony in all bending treatments.

EFFECTS ON FRUITING. Generally speaking, X.3318 had more fruit on 2YW than on 1YW, whereas there was no difference for 'Chantecler' (Table 4). The mean number of fruit per branch varied between treatments and genotypes. There was no difference among treatments for X.3318 on 1YW, whereas the control had more fruit than all bending treatments on 2YW. For 'Chantecler' bending on 23 June increased the number of fruit on 1YW, compared to other treatments and to the control. On 2YW, bending on 22 Jan. and, although more variable, on 23 June and 11 July, increased the number of fruit per branch as compared to the control.

For both genotypes, fruit on 1YW were smaller than those on 2YW regardless of bending (Table 4). For X.3318, fruit on control shoots were larger on both 1 and 2YW. For 'Chantecler', the 23 June treatment increased fruit weight on 1YW, compared to the control, 22 Jan., and 4 Aug. treatments, but there were no differences between any of the treatments on 2YW.

Discussion

Our results demonstrate that fruiting (Buban and Faust, 1982), and flowering on 1-year-old wood is affected by genotype. Control shoots of X.3318 had a high vegetative to flowering ratio, whereas the reverse was true for 'Chantecler'. Bending did not greatly affect these ratios, but, depending on the genotype and bending date, treatment influenced the number and type of buds formed during the year of bending as well as lateral development (growth and type) during the subsequent years.

In X.3318, bending had no significant effect on the proportion of laterals on 1YW, whereas in 'Chantecler', bending on 23 June or 11 July increased the proportions of laterals, especially inflorescences, on 1YW. Since this period coincided with flower primordia initiation (Huet, 1979; Longman, 1985), these results suggested there is a relationship between flowering on 1YW and the response to bending. Therefore, flowering response to bending appears to involve specific interactions between genotypic characteristics and treatment date (Meilan, 1997).

Lateral development pattern across years differed between

Fig. 2. Effects of date of bending and age of wood on the number of laterals, for genotypes X.3318 (solid lines) and 'Chantecler' (dotted lines). Results are expressed as mean percentage of laterals on 1-year-old wood (100%) for all shoots of each treatment. Each symbol corresponds to 50 shoots. Mean separation within each genotype and for age of wood 2 and 3 by Newman-Keuls multiple range test, $P < 0.05$. NS Nonsignificant.

Table 2. Effects of bending date and age of wood on multiple bourse-shoot and extinction for genotypes X.3318 and 'Chantecler'.

Age of wood (years) and bending date	Multiple bourse-shoot (μ) ^z and extinction (ϵ) ^y (%)			
	X.3318		'Chantecler'	
	μ	ϵ	μ	ϵ
1-2				
23 June	6.1 d ^{x,w}	6.7 b	6.2 a	24.3 c
11 July	6.2 d	6.2 b	4.6 a	21.9 c
4 Aug.	5.8 d	6.9 b	5.0 a	30.8 b
22 Jan.	3.3 d	6.5 b	6.6 a	31.8 b
Control	4.2 d	5.7 b	7.9 a	42.4 a
2-3				
23 June	29.6 b	12.0 b	6.6 a	14.1 d
11 July	32.2 ab	9.4 b	5.9 a	11.9 d
4 Aug.	25.8 c	10.5 b	4.7 a	12.7 d
22 Jan.	29.4 c	17.9 a	6.1 a	13.5 d
Control	33.8 a	8.6 b	6.8 a	12.7 d

^zThe multiple bourse-shoot index, μ , is the ratio $N(G)_{N+1} - N(G)_N / N(G)_N$, where $N(G)_{N+1}$ denotes the number of vegetative laterals (V) and inflorescences (I) in year N + 1, and $N(G)_N$ denotes the number of V and I laterals in year N; μ is expressed as a percentage.

^yThe extinction index, ϵ , is the ratio $N(GS)/N(G)$, where $N(GS)$ denotes the number of laterals in year N followed by an S in year N + 1, and $N(G)$ denotes the number of laterals in year N; ϵ is expressed as a percentage.

^xData are means of 50 observations.

^wMean separation within columns by Newman-Keuls multiple range test, $P < 0.05$.

genotypes, resulting in an increase in number of laterals for X.3318 and a decrease for 'Chantecler'. Apart from the multiple bourse-shoot phenomenon, which clearly appeared to be genotype-specific, our data also suggested the proportion of inflorescences on 1YW played a determining role in the response to bending of the two genotypes. Previous work (Lauri et al., 1995, 1997) showed inflorescences were the predominant extinction site, occurring mainly during the first years of lateral development. In 'Chantecler', control shoots were upright and flower buds were subjected to the competitive influence of acrotonic laterals, leading to high extinction rates. This reduced the number of laterals on 3YW by about 50%, especially in the basal two-thirds of the shoots (data not presented). This result is consistent with the findings of Walsh (1979) on erect

vigorous shoots of 'Gardner Delicious'. For treated shoots, the reduced acrotonic tendency in summer bending treatments, may have reduced this competition leading to low extinction rates between 1 and 2YW. These results support Tromp's (1970) hypothesis that enhanced flower bud formation in horizontal shoots is the result of reduced flower abortion. In X.3318, the large proportion of vegetative laterals on 1YW may partly explain the low extinction rates and therefore the small influence of bending treatments on the proportion of laterals over this 3-year study.

For X.3318, the large proportion of vegetative laterals on 1YW, together with the higher growth potential of vegetative laterals than of bourse-shoots, may also explain the growth responses in mesotonic (summer treatments) or to a lesser extent in basitonic (winter

Table 3. Effects of bending date on the number of vegetative (V) and flowering (I) laterals per branch on 1-, 2- and 3-year-old wood for genotypes X.3318 and 'Chantecler'.

Genotype and bending date	No. of V and I laterals					
	1YW		2YW		3YW	
	V	I	V	I	V	I
X.3318						
23 June	24.6 b ^{z,y}	9.5 b	7.5 a	25.2 c	16.3 b	14.8 ab
11 July	26.3 b	11.4 a	7.2 a	28.2 bc	18.4 b	15.6 ab
4 Aug.	25.6 b	9.1 b	6.8 a	25.7 c	17.4 b	13.7 ab
22 Jan.	30.6 a	8.1 b	6.5 a	30.3 b	21.9 a	12.6 b
Control	32.8 a	8.9 b	6.8 a	33.5 a	22.9 a	16.6 a
Mean	27.4 a ^x	9.2 d	6.8 e	28.0 a	19.0 b	14.4 c
'Chantecler'						
23 June	2.1 c	21.9 a	0.4 a	18.4 a	1.1 a	15.0 a
11 July	2.6 abc	20.2 a	0.4 a	17.8 a	1.1 a	14.9 a
4 Aug.	3.4 ab	16.1 b	0.2 a	13.6 b	1.0 a	11.1 b
22 Jan.	3.7 a	15.8 b	0.1 a	13.5 b	0.8 b	11.3 b
Control	2.3 bc	16.4 b	0.4 a	10.9 c	1.0 a	9.1 c
Mean	2.8 d ^x	18.0 a	0.3 e	14.8 b	1.0 e	12.1 c

^zData are means of 50 observations.

^yFor each genotype, mean separation within columns by Newman-Keuls multiple range test, $P < 0.05$.

^xFor each genotype, mean separation between columns by Newman-Keuls multiple range test, $P < 0.05$.

Fig. 3. Effects of time of treatment and age of wood on logarithmic mean of the length of V and I laterals relative to the position on the shoot (0 = basal to 1 = subapical) for genotypes (A and B) X.3318 and (C and D) 'Chantecler'. Only positions with at least 15 laterals were considered. Vertical bars represent ± 1 SE when larger than symbol size and positive.

treatment) zones. In contrast, growth of 'Chantecler', with a higher proportion of inflorescences on 1 and 2YW, responded little to bending.

Summer treatments reduced acrotony more than the winter treatment in 'Chantecler', confirming the hypothesis of Lakhoua

and Crabbé (1975b) that the gravimorphic effect is progressively superimposed on the initial acrotonic tendency, and that the longer bending is applied, the greater the response. The inverse was true for X.3318, however, in which early summer treatments induced mesotonic lateral growth without affecting the acrotonic zone. These contrasted patterns of response to bending led to different branch physiognomy. On 'Chantecler', bending especially in summer, led to a more uniform distribution of lateral shoots along the bent parent shoot. On X.3318 these shoots were typically grouped into two different zones, the acrotonic one, and depending on the treatment, a mesotonic or a basitonic one.

Results from the present study show response of genotype to bending follows no particular rule. This may partly explain the variability in results reported in the literature. Where bending is recommended as an alternative to pruning (e.g., solaxe in France), to control tree height, vegetative growth, and fruiting, these results suggest branch management practices should be adapted to the genotype. For cultivars similar to 'Chantecler' with strong flowering on 1YW, bending the growing shoot during flower primordia initiation can increase both the

number and weight of individual fruit while reducing lateral growth. In this case, the conceptual scheme that bending reduces the demand of the vegetative growing points for carbon, allowing higher exports to the fruit (Corelli Grappadelli et al., 1994) seems relevant. The same carbon allocation pattern cannot be extended to cultivars similar to X.3318, however, in which summer bending promotes lateral growth and reduces fruit number and weight. In this case, winter bending might be a good compromise to reduce lateral growth, distributing it along the shoot, to maintain good fruiting potential.

Table 4. Effects of bending date on the number of fruit per branch and the weight of fruit on 1 and 2YW for genotypes X.3318 and 'Chantecler'.

Fruiting variables and bending date	X.3318		'Chantecler'	
	1YW	2YW	1YW	2YW
No. of fruit ^z				
23 June	2.2 a ^{y,x}	11.1 c	3.1 a	1.9 abc
11 July	2.7 a	12.2 c	2.3 b	2.2 ab
4 Aug.	2.8 a	11.2 c	1.2 c	1.7 bc
22 Jan.	3.4 a	14.0 b	1.2 c	2.5 a
Control	3.2 a	15.9 a	1.8 bc	1.3 c
Mean	2.8 b ^w	12.9 a	1.9 a	1.9 a
Fruit wt (g)				
23 June	96.2 b ^x	151.0 b	157.4 a	232.4 a
11 July	98.3 b	155.4 b	149.9 ab	230.1 a
4 Aug.	98.9 b	152.2 b	140.7 b	242.0 a
22 Jan.	97.4 b	153.5 b	141.2 b	237.4 a
Control	106.0 a	164.8 a	140.7 b	230.1 a
Mean	99.4 b ^w	155.4 a	146.0 b	234.4 a

^zTotal number of fruit per branch including branches with no fruit.

^yData are means of 50 observations.

^xFor each variable, mean separation within columns by Newman-Keuls multiple range test, $P < 0.05$.

^wFor each genotype and for both variables, mean separation between columns by Newman-Keuls multiple range test, $P < 0.05$.

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