Review article

Integration of architectural types in French programmes of ligneous fruit species genetic improvement

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Integration of architectural types in French programmes of ligneous fruit species genetic improvement.

Abstract - Introduction. The main breeding programmes on ligneous fruit species run at Inra concern apricot, cherry, peach, pear, apple and walnut trees. This review aims to analyse how tree characteristics are considered by fruit breeders. Genetic variability. Characteristics most often taken into account by breeders are vigour, tree habit and type of fruiting. The variability of these main architectural criteria in the different species is discussed. Integrating tree characteristics into selection schemes. The selection criteria and their place in the different breeding programmes is displayed. The conclusions are that pest and disease resistance and fruit quality are the two main objectives of fruit breeding programmes; generally, tree habit is just considered as a complementary aim. Walnut and apple breeding programmes are the only ones that have developed specific crossing strategies aiming to release trees with an early fruit setting, and high and regular bearing. Discussion and perspectives. Criteria which are taken into account to assess for tree habit are not efficient enough: too complex, descriptive, and dependant of environmental and cultural conditions. Except in the walnut breeding programme, they are used only to describe the hybrids but not to select in the progenies. Some recent genetic, morphologic and physiologic studies should allow to find new criteria which will be more efficient for breeding purposes. Conclusion. Nowadays, tree characteristics are not taken sufficiently in selection programmes. Recent studies made on tree architecture, morphology, physiology and fruit-bearing branches should make it possible to define new criteria which will meet better the needs of breeders. © Éditions scientifiques et médicales Elsevier SAS

France / fruit trees / plant breeding / tree habit / fruit-bearing branches

Prise en compte des caractères architecturaux dans les programmes français d'amélioration génétique des espèces fruitières.

Résumé -- Introduction. Les principaux programmes d'amélioration génétique (Pag) développés sur les espèces fruitières ligneuses par l'Inra portent sur l'abricotier, le cerisier, le pêcher, le poirier, le pommier et le noyer. Cette revue analyse comment les caractéristiques de l'arbre sont considérées par les sélectionneurs. Variabilité génétique. Les caractéristiques les plus utilisées sont la vigueur, le port de l'arbre et son mode de fructification. La variabilité exprimée par ces principaux critères architecturaux pour les différentes espèces étudiées est discutée. Intégration des caractéristiques de l'arbre dans les schémas d'amélioration. Les critères de sélection et leur place dans les différents Pag sont exposés. Dans les faits, la résistance aux bioagresseurs et la qualité organoleptique des fruits sont les deux principaux objectifs d'amélioration ; le port de l'arbre n'est qu'un objectif complémentaire. Seuls les Pag du noyer et du pommier ont développé des stratégies spécifiques de croisement visant la créa-tion de nouvelles variétés à mise à fruits rapide et de production régulière et forte. **Discus**sion et perspectives. Les critères aujourd'hui utilisés pour apprécier l'architecture des hybrides sont souvent trop complexes, descriptifs, intercorrélés et dépendants des conditions pédoclimatiques et culturales. Sauf pour le noyer, ils ne servent qu'à décrire les hybrides et non à effectuer des sélections parmi la descendance. D'autres études en cours devraient per-mettre de disposer de nouveaux critères plus efficaces pour la sélection. **Conclusion**. De nos jours, les caractéristiques de l'arbre ne sont pas suffisement utilisées en sélection. Les études faites sur l'architecture, la morphologie, la physiologie et la branche fruitière de l'arbre devraient permettre de définir prochainement de nouveaux critères mieux adaptés aux attentes de l'améliorateur. © Éditions scientifiques et médicales Elsevier SAS

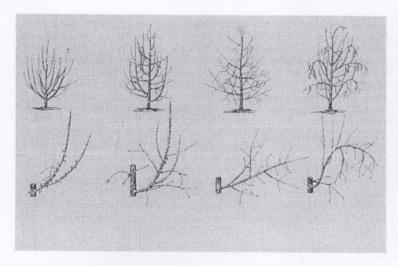
France / arbre fruitier / amélioration des plantes / port de la plante / branche fruitière

1. introduction

The main breeding programmes on ligneous fruit species run at the Institut national de la recherche agronomique (Inra) in France concern apricot trees (Prunus armeniaca L.), cherry trees (Prunus avium L. and Prunus cerasus L.). peach trees (Prunus persica L. Batsch), pear trees (Pyrus communis L.), apple trees (Malus domestica Borkh) and walnut trees (Juglans regia L.). Two priority goals are common to these programmes: bio-aggressor resistance and fruit organoleptic quality (attractiveness, size, taste, storage ability, etc.). In general, criteria concerning tree architecture are of an only secondary interest. Such criteria still have an impact on essential features: productivity (walnut, apple, apricot), regularity of production (apple, pear), production "durability" (peach), rapidity of fruit bearing (walnut, cherry, pear), flowering and harvesting periods (cherry, apricot), geographical adaptation (apricot). The organoleptic quality of fruit is, as well, closely tied to tree architectural characteristics and types of training [1-6].

The outline of this presentation will follow the interests of the breeder: the variability of the main architectural criteria will first be discussed. The selection criteria and their place in the different breeding programmes will next be displayed. A critical





and prospective analysis will then be made on the consideration of tree characteristics by breeders.

2. genetic variability

The variability found in marketed cultivars represents only a tiny part of the total genetic variability present in cultivated species. This situation concerns all the characteristics of both fruits and trees. Still, it seems that in certain species, the apple, for instance, selection in the most intensely marketed cultivars has focused mainly on fruit characteristics with little interest for the diversity of tree habit. Even though a large number of "standard" habit cultivars are found, such as Golden Delicious, extreme fruiting types exist among often grown cultivars: a weeping habit type of Granny Smith, a sought-after spur type among the mutants of widely-marketed cultivars (Red Delicious, Golden Delicious) (figure 1).

The main features of trees present a large scale variability. Those characteristics most often taken into account by breeders are vigour, tree habit and type of fruiting.

2.1. vigour

Vigour has a strong impact on many characteristics linked to production: rapidity of fruit bearing, productivity and fruit size. It can also considerably affect tree shape and, thus, tree training. There is, in fact, a complex relationship between vegetative growth and fruiting in all fruit species. This situation is particularly noticeable in pears, walnuts and cherries. These species are characterized by extreme vigour and a long juvenile period. The walnut was originally a small fruit-bearing tree which, through natural selection, developed in forests before being once again selected for fruit bearing. The cultivated cherry has been derived directly from forest species.

Inside every cultivated species, there is a large range in vigour. This characteristic depends as well, however, on numerous environmental factors. The choice in root-

stock is also important in determining its expression.

2.2. tree habit

This criterion characterizes the overall form of the tree. All species have a wide range of tree habits, varying from erect to weeping. It is a characteristic which generally shows progressive variation, as in the descriptions of numerous species when notation grids [7, 8] have been used. There is considerable variability in walnut trees, even if most of the cultivars of this species have a semi-erect to semi-spread habit.

There are types with limited development, with short internode lengths: one speaks of "dwarf" peach trees [9], a characteristic expressed under simple genetic control [10]. Such types are not presently used for production in France. Weeping habit peach trees have also been described [11].

In apple trees, there are mutants called "spurs" in all largely grown cultivars. This monogenetic characteristic gives the tree a more compact appearance and is sought out by fruit growers wishing to make their orchards denser. There is, however, a drop in flavour quality linked with this habit [12] and a marked tendency towards biennial bearing [13]. The extreme habit type in apples is the columnar habit represented by MacWijcick, a mutant of the MacIntosh variety [14], which displays very marked biennial bearing. Spur types can also be found among apricot trees (Stark Early Orange variety). In pear and walnut trees this type of characteristic does not seem to be linked to the biennial bearing phenomenon.

Tree habit within a given variety still appears to vary, depending notably on vigour. In apricot trees, poor pedoclimatic adaptation can modify the natural habit of a variety towards that of a weeping habit.

It is even possible to witness habit modification over the life of a tree. The Fercer variety of cherry, due to its excessive vigour the first few years after planting, initially has an erect habit whereas it has a weeping habit during production.

2.3. type of fruiting

It is, in fact, very difficult to dissociate "tree habit" and "type of fruiting"; the latter has an obvious influence on the former. This section will treat specifically fruit-bearing branches. Several factors intervene in their functioning: the type of the wood (length and position on the tree), the age of the wood, the position of the fruiting (lateral or terminal bud), etc.

Each species has its own specificities; the present study of fruiting has not, however, been carried out in equal depth for all species.

2.3.1. cherry

Cherry fruiting takes place on two types of shoots:

- at the base of 1-year old shoots, where the presence of five to ten buds assure the tree's first years of production,

- on spurs, short productions composed of seven or eight flowering buds around a central wooden bud which assures the perpetuation and autonomy of the branch.

There is a fundamental difference between acid and sweet cherry trees: acid cherry trees fructify mainly on 1-year old wood. For sweet cherry trees, both types are found: some cultivars have a natural tendency to privilege production on lateral spurs (Van), others at the base of 1-year old shoots. The density of spurs on shoots also varies considerably depending on the cultivars: Van possesses very tightly bunched spurs at the top of the shoots; in Fercer, May buds are more widely spaced and all along the shoots.

2.3.2. almond, apricot, peach

Fruiting mechanisms are quite similar in these three species. Variability of this characteristic has very rarely been described and, even then, with very limited precision [15]. It would appear to be of relatively low level.

Fruit peach tree production takes place mainly on mixed shoots (long shoots carrying both flowering and wooden buds). The branches selected for peach production are the 1-year old ones that have been inserted near the scaffold branches of the tree.

Apricot tree fruiting takes place on two types of shoots: long shoots which are similar to the mixed shoots of peach tree; short shoots which, depending on their length, are called "spurs" (5 cm), or brindles or slender brindles with wood and fruit buds (5 – 10 cm).

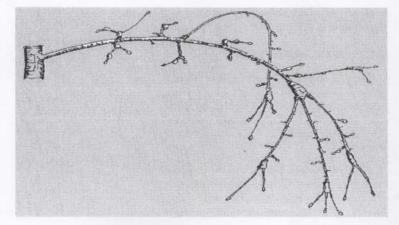
These shoots, depending on their position and organization, result in tree structures covering the entire range of possibilities varying from exclusively "spur" types, as in the Stark Early Orange variety, to types such as the Beliana variety which produce exclusively on mixed shoots.

2.3.3. apple

On the basis of extensive onsite observation, Lespinasse and Lauri have succeeded in analyzing the main characteristics of fruit-bearing branches and in describing the variability found in a few cultivars [16–18]. Three characteristics are necessary in defining the agronomic quality of the fruiting branch (*figure 2*): precocity and quality of flowering, autonomy of lateral spurs and reiteration.

a) precocity and quality of flowering

Terminal bourse has a very strong influence on the development of lateral fruiting spurs. Cultivars with the highest production regularity also generally have very efficient



terminal flowering. A positive relationship between the volume of the terminal bourse and production regularity has been identified [13].

b) autonomy of lateral spurs

Lateral spurs are composed of small preformed and stacked shoots in a lateral position on a fruit-bearing branch. Their nature and functioning are closely linked to the type of branch which is carrying them. Branches with high spur density (Reine des Reinettes, Red Delicious spur mutants) are usually unable to produce fruit annually and function synchronically: flowers one year, vegetative buds the next, that is to say, biennial production. On the opposite, on branches carrying less spurs, the spurs become autonomous and have the possibility of bearing fruit annually (Granny Smith, Red Winter). The nonfunctioning of a high proportion of axillary buds through dormancy or death (extinction) would, therefore, assure good production regularity.

c) reiteration

Production of young shoots at bends or at the base of a branch generally takes place after fruiting and reveals a separation between vegetative growth and fruiting. This separation is more marked on cultivars for which apical dominance lasts and terminal flowering is delayed. Such a situation results in serious impoverishment of the fruiting zone.

In apple trees, a wide range of fruit-bearing branches can be observed. This situation can be related to tree habit (figure 1): in quite erect cultivars, terminal vegetative growth remains a priority for a long time and terminal bourse only appears thereafter. Fruiting develops from the base towards the tip of the branch and is principally composed of short spurs. In natural habit, such trees usually produce biennially. Acrotonic cultivars can also have erect habit. However, the early appearance of terminal bourse and the presence of crown brindles along with acrotonic development leads to rapid sagging of young branches. In contrast to the case described above, fruiting develops basitonically, from the top

Figure 2. Drawing of an apple tree fruiting branch (by Lespinasse).

towards the base of the branch. Such trees naturally diffuse most of their vegetative growth among their spurs, which become autonomous very rapidly: they can easily regulate annual production, as is the case for Granny Smith and hybrids presently under selection.

2.3.4. walnut

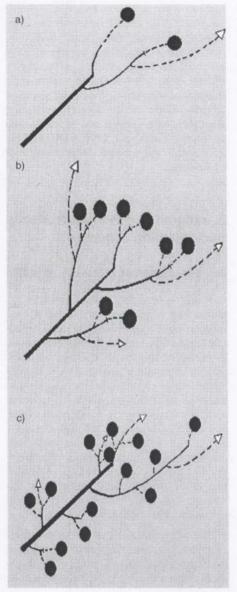
The common walnut tree, *Juglans regia*, has three main types of fruiting depending on shoot-bearing as well as on the positioning and number of flowering buds on 1-year old shoots [19]: terminal position fruiting, intermediate type fruiting and lateral branch fruiting.

a) terminal position fruiting

The terminal position fruiting (figure 3a), representative of French walnut populations as well as those of eastern and northern Europe, is, by far, the most widespread. On 1-year old shoots, fruit buds are found only in terminal or subterminal position. Due to the strongly acrotonic tendency of these shoots, the only buds to open are those situated on the distal section of shoots, while those in the median or basal positions are cancelled. Few secondary branches are found and considerable shedding can be observed along the branches. Fruiting is limited to the extremities of the tree. Fruit-bearing comes slowly and the production potential is low.

b) intermediate type fruiting

As in the preceding case, in the intermediate type fruiting (figure 3b), female floral induction interests only the buds located at the terminal or subterminal positions on 1-year old shoots. In contrast, apical dominance along these shoots is weak, making it possible for a large number of vegetative lateral shoots to start up in spring. These shoots bear fruit in terminal position (tip bearing) the following year. Production is, thus, well distributed throughout the tree along the branches, with fruit placed at the extremities of long lateral shoots. This fruiting type permits relatively rapid fruiting and a level of production which is considerably higher than that of trees with terminal fruiting.



c) lateral branch fruiting

In the lateral branch fruiting (*figure 3c*), fruit buds are situated along 1-year old shoots where the apical dominance is weak. The majority of flowering buds start up therefore in spring and produce mixed shoots of varying length in terminal position at regular intervals the same year. When they have been well pruned these short lateral branches continue to produce for sev-

Figure 3.

Types of fruiting in walnut trees (by Germain). a) Terminal position; b) Intermediate type; c) Lateral branch. eral years. Production is, thus, distributed in "sleeves" along the branches. These cultivars bear fruit much more rapidly than those with terminal fruiting, and their production potential is at least twice as high. Such production, relatively rare in the *Juglans regia* L. species, is found in local walnut populations around the Mediterranean: Spain, Portugal, Sicily, Greece and Israel, as well as in Iran, Tadjikistan, Khirzistan, Ouzbekistan and in the western Chinese province of Xinjiang.

3. integrating tree characteristics into selection schemes

3.1. description of selection schemes

Running breeding programmes in ligneous fruit species involves facing several morphological, physiological and cultural constraints. The length of the juvenile phase is certainly the most limiting for most species. During this period, the duration of which varies according to the species and the type of training (peach = 1-2 years: apricot = 4 years; apple = 4-5 years; cherry = 5-6 years; walnut = 4-7 years; pear = 5-7 years), the tree acquires its adult characteristics. The most obvious manifestations of this period are the lack of flowering, impressive vegetative growth and the presence of specific morphological traits (thorns on pear trees).

The tree thus has rather different behaviour from that it will have as an adult, which limits the selection works during this phase. In fact, even if early selection for parasite resistance is possible for most species, selecting for good fruit quality or describing tree architecture can only be carried out on the adult tree: no early, reliable indicator is presently available. The length of the juvenile period therefore has a direct impact on the length of the selection cycle.

The steps in the selection process remain, however, similar for all species (*table D*. The first years are used for the steps of early selection: in the walnut, selection for late bud opening; in most species,

tests of resistance to the main pests and diseases [scab (Venturia inaequalis) and powdery mildew (Podosphaera leucotricha) for apple trees; fire blight (Erwinia amylovora) and scab (Venturia pirina) for pear trees: powdery mildew and green aphids (Myzus persicae) for peach trees. The resistance tests are usually run in greenhouses and/or in nurseries. These initial steps also make it possible to eliminate subjects which are "outside the norms", such as too fragile ones. The selected trees are then planted in hybrid plots where fruit and tree descriptions are made as soon as the subjects have reached adulthood and for at least 3 years of fruiting. Trees with the highest levels of performance are then tested within the framework of multi-site test networks (characterization, level 1 assessment, level 2 assessment) managed, for each species, by Inra and Ctifl (Centre interprofessionnel des fruits et légumes) in the context of the national experimentation charter.

3.2. notation of tree characteristics

Vigour, tree habit, type of fruiting and branching (quantity, angles, etc.) are characterized for most species (*table II*). All are judged using a qualitative notation system based on a scale of four to seven classes with reference to known cultivars. Only one characteristic is quantitatively assessed: trunk diameter which gives an indication of vigour.

These criteria are integrated at different moments of the cycle: both in the hybrid plots and thereafter during level 1 experimentation (table 1). Such notations are not made systematically on all hybrids in the apricot and peach selection schemes. For the pear and the cherry trees, architectural notations are made only once during the life: in the hybrid plot and on all subjects. For apple trees, an initial notation on tree architecture is made for all trees in the hybrid plot, followed by a second notation for the best selections within the framework of level 1 experimentation. The most complete notations are made for the walnut: tree vigour, tree habit and type of fruiting are observed for all subjects several times during the selection cycle.

Years ¹	Apricot	Cherry	Walnut	Peach	Pear	Apple
0	-		-	Greenhouse Mildew, green aphids		- 1
1	Nursery	Greenhouse	Nursery	Hybrid orchard		Greenhouse Scab
2	Hybrid orchard	Nursery → grafting	Vigour Early budding	Fruit (5) ²	Greenhouse Bacterial blight, scab	Nursery Mildew Tree (vigour)
3	- State Departure	Hybrid orchard	Hybrid orchard		Nursery	Philip Serk
			Tree (vigour)		→ grafting	\rightarrow grafting
4	Plum pox (3) ²		Toutes distant	-	Hybrid orchard	Hybrid orchard
5	Fruit (3) ²	Phenology	Tree (vigour, habit)	- 19 5 5 5 5 5	-	Resistance (4) ²
6	→ grafting		Tree (fruiting) $(4)^2$ Fruit $(4)^2$	\rightarrow grafting	Juvenil characteristics	Fruit (4) ²
7	National experiment	Fruit (3) ² Tree Parasite tests	Tree (vigour, habit)	National experiment		
8	Fruit (3) ²		→ grafting	Fruit (5) ²	Fruit (4) ² Tree (vigour, habit, branching)	Tree (vigour, habit)
9		-	Tree (vigour, habit)	Tree (habit)		National experiment
10		- second - second	National experiment		-	Fruit (3) ²
11		4 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	-			
12	Tree	-	-	-	National experiment	Tree (vigour, habit, branching)
13			Fruit (4) ² Tree (4) ²	-		-
14		\rightarrow grafting				
		(/classical rootstock)	-	The second second	- In In	17000
15	+	National experiment	- 11		Fruit (3) ²	
Varietv ³	> 15 years	> 20 years	20 years	10 years	20-25 years	15-20 years

¹ Years after pollinisation.

² Number of test years or of observation for the trait in question; no parentheses = 1 observation.

³ Total length of cultivar cycle.

where types with terminal fruiting are set characteristics judged to be redhibitory can aside, the architectural notations carried out lead to elimination: apple trees which are too during the selection scheme are only informative: no hybrids are eliminated on the basis

For all species other than walnut trees, of solely morphological criteria. Still, a few fragile while still in the nursery, cherry trees which are extremely erect or genetic dwarves.

F. Laurens et al.

Table II.

Architectural criteria taken into account (+) in various French programmes of ligneous fruit species genetic improvement.

Criteria considered	Apricot	Almond	Cherry	Peach	Walnut	Pear	Apple
Vigour							Signa -
Trunk circumference	+	-	-	-	+	+	+
Global note	+	1.4	+	-	+		+
Free habit	+	-	+	-	+	+	+
Type of fruiting	+	-	+	-	+	-	+
Branching							
Importance		+	-			+	+
Angles of branching	-	-		-		+	-
deotypes	Contraction of the	-		-	-	-	+
Other characteristics							
Juvenility	A State State	- 1 -				+	
Shedding			- 11	-121	-	1	+
Fruit / corymb		-			-	+	+

All of the information is used at the end of selection to give advice on the best adapted training methods (choice of rootstock, form, pruning) for the architecture of the best hybrids. progenies by relying upon parents carrying the "one fruit per corymb" trait, which assures auto-regulation of fruiting at the level of individual flower clusters.

Scab resistant hybrids with good taste and meeting the previously described agro-

nomic criteria are today the subjects of large

3.3. results

3.3.1. apple trees

The apple tree breeding programme at Inra is based on close collaboration between the Fruit and Ornamental Shrub Breeding Unit, Angers, and the Fruit and Vine Species Research Unit (UREFV), Bordeaux. The goal is to release cultivars with high quality flavour and parasite and pest resistance (scab, mildew, rosy apple aphid, fire blight). A complementary goal is also sought: finding trees with regular, high production which can adapt to pedestrian orchards. Approximately 15 % of the crossings made each year are carried out for this reason [20]. Such goals can be reached by implementing specific crossing action plans between weeping habit genotypes (Granny Smith, Red Winter) and those of standard habit (Golden Delicious type). Production regularity has been transmitted to several

scale (level 2) experimentation.

3.3.2. walnut trees

Since 1977, the UREFV in Bordeaux (France) has been engaged in a programme of variety creation through interspecific hybridization. The two main goals of this study concern the architectural characteristics of trees: on the one hand, fruiting on lateral branches, a sign of rapid fruit-bearing and high productivity, and, on the other hand, late flowering. Thirty eight crossings have been developed and over 2 000 hybrids have been characterized. In the past 3 years, two cultivars have been included in the species catalogue: Fernor and Fernet. Each of them possesses the following qualities: fruiting on lateral shoots, late flowering, low bacterial sensitivity and good fruit flavour. Three new cultivars should be added within the next 5 years.

4. discussion and perspectives

In all ligneous fruit species treated at the Inra, except for walnut trees, observations on vigour, habit, branching and fruiting made during selection have no impact on the choice of the most efficient hybrids: selection focuses on fruit sensu stricto. Only apple and walnut tree breeding programmes have implemented crossing strategies including parents chosen both for fruit quality and for their fruiting characteristics. Even for these two species, the choice in criteria measured has remained empirical. There are several limitations to their effective use in selection:

- Such assessments are generally made during rather global observations grouping very numerous, different and closely interconnected traits on a single grid (cf. tree habit notation by class or ideotypes in apple and pear trees). Such data is of course informative, but it is difficult for the geneticist to exploit due to its complexity.

 They are descriptive, rather than being concerned with the physiological functions producing fruiting or regulating it.

 They are strongly inter-correlated and highly dependent upon pedoclimatic conditions and cultural factors.

– The observations are made late in the selection scheme, after the juvenile period of the plants. Breeders would like to find earlier and more reliable criteria. In certain species, a poor correlation can be found between a plant behaviour on its own root and after grafting, particularly as concerns the fruiting site trait in apricot trees as well as vigour in walnut trees.

Several recent approaches have been developed to take tree characteristics more into account in improvement programmes.

- Genetic studies: a large amount of data on tree architecture has been recorded over the last few years for numerous species (apple, pear, cherry, walnut trees). In most cases, this data has never been analyzed. Genetic studies would make it possible to take advantage of this information. The genetic parameter estimation such as the heritability or genetic correlations does, in fact, make it possible for breeders to choose the most informative characteristics. Moreover, this type of analysis supplies information on the genetic value of the parents involved in the breeding programmes. Such work has been carried out on the walnut [21] and the apple [22] trees. It could be developed for other species.

- Morphological and physiological studies: work carried out on fruiting branches of the apple trees should lead to the proposal of new criteria for better predicting the capacity of branches to regularly produce quality fruit. The length of the bourse, the importance of the extinction, the autonomy of the lateral spurs and the importance of reiteration are a few of the criteria which could henceforth be integrated into the systematically run notations during apple tree selection schemes. The same type of morphological studies as those carried out for apple trees are presently underway for pear, cherry and walnut trees. They could also result in the definition of new criteria close to breeder needs.

Work is underway to find very early developmental indicators for apple trees. Morphological (shoot length and diameter; internode quantity and length; sylleptic shoot quantity and characteristics) and descriptive (branch positioning) measurements have been made on 2-year old hybrids. A follow-up will be run on these trees throughout the selection cycle [23].

Analytical approaches are also being run on peach trees at the Inra Avignon Mediterranean Fruit Research Unit, with the goal of defining early selection criteria on peach tree growth and development. Fruit-bearing branch studies deal with size assessment and analysis of flower distribution along the branch's full length. In numerous species, it has been shown that the thickest shoots could support heavier fruit loads [24] and make better water and mineral supply to the fruit [24], thus assuring fruit of higher quality. The studies undertaken in Avignon, France, have shown that the shoot/diameter length criterion on 1-year old pot-grown trees was well correlated with that of the average size for shoots on 5-year old trees. This criterion is, thus, a good early indicator in estimating shoot size variability among cultivars [24, 25].

F. Laurens et al.

In parallel, a study is being made to analyse flower distribution along fruit-bearing branches. Fruits at the base of a shoot are, in fact, the best nurtured, whereas floral buds are more frequent on distal sections. The relationships between the node appearance context and the nature of axillary productions have been studied to analyse the propensity of each node to produce vegetative or flowering buds. These analyses should lead to the definition of new selection criteria.

- Modelling the relationships between inter-correlated developmental characteristics or between developmental characteristics and environmental parameters makes it possible to understand better such phenomena. In this way, in peach trees, it has been possible to evaluate branching propensity independently of growth speed [26]. A detailed breakdown of the characteristics enables us to make more judicious choices in parents to associate.

Research into models taking flowering and branching distribution into account, presently under development at the Inra Montpellier Arboricultural Laboratory, will, in time, reach the goal of comparing hybrids in the selection process with cultivars which are already cultivated. This research is being run in collaboration with various selection programmes on peach [27] and apricot [28] trees, on apple scions [20] and on walnut trees.

5. conclusion

Nowadays, tree characteristics are not taken sufficiently into account in selection programmes. Their assessment often remains very empirical.

Recent studies made on tree architecture, morphology, physiology and, most particularly, on fruit-bearing branches, associated with adapted quantitative statistical or model-based processing, should make it possible to define new criteria which will meet better the needs of breeders.

In fact, numerous morphological (tree volume), physiological (juvenile period)

and genetic (the case of heterozygous species) constraints slow genetic improvement of ligneous fruit species. To limit the duration of selection schemes and lower costs, breeders are seeking early criteria.

Molecular markers are being developed for numerous species, particularly peach and apple trees. Such work is certainly a path for the future. But, beforehand, it is necessary that techniques be made applicable, that tree characteristics and the physiological mechanisms of fruiting be clearly defined and better understood.

All of these techniques should be taken into account by breeders in order to select not only fruit, but also the tree which carries it.

references

- Audergon J.M., Monestiez P., Habib R., Spatial dependences and sampling in fruit tree: a new concept for spatial prediction in fruit studies, J. Hortic. Sci. 68 (1993) 99-112.
- [2] Génard M., Bruchou C., Multivariate analysis of within-tree factors accounting for variation of peach fruit quality, Sci. Hortic. 52 (1992) 37–51.
- [3] Lespinasse J.M., Delort F., Carbonneau A., Conduite de Royal Gala. Étude comparative de différents systèmes, Arboriculture Fruitière 449 (1992) 30–37.
- [4] McLaren G.F., Knowler S.E., Glucina P.G., Alspach P., The influence of rootstock on tree habit and fruit quality in apricot cv. Sundrop, Acta Hortic. 384 (1995) 483–486.
- [5] Marguery P., Sangwan B.S., Source of variation between apple fruits within a season and between seasons, J. Hortic. Sci. 68 (1993) 309–315.
- [6] Robbie F.A., Atkinson C.J., Wood and tree age as factors influencing the ability of apple flowers to set fruit, J. Hortic. Sci. 69 (1994) 609–623.
- [7] Lespinasse J.M., La conduite du pommier, Brochure Invuflec-inra, Paris, France, 1977, 80 p.
- [8] Jay M., Cerise. Les variétés et leur conduite, Ctifl, Paris, France, 1997.
- [9] Scorza R., Characterization of four distinct peach tree growth types, J. Am. Soc. Hortic. Sci. 109 (4) (1984) 455–457.

- [10] Kester D.E., Asay R.N., Inheritance in F1 and F2 seedling populations of almond crossed with Dw/Dw and dw/dw peach. I. Growth habit traits, Hortscience 20 (3), abstract no 284 (1985) 561.
- [11] Monet R., Bastard Y., Gibault B., Étude génétique du caractère « port pleureur » chez le pêcher, Agronomie 8 (1988) 353–358.
- [12] Le Lezec M., Babin J., Lespinasse J.M., Masseron A., Tronel C., Chartier A., Les Delicious Rouges, Publication Inra/Ctifl, Paris, France, 1983, 68 p.
- [13] Lespinasse J.M., Delort F., Regulation of fruiting in apple. Role of the bourse and crowned brindles, Acta Hortic. 349 (1993) 229–246.
- [14] Kelsey D.F., Brown S.K., McIntosh Wijcik: a columnar mutation of McIntosh apple proving useful in physiology and breeding research, Fruit Var. J. 46 (2) (1992) 83–87.
- [15] Kester D.E., Gradziel T., Growth habit trait nomenclature in almond and peach phenotypes, Hortscience 25 (9) abstract no 64 (1990) p. 1072.
- [16] Lauri P.É., Lespinasse J.M., Delort F., Térouanne E., Rodriguez R., Analyse des branches fruitières et régularité de fructification, Fruits Légumes 146 (1996) 23–27.
- [17] Lauri P.É., Lespinasse J.M., Delort F., Térouanne E., Rodriguez R., Régulation de la ramification et fructification, Fruits Légumes 147 (1996) 26–28.
- [18] Lauri P.É., Lespinasse J.M., Térouanne E., Relationship between the early development of apple fruiting branches and the regularity of bearing. An approach to the strategies of various cultivars, J. Hortic. Sci. 72 (4) (1997) 519–530.
- [19] Germain É., Le noyer. In: Gallais A, Bannerot H. (Éds), Amélioration des espèces végétales. Objectifs et critères, Inra, Paris, France, 1992, pp. 620–632.

- [20] Laurens F., Use of apple genetic resources in apple breeding programmes at Inra: present status and perspectives, In: Case H.J. (Ed.), European Malus Germplasm, Proc. ECP/GR meeting, June 21–24, 1995, Wye college, London, UK, IPGRI, 1995, 69–73.
- [21] Germain É., Inheritance of the late leafing and lateral fruitfulness in walnut (*Juglans regia* L.). Phenotypic correlations among some traits of the trees, Acta Hortic. 284 (1990) 125–134.
- [22] Durel C.E., Laurens F., Fouillet A., Lespinasse Y., Utilization of pedigree information to estimate genetic parameters from large unbalanced data sets in apple, Theor. Appl. Genet. 96 (1998) 1077–1085.
- [23] Lauri P.E., Lespinasse J.M., Laurens F., What kind of morphological traits should be sought in apple seedling progenies in order to select regular bearing cultivars?, Acta Hortic. 451 (1997) 725–729.
- [24] Kervella J., Pfeiffer F., Pagès L., Génard M., Serra V., Taking into account relationships between ecophysiological processes in the breeding for peach tree characteristics, Acta Hortic. 465 (I) (1998) 145–154.
- [25] Kervella J., Pagès L., Génard M., Genotypic differences in the length-diameter relationship of branches of one-year-old peach and nectarine trees, J. Am. Soc. Hortic. Sci. 119 (3) (1994) 616–619.
- [26] Génard M., Pagès L., Kervella J., Relationship between sylleptic branching and components of parent shoot development in the peach tree, Ann. Bot. 74 (1994) 465–470.
- [27] Fournier D., Guédon Y., Costes É., A comparison of different fruiting shoots of peach trees, Acta Hortic. 465 (2) (1998) 557–565.
- [28] Costes É., Guédon Y., Modelling the annual shoot structure of the apricot tree (cv. Lambertin) in terms of axillary flowering and vegetative growth, Acta Hortic. 416 (1996) 21–28.
- [29] Costes É, Guédon Y., Modelling the sylleptic branching on one year-old trunks of apple cultivars, J. Am. Hortic. Sci. 122 (1) (1997) 53–62.

Inclusión de los caracteres arquitectónicos en los programas franceses de mejoramiento genético de las especies frutales.

Resumen - Introducción. Los principales programas de mejoramiento genético (Pmg) llevados a cabo sobre especies frutales leñosas por el INRA conciernen los albaricoqueros, cerezos, melocotoneros, perales, manzanos y nogales. Esta revista analiza cómo los seleccionadores consideran las características del árbol. Variabilidad genética. Las características más utilizadas son el vigor, el porte del árbol y su modo de fructificación. Se analiza la variabilidad expresada por estos principales principios arquitectónicos para las diferentes especies estudiadas. Integración de las características del árbol en los esquemas de mejora. Se exponen los criterios de selección y su lugar en los diferentes Pmg. La resistencia a los bioagresores y la cualidad organoléptica de los frutos son los dos objetivos principales para la mejora; el porte del árbol es sólo un objetivo complementario. Únicamente los Pgm de nogales y manzanos han desarrollado estrategias específicas de crecimiento con el objetivo de crear nuevas variedades de fructificación rápida y de producción alta y regular. Discusión y perspectivas. Los criterios actualmente empleados para apreciar la arquitectura de los híbridos son a menudo demasiado complejos, descriptivos, interrelacionados y dependientes de las condiciones edafoclimáticas y de cultivo. Exceptuando el nogal, sólo sirven para describir a los híbridos y no para efectuar selecciones entre la descendencia. Los nuevos estudios que se están realizando deberían aportarnos nuevos criterios más eficaces para la selección. Conclusión. Actualmente, las características del árbol no se emplean suficientemente para la selección. Los estudios realizados sobre arquitectura, morfología, fisiología y rama fructífera del árbol deberían permitir la próxima definición de nuevos criterios más adaptados a las esperanzas del mejorador.© Éditions scientifiques et médicales Elsevier SAS

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152 Fruits, vol. 55 (2)