Basic considerations about pruning deciduous fruit trees

C. Giulivo

Dipartimento Agronomia Ambientale e Produzioni Vegetali - Agripolis, Università degli Studi di Padova, Via Romea, 16, 35020 Legnaro (PD), Italy.

Abstract: Crop yield and fruit quality performance determine the economic value of the orchard system. Once the basic traits of the orchard design are defined, pruning may represent a powerful tool to modulate the vegetative and productive behaviour of the trees. The various pruning manipulations involve variations in growth, size and geometry of the plant and their effects are explained in terms of correlate functions among the tree organs. In spite of its potential, pruning can not overcome the effects of some basic mistakes made in design and management of the orchard. Basic concepts about pruning developed in the past are reassessed in light of recent knowledge on architecture and growth of the tree.

1. Introduction

Yield and quality performance of fruit crops results from the co-ordinated and integrated functioning of several components which constitute the "orchard system". This system must be carefully assembled in all its components in order to respond to the diverse environmental, social and economic constraints.

Designing the system means to define the physical arrangement of the trees, their shape and all the agronomic practices to apply during the entire life span of the orchards. All the system components must be implemented at the time of the orchard design determining its basic traits such as planting density, training system, and scion and rootstock combination. In addition to these physical traits it is necessary to define the proper pruning strategy to be adjusted year by year to the chosen training system taking into account also the agronomic operations direct to the management of the soil root relationship.

Pruning is the basic tool to manipulate fruit tree architecture and behaviour in order to achieve economically sound crop yield and fruit quality. "Pruning" includes a very large and diversified number of operations involving the aerial organs and the root system, performed both during rest and vegetative season (for a glossary of pruning terms see: Baldini and Scaramuzzi, 1962; Liebster and Pesserl, 1982; Ingels *et al*., 2002). Once the major traits of the orchard have been defined, the pruning strategy may then enter into discussion. The main objective in training fruit trees is the modulation of competition among the vegetative and reproductive parts of the tree, which essentially means the manipulation of the source-and-sink relationships occurring in the plant taking into account other basic objectives such as light interception and distribution in the canopy, and biomass partition properly directed toward the fruits.

The relationships between pruning and processes of growth, fruit bearing and senescence assume a strategic relevance as almost every pruning operation affects the growth of a tree or its organs on either a short- or long-term scale. Pruning is a very powerful tool but it cannot overcome the effects of basic mistakes in design and management of the orchard. The significance of the architecture and growth traits of trees and their relationships with reproductive activities are essential to understanding how pruning may affect the functioning of the orchard system.

In this paper the principal aspects of plant architecture and growth relevant to pruning are examined; since "pruning" includes many diverse operations, a large range of combinations of winter and summer pruning manipulations is possible and therefore their potential effects on tree behaviour are considered and explained in terms of the source-and-sink relationship and competition among sinks.

A number of the references cited in this paper may seem dated, but it must be said that studies and experiments on pruning have recently become rare whereas during the 1980s and '90s scientists, researchers and field experts paid great attention to this inalienable orchard management practice. Italian contributions to the knowledge of the physiological and practical basis of pruning have been particularly important, as shown by fundamental papers and reference books on this topic (Dotti, 1949; Morettini, 1963; Bargioni, 1992; Sansavini and Errani, 1998; Branzanti and Ricci, 2001). It seems, however, useful to reas-

sess these contributions in light of recent knowledge on the architecture and growth of trees.

2. Tree architecture

The identification of tree architecture traits is relevant to the pruning strategy. According to Costes *et al*. (2006) plant architecture includes two independent notions: branching and connection between plant units (topology), and the spatial location, orientation, size and shape of the vegetation elements (geometry). Tree architecture includes physical structures and physiological functions of fruit trees, and is therefore related to space and time aspects. The multilevel approach of the tree (whole tree, branch, leaf and fruit) should be stated and tree architecture should be described by canopy height, width and shape, by fruiting and vegetative shoot types and their relative proportions, spatial distribution, branching, and growth dynamics. Canopy porosity or density should also be considered as light interception and distribution, and pest occurrence are concerned (Simon *et al*., 2007).

The orchard structure, function and production may be understood if, in addition to tree architecture, phenotypic plasticity and phenology are considered. Trees are modular organisms which develop by reiteration of elementary botanical elements whose anatomical, morphological, dimensional and functional traits change during ontogeny and accordingly to various life stages (Bathélémy and Caraglio, 2007). During ontogeny plant appearance varies with form and/or structure and with temporal and/or topological changes and, therefore, it is of high practical relevance to orchard design and management (Fig. 1).

Tree architecture depends on the nature and relative arrangement of each of the tree's parts. At any given time, the architecture is a result of equilibrium between internal growth events and external environmental constraints. Pruning must take into account this natural fact and hence it must follow the natural behaviour of the fruit tree and direct it toward the desired economic goals.

The main morphological traits used in describing tree architecture are the growth processes, branching modalities, morphological differentiation of axes and location of the reproductive structures (Barthélémy and Caraglio, 2007).

Growth processes. Organogenesis and extension are two distinct but co-ordinated morphogenetic events that result in the primary growth of a plant. These events basically determine the stem of a plant, which can be considered a succession of internodes and nodes, on which a leaf (or leaves) and axillary bud (or buds) are located; the node and the subtending internode represent the basic structural unit of the plant body (metamer or phytomer).

A tree, whatever its final size, is initially formed by the activity of at least two primary meristems, one to develop the aerial part and one the root system, but the subsequent increment in diameter of woody axes (aerial and subterranean) is determined by the activity of secondary meristems.

In many species, the apex of the aerial axes may abscise or abort after a time of functioning or it may shift
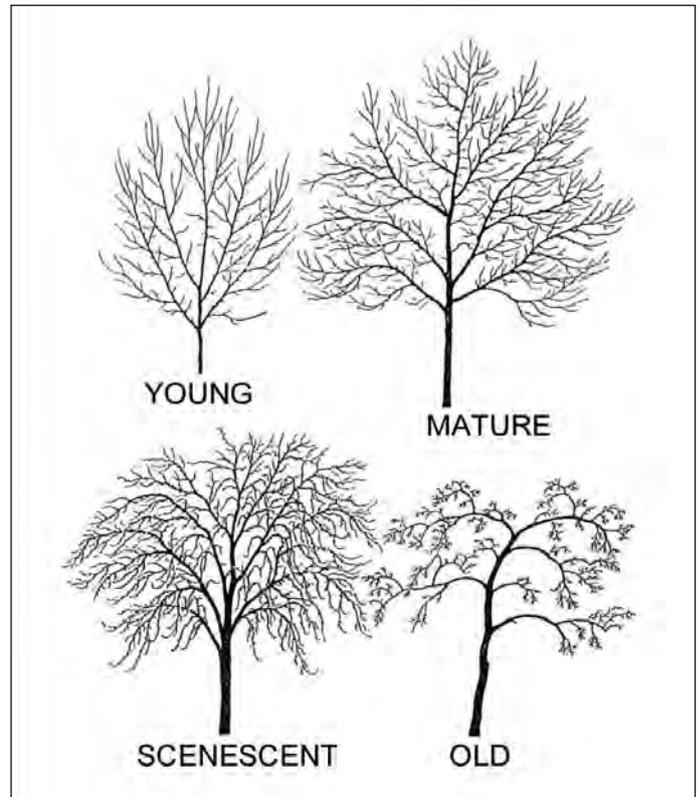

Fig. 1 - Evolution of the tree crown during plant life (from Hilkenbäumer, 1953).

into reproductive structure or other organs: this behaviour is defined as determinate growth. On the other hand, when the apical meristem of the axes maintains indefinitely its growth potential, an indeterminate growth (or extension of the axis) occurs.

Continuous growth occurs when a shoot does not show a marked endogenous cessation of extension, a case usually occurring in uniform equatorial climates or environments. When a shoot shows marked endogenous extension periodicity and cessation, rhythmic growth occurs. Rhythmic extension of leafy shoots is the typical pattern of deciduous fruit trees in which meristem activity shows an alternation of periods of rest and of active extension. The rest period marks on an axis portion a zone of short internodes and/or cataphylls corresponding to the protective organs of the bud from which the axis derives. Rhythmic growth of the stem may combined with continuous or more frequently with a rhythmic organogenesis pattern.

Preformation and neoformation. When metamers and organs of a shoot are already present in the bud before the elongation of the axis deriving from it, the shoot is called preformed. In other cases, more metamers and organs than those included in the bud appear on the shoot and are neoformed by the apical meristem. Fruit trees show a strong polymorphism in axis development (Costes *et al*., 2006) (Fig. 2). Preformed shoots are usually short axes (brachyblast) which after bud burst elongate slightly due to the extension of the preformed metamers. In horticulture short shoots are referred to different names according to the species and to their reproductive or vegetative structures. In stone fruit

species, they are called 'leaf rosettes' or 'clusters' if they bear, respectively, only leaves or an apical vegetative bud and a variable number of lateral flower buds. In pome fruit species, the short preformed shoots are called 'dards' when they are vegetative or 'spurs' when they bear also flowers (Fig. 2). In many fruit species (cherry, apple and pear trees in particular) the spurs can be one-year-old brachyblasts or consist of a perennial set of branched shoots, which have all remained brachyblasts. Longer shoots may be also preformed (mesoblasts) and in this case their limited length derives only from the elongation of internodes; mesoblasts can carry only vegetative buds or carry some lateral flower buds (stone fruits) or an apical fruit bud (pome fruits) and, in any case, are called 'brindles'(Fig. 2). Preformation and neoformation can also be combined to produce much longer shoots (auxiblasts) in fruit trees; they are usually vegetative axes in pome fruits (Fig. 2), whereas in stone fruits they can bear numerous lateral flower buds as in peach tree.

Fig. 3 - Evolution of a one-year axis (A) into two-year (B) and three-year (C) branches.

Fig. 2 - Polymorphism of the axes on an apple branch. *Left*: S (brachyblast) and BS (brachyblast on a bourse) and BR (mesoblast) are preformed shoots, LS (auxiblast) are preformed and neoformed shoots. *Right*: Long shoot, brindles and spurs on a bourse.

Branching process. The complex architecture of a tree consists of several axes, one derived from another by repetitive processes (Fig. 3). The branching process is based on axillary meristems located just beside the initiated leaf at a node. More than one axillary bud may be found at the axil of a leaf as in the case of mixed shoots of peach trees or other stone fruit species.

The branching pattern of an axis can be monopodial or sympodial according to its indeterminate or determinate growth pattern, respectively. In the case of a sympodial pattern, one, two or more branches may develop after the death, abscission or transformation of the apex. In fruit trees one or two branches arise more commonly. Rectilinear stems may be composed of a succession of metamers or growth units or annual shoots, all produced by a single meristem or by a linear succession of sympodial modules (Barthélémy and Caraglio, 2007).

Continuous branching occurs when all the axillary meristems of a stem develop into lateral shoots; rhythmic branching occurs when lateral axes are grouped as distinct tiers with an obvious regular alternation of unbranched and branched nodes on the parent stem. Branching may be diffuse if only some nodes of the parent axis bear a lateral
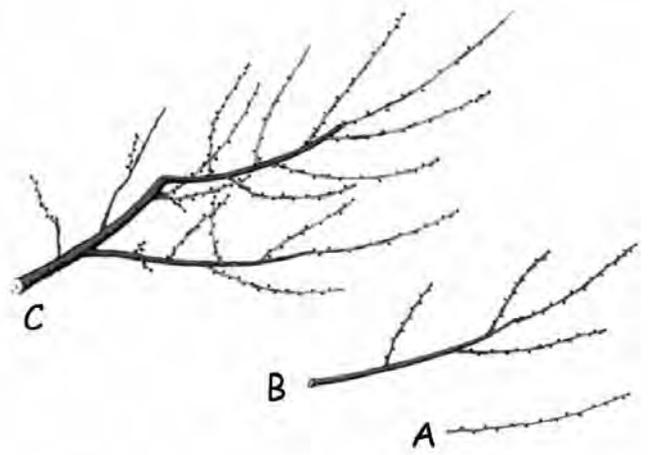
axis or if a regular distribution of branches in tiers is no evident.

Acrotony, basitony and mesotomy. The positional preferential development of lateral branches on a vertical parent axis may be classified into three categories. Acrotony is the prevalent development of lateral axes in the distal part of the parent axis or shoot, whereas basitony consists in the prevalent development of branches on the proximal part; mesotony is used to denote a privileged development of branches in the middle part of the axis. The topological arrangement of lateral branches along a parent axis is often associated with an increasing or decreasing gradient in length and/or vigour of the branches. In fruit trees, all three categories of lateral axis development are present with some variations even in the same species. The topological arrangement of branches in the tree crown can be strongly modified by pruning.

Hypotomy, epitomy and amphitomy. Considering that an axis may diverge from the vertical, the privileged arrangement of lateral axes on a parental axis is very different if this is horizontal, curved or slanted. The privileged zone may be the upper, lateral or basal position of the parent axis and the terms are respectively epitony, amphitony and hypotomy (Fig. 4). In many fruit trees epitony is

Fig. 4 - Development of lateral axes on an axis. Slanted parent axis of peach tree (left) and curved parent axis of apple tree (right).

a very common feature (Costes *et al*., 2006), it is often associated with the survival of old branches in old trees (Fig. 5). Hypotomy is characterized by a privileged development of lateral axes in the curvature zone of a branch. Amphitony occurs frequently on rectilinear horizontal or slightly slanted branches. The latter two features may be combined in slanted and curved branches and their incidence in the expansion of lateral branch complexes is of the outmost importance in the aerial architecture of many woody plants. Amphitony is a frequent behaviour in rectilinear branches while epitony and hypotony are characterized by the predominant development of lateral axes on the convex side of the curved, downwardly- or upwardly-oriented branches. As they are highly influenced by axis orientation, these branching features are frequently combined with topological arrangement along axes (acrotony, basitony, mesotony) and these combinations can strongly influence the bud fate according to their topological position and space orientation within the tree canopy.
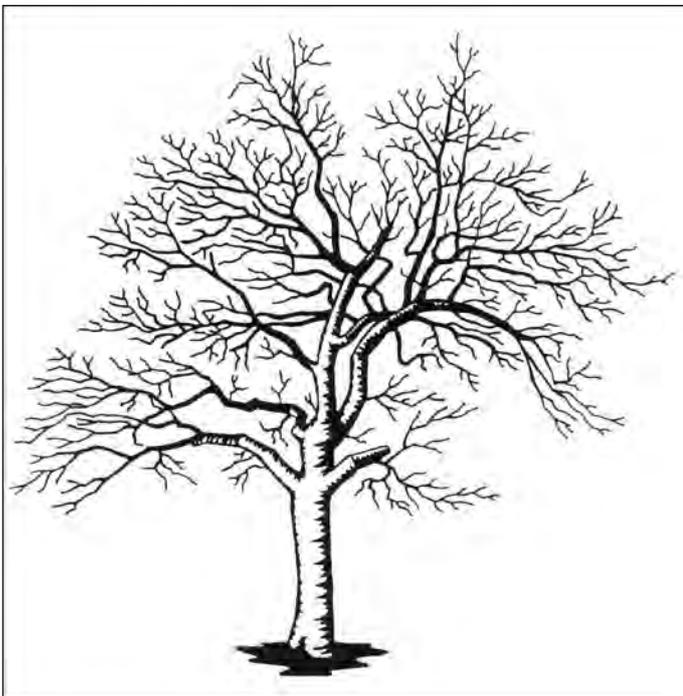

Fig. 5 - Evident epitomic behaviour in an old apple tree (from Liebster and Pesserl, 1982).

Polymorphism of axes. The orientation of an axis and the spatial disposition of its leaves are of major importance in the growth strategy of a tree. Within a single tree, some of these axes are essential in plant skeleton edification; some are involved in space exploration whereas others are more directed toward reproductive function or light interception and photosynthesis. The differentiation of axes and bud fate may be highly specialized and very different structures (i.e. flowers, inflorescences, spine, shoot, etc.) may be found in a single leaf axil and in a precise position, but the differentiation of an axis may not be an irreversible process. Depending on modifications of internal or external conditions or after architectural traumatism or ma-

nipulation (pruning), reversion of axis differentiation may frequently occur, indicating that shoot differentiation and bud fate are controlled by a whole plant network of correlated and environmental conditions. The polymorphism of axes is common in fruit trees and represents a morphological differentiation determined by meristem expression and activity. It is common that several types of axis coexist on the same individual tree. However axis specialization is very significant when a tree is trained and pruned for fruit production since in this tree a balanced distribution among skeleton axes, reproductive axes and vegetative axes used for renewal fruiting shoots (Fig. 6) must be found.
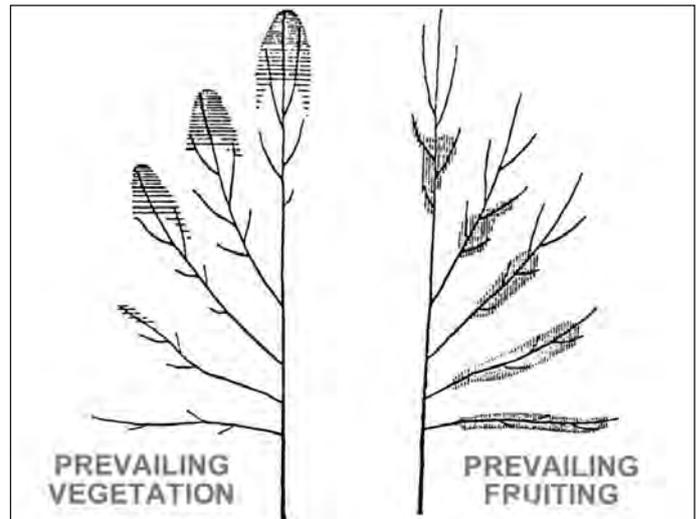

Fig. 6 - In the tree canopy the polymorphims of axes is differently located. In some parts vegetative structures prevail and in others reproductive structures are predominant (redrawn from Hilkenbäumer, 1953).

Orthotropy, plagiotropy, and mixed axes. Orthotropic axes are generally erect to vertical with a radial symmetry, bear leaves in spiral, opposite or verticillate disposition, and lateral axes in all spatial directions; orthotropy is generally associated with plant skeleton edification and the colonization or exploration of vertical space. By contrast, horizontal to slanted oriented axes (plagiotropy) show a bilateral symmetry with distichous phyllotaxis and lateral axes arranged in one plane; plagiotropy is generally concerned with exploration and exploitation of the horizontal space and reproductive functions.

In many trees an axis may present an orthotropic proximal portion and a plagiotropic distal end or vice versa. The superimposition of such "mixed axes" is a distinctive feature of trunk edification in trees, but it can be strongly manipulated by pruning (Fig. 7).

The position of sexuality and reproductive organs can be terminal or lateral and the onset of these organs involves dramatic changes in the architecture of the trees because its impact on plant growth and branching. The lateral or terminal position of reproductive organs is of great relevance for the orientation of the axis that supports the organs (Fig. 8).
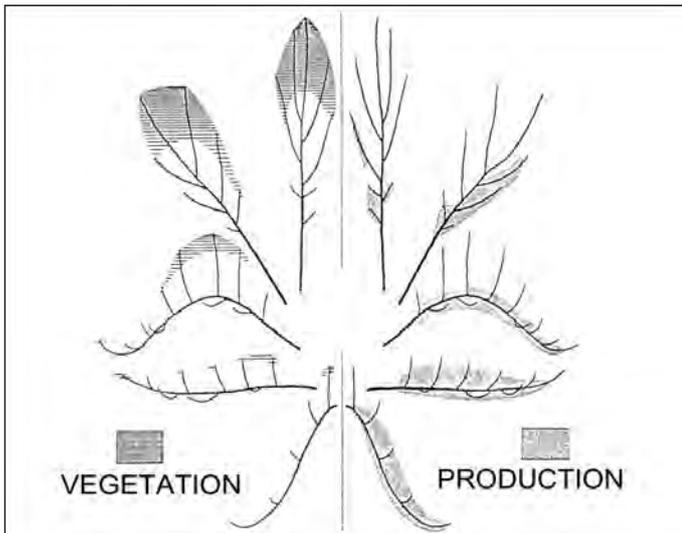
132

Fig. 7 - The relative location of vegetative and reproductive activities may be changed by variations of growth direction of axes imposed by pruning.
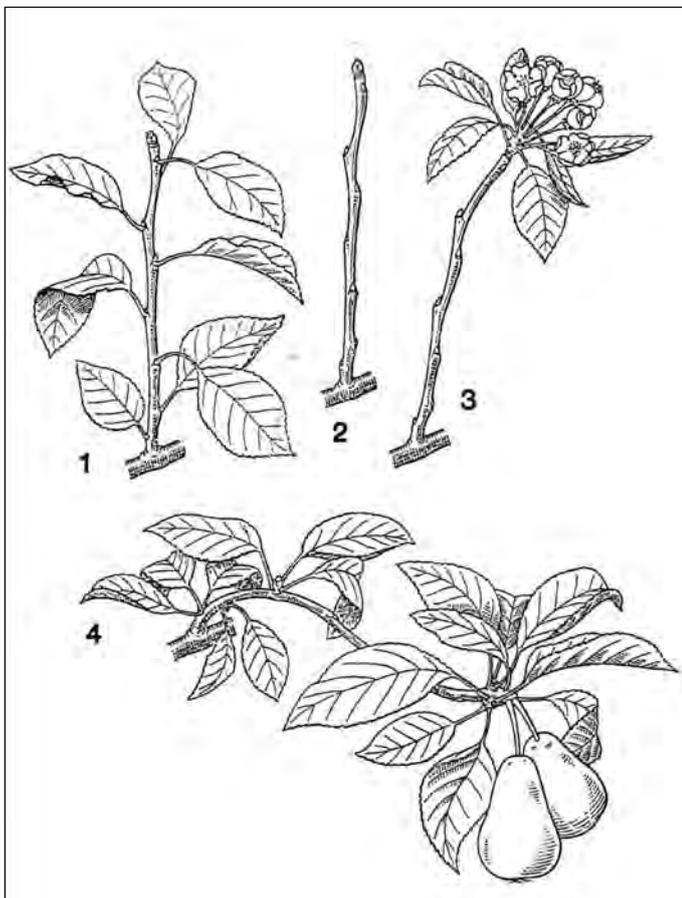

Fig. 8 - Natural variation in growth direction of a pear brindle with an apical fruit bud (from Grisvard, 1957).

Architectural model. The growth pattern of a fruit tree species which determines the successive architectural phases must be taken into account if a proper and specific training and pruning is to apply to the trees. The architectural model derives from an inherent strategy that defines both the manner, in which the plant elaborates its form, and the resulting structure. The model results from the nature and the sequence of activity of endogenous morphogenetic processes as determined by the basic growth program on which the entire architecture is established and realized under the environmental and cultivation constraints.

A particular combination of simple morphological features may identify typical architectural models: a) the growth pattern (determinate vs. indeterminate growth; rhythmic vs. continuous growth); b) the branching pattern (terminal vs. lateral branching vs. no branching; monopodial vs. sympodial branching; rhythmic vs. continuous vs. diffuse branching; immediate vs. delayed branching; c) the morphological differentiation of axes (orthotropic vs. plagiotropic vs. axes with orthotropic and plagiotropic portions); d) the position of reproductive structures (lateral vs. terminal fruiting) (Barthélémy and Caraglio, 2007).

The tree architecture can be considered a hierarchical branched system in which the axes are grouped into categories according to their morphological, anatomical or distinctive functional features. This branch system, even if very complex, is composed of a simple sequence of axes characterizing its basic architecture. The simple architectural unit lasts during the whole life span of some tree species while in most trees it is possible to recognize repeated architectural units during their development, late in ontogeny, or under particular conditions. This process is called "reiteration"; more precisely it is a morphogenetic process through which the tree duplicates its own elementary architecture. This process may be demonstrated in several structures such as water shoots, root suckers, etc. These reiterated structures may derive from dormant meristems and in this case are called proleptic or delayed. In other cases, reiteration may be a consequence of a shift in the functioning of the apical meristem of a growing shoot that will finally produce a less differentiated structure; in this case, the reiteration is described as sylleptic or better immediate.

The trees develop by the repetition of elementary construction units conforming to their model and a differentiation sequence in the activity of their whole set of meristems. The specific and exact structure of a particular organ in a given location within the architecture of the tree may be considered as the result of a complex of several ontogenetic and morphogenetic factors that influences all plant organization levels, at each stage of plant development and during its whole life span. Although environmental factors may modulate these sequences of differentiation, they almost never modify the inherent morphogenetic and ontogenetic constructional project of the plant organization. This is also true for horticultural manipulations such as training and pruning, confirming that it is advisable to follow the fruit tree's development without radically changing its vegetative and reproductive behaviour. In other words, the branching order of an axis must be respected since the higher the order, the higher its degree of differentiation. When the architecture of a branched tree must be manipulated, the modification must be carefully considered according to the specific branching pattern, gradients (acrotony, basitony, mesotony) and the axis spatial orientation and/or geometry (hypotony, epitony, amphitony). In a given plant species, or even in a

133

single tree, very different situations may be observed: at a given stage of development, homologous botanical structures with different features coexist on the same individual (e.g. short vs. long shoots or reproductive vs. vegetative shoots) whereas, by contrast, similar elementary structures with the same morphological features (short shoots with vegetative or reproductive features) may be observed in very different plant ages or stages of development.

This may be defined as the physiological age of the meristem, which may generally be characterized by a particular combination of several morphological, anatomical and/or functional attributes of a given plant structure derived from this meristem. The physiological age of the meristem depends on its location in the plant architecture and on the stage of development of the plant; its expression may be modulated by environmental factors and obviously by cultural practices, particularly by pruning (Fig. 9). The physiological age of a meristem relates to the degree of differentiation of the structure it produces. Typical features of the physiologically aged structures are, for example, the short axes of many trees: growth units are short, bear flowers and may have a short lifetime. These highly differentiated axes may be considered physiologically old whatever their moment of appearance. By contrast, main axes consisting of vigorous growth units and/or annual
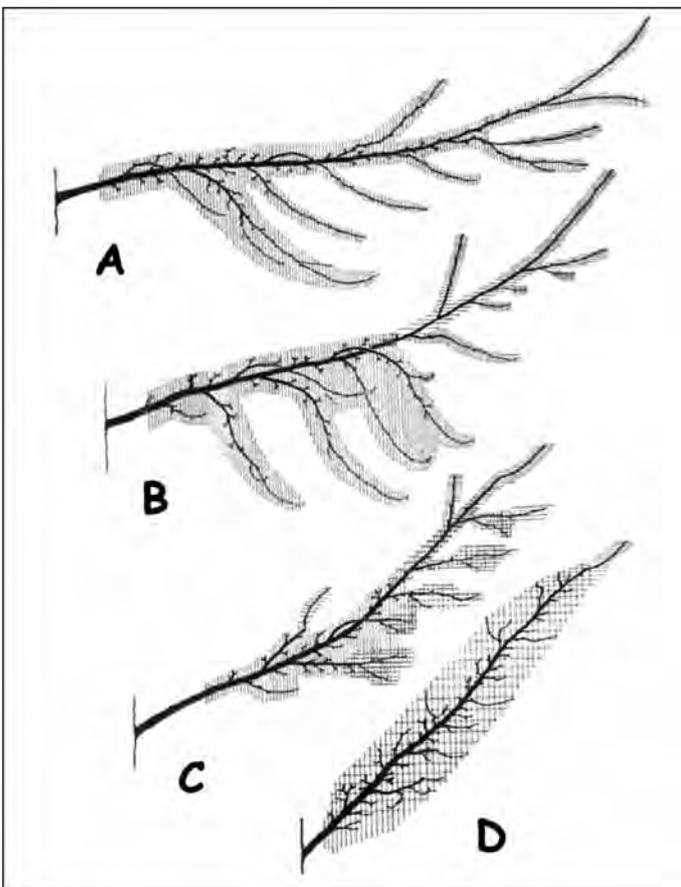

Fig. 9 - Formation of lateral axes of different types and ages on an apple tree branch pruned according to the various pruning criteria used in four training systems, which diverge from the natural behaviour very little (A) to very much (D) (redrawn from Hilkenbäumer, 1953).

shoots may be considered physiologically young products and generally appear only in young trees or in strongly pruned fruit trees. Identification of meristem age of is very important in order to understand the comprehensive architecture of a plant or even its plasticity, i.e. the effects of the environment and/or of cultivation practices on its development and structure (phenotypic plasticity).

3. Tree growth

The growth of a living being means the irreversible increase of dry matter, and more currently the term is used for any positive variation in shape, size or fresh weight of an individual or a part of it. Trees are characterized by secondary growth processes and by a continuous formation of woody tissue, part of which is non-living biomass. The woody part has the essential functions of tree support, sap transport, and storage of water, nutrients and carbohydrates. From the stand point of modern horticulture, trees of large size are not desirable because they invest a large part of energy and resources in building up and maintain their woody frame. The growth rate of the whole tree is of great economic meaning since it determines, in addition to dry matter accumulation, other important events such as the overcoming of juvenility (if the tree develops from a seed), the duration of the initial low productivity stage, and the acquisition of high fruiting and competing capability. Practically speaking, in a grafted fruit tree a fast initial growth rate is an economic advantage for rapidly attaining its definitive size, which in modern fruit trees should be as small as possible in order to realize a high ratio between fruit load and woody frame (Bargioni, 1988).

Tree growth (i.e. permanent increase of dry matter) is balanced between the development of new leaves and new roots. The new leaves exert a positive feedback on the assimilate production and similarly the new roots a positive feedback on absorption of more water and nutrients.

At the beginning of a tree's life, the major part of assimilates produced by the leaves is invested in the construction of the root system. As long as the root system does not achieve an adequate size to supply a sufficient amount of water and nutrients, the reproductive potential of the tree remains zero or extremely low. During maturity the canopy-root ratio is relatively stable and fruiting is kept more or less constant. When the tree attains a given size, the costs of maintaining the structure become very high and fewer and fewer resources are available to sustain root system growth, since its competition potential is weak in relation to other plant organs, particularly fruits. Less water and nutrients are then available to the crown, reducing net photosynthesis and assimilate potential and, as a consequence, senescence of the tree is triggered. The net investment of the various resources which enter in and exit out of the tree and partition of the biosynthesis products are two important determinants of the balanced growth of a tree. Water, nutrients, carbohydrates, organic acids, lipids, proteins, hormones etc. may be utilized in different

134

ways and times in relation to the physiological balance of the tree. The amount and partition of photosyntates gives a good indication of the growth potential of the tree or of its organs because they are the source of energy which can be used at the time or stored. Source-sink interactions, that is the transitory destination of assimilates and their final partition, determine the rate and expression of the relative growth of the plant organs and therefore the architecture and size of the tree.

The aim of tree and orchard management is to channel the major part of assimilates toward the reproductive structures, limiting that directed toward other plant organs without affecting the functioning of the whole system.

Individual tree architecture can vary greatly based on the growth strategy of the plant but can be modified by the environment and cultivation conditions (phenotypic plasticity). An example related to orchard design is the competitive stress induced by planting density (Fig. 10). In comparison to a widely spaced population, closely spaced tree populations have a more limited volume of soil available for the individual root systems and thus fewer resources are supplied to the tree canopy. With close spacing, individual trees are smaller and less branched, but the ratio between fruits and woody structure (or volume of the crown) is higher than in individuals in a widely spaced population. Not all plant characters are affected equally by the competitive stress, and some effects tend to be species- and environment-specific (Cannel, 1983). Light interception and distribution in the canopy may play a concomitant role in plant growth; in the tree canopy the behaviour at high incident irradiance depends on the degree of light saturation of the leaves, which in turns depends on their geometrical arrangement and the geometry of the tree, which determine the ratio between direct and diffuse radiation (Connor, 1983). From outside to inside the canopy the quantity of light decreases sharply, as does the light quality (Proctor, 1978). Taking into account the variation of light quality inside the canopy (visible light, red/far red, UV), plant form and reproductive performance may be different in dense or open canopies because of the photomorphogenic and photoperiodic effects (Connor, 1983). In stands composed of genetically identical trees, like orchards, the effects of competitive stress can be even more emphasized if appropriate pruning and management practices are not applied. The contribution of pruning to the shape, growth and functioning of the tree can be relevant but it does not introduce dramatic variations in the natural vegetative growth habit of the fruit tree.

4. Correlative functions

The correlative functions within an individual tree (i.e. competition and cooperation among the plant organs) deserve particular attention because they offer some basic concepts for pruning, which L.H. Bailey illustrated very well a long time ago in "The Pruning Manual" published
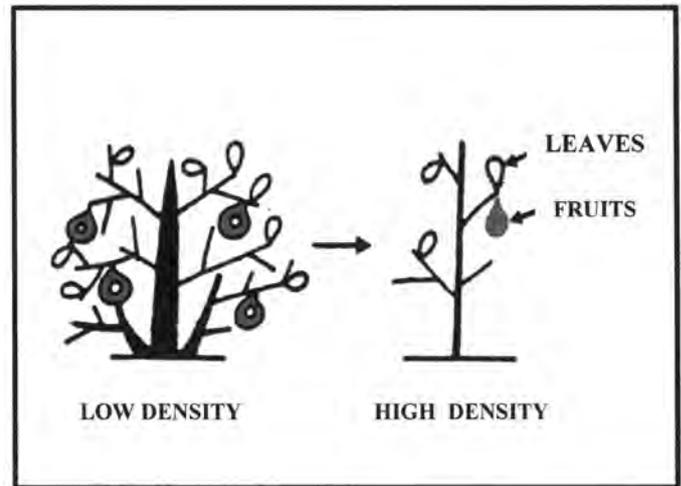

Fig. 10 - Effect of planting density on tree structure. Closely planted trees bear more fruits per unit canopy volume than widely spaced trees because of phenotypic plasticity (Cannel, 1983).

as first edition in 1898. It is worthwhile to report exactly what he wrote.

"A tree is essentially a collection or a colony of individual parts. Every branch, even every joint of the branches, may do what another branch does - it may bear leaves, flowers and seed. Every branch competes with other branches; and there are more germs of branches - that is, more buds - than there can be branches on any tree, or in any other plant that by its nature produces many branches. No two branches of a tree are exactly alike, but are what their position or condition or heredity makes them to be. Some are strong and some are weak. That is, there is no definite or proper size or shape for any branch, as there is for different members of an animal or of a flower. The limbs and organs of an animal are not competitors but co-partners, each performing some functions or office, that another does not, and they all attain a definite maturity of size and shape. But a branch in a tree-top never attains its full size until it ceases to grow and thereby begins to die. Branches are not so much organs as competing individuals. If all these statements are true, then three conclusions follow: there is a contest among the branches of a plant, and some of the contestants perish; the destruction of these branches may conduce to the betterment of those remaining; all the branches of a tree are not necessary to it, but some of them may be superfluous or detrimental to it. In other words, pruning may follow as natural course."

In this context the manipulation of trees by pruning is amply justified in an orchard. Citing again Bailey, "Of course there is a kind of partnership between the branches of a tree, for we assume that each strong branch makes a contribution to the development of the root-system and trunk-system, and there is not the same separateness as between wholly different plants; yet the contest between these branches is apparent, and it has special significance to the present discussion."

Of course these considerations may be extended to the other organs of the tree: buds, twigs, shoots, flowers, fruits and roots.

Taking into account the functional equilibrium between the size and activity of the shoots (carbon fixation) and size and activity of the fine roots (absorption of water and nutrients), that in a constant environment, favouring continuous growth, tends to maintain a constant ratio of root/shoot relative growth rates (Cannel, 1985), it is evident that removing a part of a tree by pruning represents a loss of a given amount of tissue and in replacing the lost part the tree expends a certain amount of assimilates. This may seem nonsense, but it is necessary to keep in mind the goals of the orchard, which are the economics and adjustment of tree-environment interactions. Tree vitality is not impaired by removing a part of it unless the removal is so great that it interferes with nutrition (growth) of the remaining parts, for example a great removal of photosynthetic leaf surface or of adsorbing roots.

Taking into account plant homeostasis, it is obvious that if part of the shoots or branches are removed, assimilates are devoted to rebuilding the lost part and fewer are directed toward the root system, and vice versa. If part of the roots are suppressed, the shoots resume their growth only when the pruned part of the root system is rebuilt and the root/shoot equilibrium is re-established, other aspects remaining constant (Richards and Rowe, 1971). Therefore, shoot pruning temporarily checks root growth, while root pruning temporarily checks shoot growth: the more pruned off, the greater the check in growth, and the longer it takes for the plant to recover the root/shoot relationship that existed before pruning. Thus, shoot pruning is a means of promoting new shoot growth, and root pruning is a means of promoting new root growth (Cannel, 1985). Therefore when part of the treetop is cut away, if not too severely, the tree resources are directed toward the remaining growing points and the tree develops, for example, more vigorous shoots. The consequence is that a correctly pruned tree appears more vigorous and also, as reported by Dotti (1949), more productive and long-living than an unpruned tree.

For the purpose of this paper, the genetic and metabolic processes causing and governing these correlative functions will not be considered but instead some of the most relevant organ and function competitions for the tree resources are addressed from a phenotypic point of view. Hierarchic but not univocal relationships are often established among tree organs and they contribute to the correlative functions that may involve organs of the same or different type.

5. Correlative relationships between organs of the same type

In this section relationships between meristems, buds, shoots, branches, flowers and fruits are considered. The most important correlative functions are those among the meristems present on a shoot since they originate all the organ typologies. The role of apical dominance, that varies amply according to genotype, development stage and environmental conditions, is known. Apical dominance also affects the functional relationships of the buds, determining different vegetative gradients along the shoot. These phenomena offer an important basis for pruning practices.

In peach the number of sylleptic shoots appeared to be related to the growth rate displayed by the parent shoot during the early part of the growing season (four to five weeks after bud break). Parent shoots with high growth rate formed sylleptic shoots in a greater number than the pinched back ones in which apical dominance was completely abolished. Therefore growth rate in the early growing season may play a stronger role than pinching in feather formation. Apex removal by pinching (summer pinching) changes the physiological status of a growing shoot, whereas bending affects only the shoot growth rate, thus its feathering (Giulivo and Ramina, 1974).

An interesting case, reported by Hilkenbäumer (1953), regards the number and distribution of buds on a tree. Three cases are considered and are shown in figure 11: a) when a tree carries a very high number of buds, on each axis a large number of weak shoots are produced and a part of buds remain silent; b) if all the axes are heavily and evenly pruned back, the number of buds is reduced and fewer but vigorous shoots originate in the same manner on each branch; c) if one axis is heavily pruned back and the other two lightly, weak shoots are produced by the former and strong shoots by the latter axes in contrast with case b. Cases a and b may be explained by the assimilate partition among many or few buds (Hilkenbäumer, 1953). For case c, which is more difficult to explain, it is suggested that the less pruned axes dominate the heavy pruned axis because they bear more buds and sprout earlier, becoming thus stronger sinks. This may be considered an example of the independence-competition among axes of a tree.

The fewer the shoots are allowed to grow with a severe pruning, the longer they are (Fig. 12). When only very few shoots are present on the tree, not only are they thicker with larger leaves and have longer internodes, but some of the lateral buds grow out to form short shoots or feathers (Abbot, 1984). The leading shoot (dominant position) is however always longer than those below it (Fig. 13). Whichever parent axis is manipulated (Fig. 14), there is
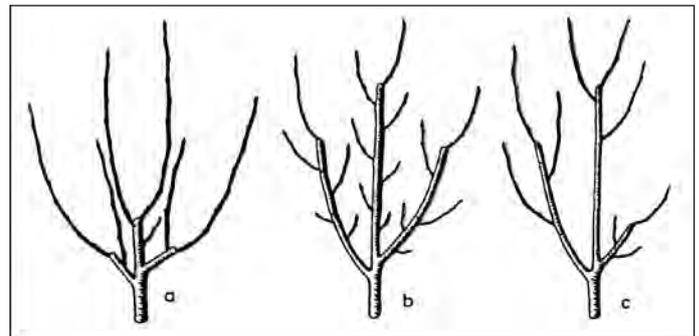

Fig. 11 - Vegetative responses of branches headed back with different intensities (A and B) or uneven intensity (C) (redrawn from Hilkenbäumer, 1953).

always one lateral axis that assumes dominance over the other axes. These factors clearly indicate the competition between homologous vegetative organs.
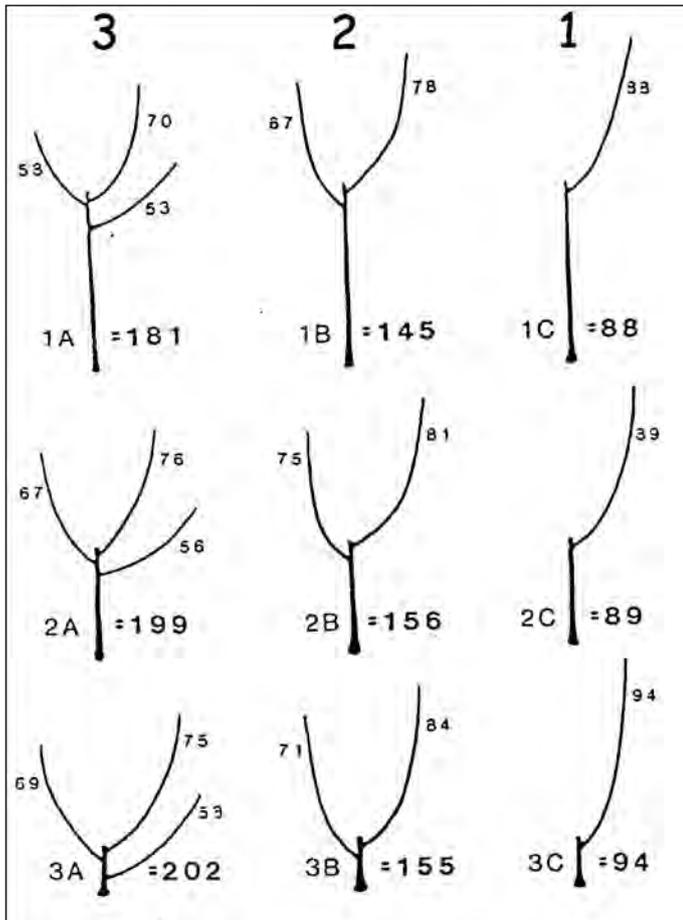

Fig. 12 - Effects of light, medium and severe pruning (one, two, three shoots on a headed-back one-year-old apple tree) (Abbott, 1984).

Fig. 13 - Elongation in apical (A), sub-apical (B, I) long shoots and in brindle (Br) shoots of three cultivars of peach tree with different ripening time (Giulivo *et al.*, 1981 a).
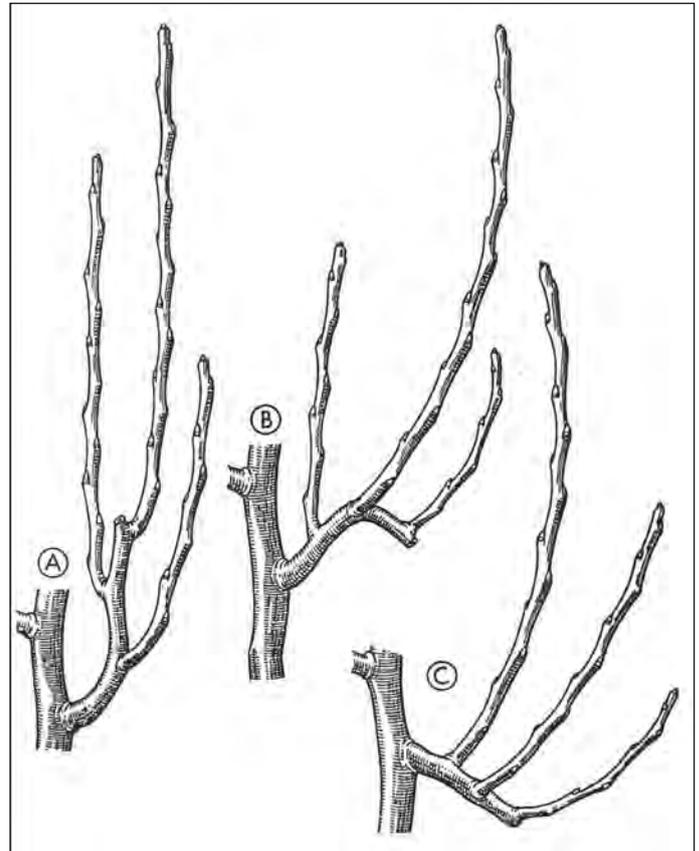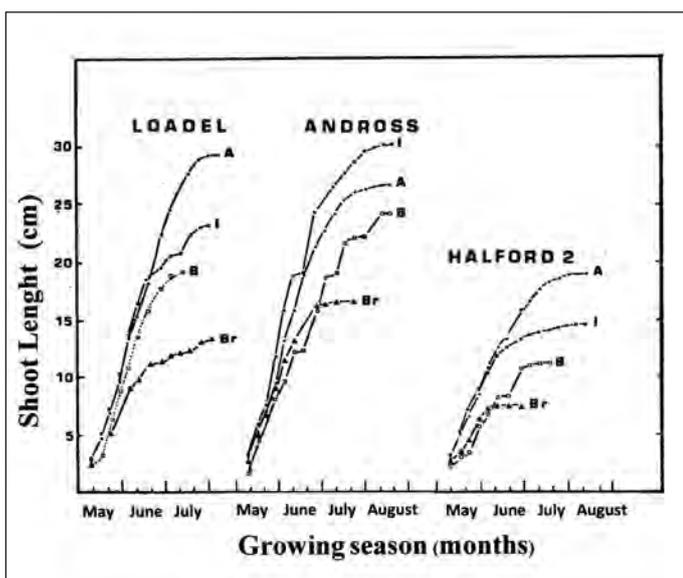

Fig. 14 - Position of the dominant shoot in headed-back vertical (A), curved (B) and slanted (C) parent axes (da Grisward, 1953).

A typical case of competition among homologous organs is the high abscission potential or reduced development and growth of fruits that are located, respectively, below or above the fruit that sets first in the corymbs of apple and pear trees (Fig. 15). The effect of fruit set priority on competition was also reported in peach tree where the fruitlets which set first and start to grow rapidly have the lowest probability of abscission (Ramina 1981; Giulivo *et al.*, 1981 b).

6. Correlative relationships between organs of different types

The strength of relationships among organs are dynamic and change over the growing season and year. Usually the organs that have the larger mass (size) and grow more actively dominate the other organs of the plant. The relationship between vegetative and reproductive structures is a typical case. When shoot growth is very intense, fruit growth is limited and vice versa (Fig. 16) (Giulivo *et al.*, 1981 b; Pitacco and Giulivo, 1992).

In an unpruned tree parts of canopy exist where vegetation dominates and parts where fruiting is prevalent. The position of a vegetative axis in space determines the vegetative-reproductive relationship (Fig. 6); in a vertical axis the vegetative activity is strongly favoured and fruiting is repressed. If an axis occupies a lower position in

Fig. 15 - Competition of the first setting fruitlet over the other fruitlets of the same corymb of pear (left) and apple tree (right).
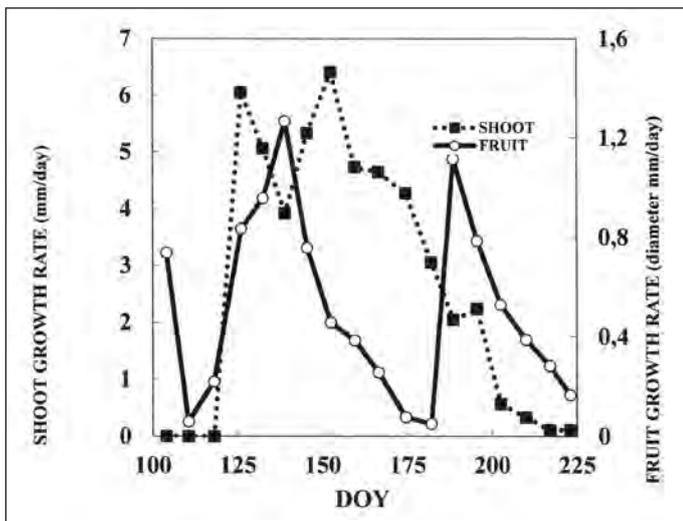

Fig. 16 - Seasonal growth rate of shoots and fruit of peach tree, cv. Andross. When the former is high, the latter is low, and *vice versa* (Pitacco and Giulivo, 1992).

the crown and tends toward a plagiotropic position, the relationship is reverted. This phenomenon obviously offers a great opportunity to manipulate a tree with winter and summer pruning. It can be assumed that every manipulation limiting growth can increase the reproductive activity, i.e. fruit bud differentiation and fruit development and growth. Two typical cases may be reported: a) by bending, the elongation rate of a growing shoot is decreased but bud differentiation is favoured; b) with limited nitrogen availability the vigour of the tree is depressed but the fruiting capability is increased (Hilkenbäumer, 1953).

The relationship between fruitlets and shoot carried by a bourse of apple tree can be an interesting case of transient competition between a leafy shoot and a reproductive organ carried by the same plant structure (brachyblast). Usually the fruitlets carried by the bourse corymb present a steady abscission for some weeks after full bloom but, if the shoot of the bourse is removed early, fruitlet abscission is delayed and reduced; the fruits on bourse deprived of the shoot growth less and at their final size results much smaller than that of fruits on a normal bourse carrying a shoot (Abbot, 1984). This is a consequence of fruit abscission in the

corymb, but it may also be an effect of the transport of assimilates to the fruit which takes place when the leaves of the bourse shoot become active exporting organs.

As the season progresses, the developing fruits have an increasing demand for assimilates: after some weeks from fruit set they are diverted from shoot and root growth, bud differentiation and later from reserve storage. Increasing the fruit load has a dramatic effect: fruit bud differentiation is progressively reduced to a certain threshold, beyond which it is completely abolished (Fig. 17).
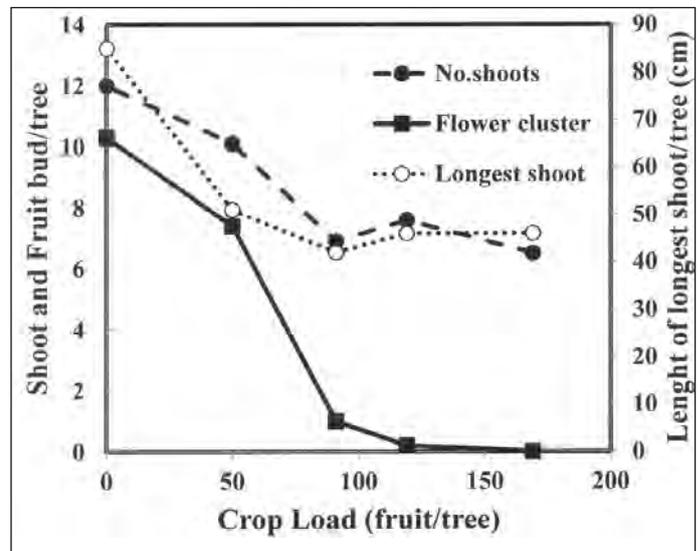

Fig. 17 - Effects of increasing fruit load of apple tree on shoot and fruit bud formation and on elongation of the longest shoot. (Abbott, 1984)

The presence of fruits on the tree slows down the formation of fruit buds as long as the fruits remain on the tree (Fig. 18); the later the harvest, the stronger the effect (Giulivo *et al.*, 1981 a).

A heavy crop load, induced by a very low fruit load during the previous year, strongly reduces shoot growth, flower differentiation for the next year and storage of reserve
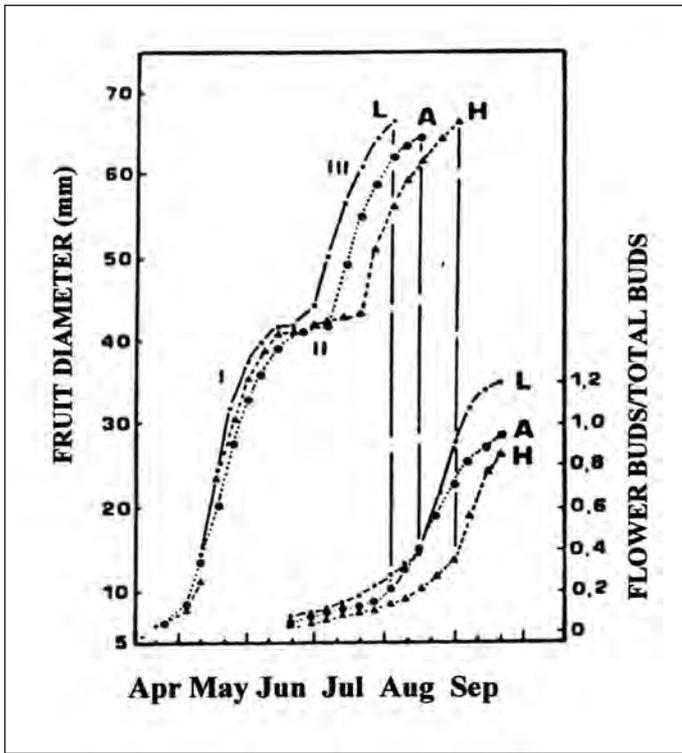
Fig. 18 - Fruit growth and percent of fruit bud formed on shoots of three cultivars of peach tree with different ripening times (Giulivo *et al.*, 1981 a).
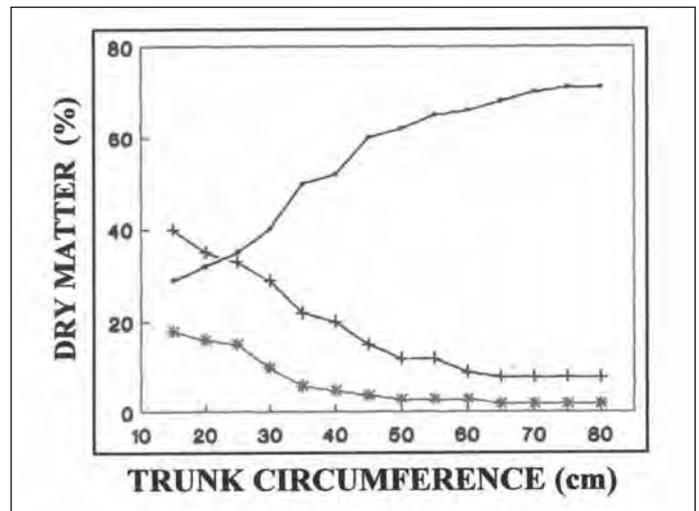

Fig. 19 - Dry matter partition among fruits (points), tree crown (crosses) and root system (asterisks). At increasing tree age represented by the trunk circumference less and less dry matter is allocated in the permanent structure of the tree (redrawn from Chalmers and Van den Ende, 1975).

materials (Giulivo, 1990). This can explain the succession of on- and off-years. A large number of developing fruits requires a great amount of assimilates which are diverted from vegetative growth and bud differentiation and this is a clear example of competition between different plant organs or functions. Flower or fruit thinning in the on-year is a powerful tool for modulation of the competition exerted by the fruits (Ramina, 1981; Abbot, 1984). Over-cropping and under- cropping, subsequent to off- and on-years, can be to some extent overcome by winter pruning, decreasing or increasing the number of fruiting structures of the tree.

The onset of fruiting is a dramatic event in the behaviour of a tree and the relative growth of plant parts is radically changed (Chalmers and Van den Ende, 1975): as the crop potential of the tree increases with time (Fig. 19), fewer and fewer resources are allocated in the permanent structures of the tree (trunk, branches and root system). This means that cropping of the tree is over time an aging factor and its regulation is a way to delay senescence of the plant. The regulation of cropping by summer and/or winter pruning represents a powerful tool for the maintenance of long-lasting economic performance of fruit trees.

During the growing season a heavy fruit load reduces root growth; very strong vegetation acts in a similar way, limiting fine root formation (Willianson and Coston, 1989). The partitioning of assimilates between shoots and roots is strongly affected by the water status of the tree (Schultze, 1982).

In many cases and in some stages of development the competition between tree organs is often connected with

cooperation. The dynamic relationship between shoots and fruit within the whole tree, and also within a single leafy shoot, is particularly relevant. In fact, in an early stage of fruit growth (Fig. 20) the relationship shoot/fruit depends on the number of sinks and their relative position along the mixed shoot, as shown by an experiment on one-year-old peach shoots (Giulivo and Ramina, 1975).

Complex relationships among sinks occur, even within a single node of a shoot as observed in peach tree. It is
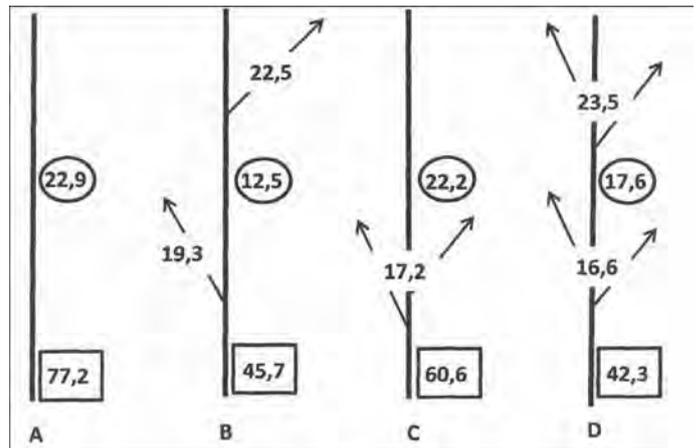

Fig. 20 - Fruit- shoot correlative relationships on peach one-year-old mixed shoots 0.2 m long. (Circles = fruit; arrows = shoots; square = basal leaf of mixed shoot treated with 14C, all other organs were removed). The organ (or organs) at the higher position was always the strongest sink. The fruit was a very strong sink (situation A); when the fruit was in between two shoots its strength was strongly reduced (situation B); when the fruit was above two shoots it was dominant (situation C) and therefore the relative organ position changed the sink relationship; the number of shoots above and below the fruit change the relationship between the organs (situations B and D). (Giulivo and Ramina, 1975).

known that different combinations of vegetative and flower buds occur at the nodes of peach mixed shoots; if a single fruit originates at a node initially it grows faster than the one or two fruits which are associated with a node with a growing shoot, but after some time, when the shoot rate decreases, these fruits attain a larger size (Casella, 1949; Giulivo, data not published). This may be explained by the contribution of the shoot leaves to the assimilate requirement by the fruits, in agreement with the results reported by Abbot (1984) on the shoot/fruit relationship carried by an apple bourse.

It would be possible to mention many other correlative functions, but the cases mentioned here should be adequate to stress the significance of these relationships in pruning management.

7. Conclusions

The efficiency of the orchard system is a primary requirement for economic success in fruit growing and therefore the architecture of the stand, with an appropriated use of the space available, can permit an efficient use of light, water and nutrients to sustain the basic physical and physiological processes involved in the functioning of the system. Sometimes space utilization (planting density) is too low or too high; in the former case light interception by the canopies becomes too scarce and soil evaporation too high; in the later, reciprocal shading of the trees assumes considerable weight. Sometimes the structure of the canopy is not optimal, as it may be too dense or too sparse and consequently the conditions inside the canopy are such that leaf and fruit functioning may be modified, pest proliferation may be promoted or light interception may be too scarce to maintain the various functions and processes of the canopy. In designing tree architecture, three basic indexes must be considered: the ratio between the tree parts above and below the ground, the ratio between leaf area surface and canopy volume, and the leaf area surface per unit of fruit weight. These indexes are satisfied differently in the various orchard models in relation to the applied training system and pruning criteria. Different training systems with a similar pruning criterion tend to have more or less the same production behaviour while different pruning criteria applied to the same training system tend to induce different crop performance (Sansavini and Musacchi, 1994). Pruning practices are thus a powerful means to modify tree functioning: pruning generally reduces the primary production of the orchard but may induce a great improvement of the performance of the system. The details of pruning for maximum fruit bud production and adequate fruit size and ripening differ for different species but it is possible to identify some general principles.

The various pruning techniques have very different effects on the growth and fruiting of a tree; heading-back or removal of organs, variations of spatial position and/or orientation of vegetative axes and transient modification of sap transport induce very different reactions. Interventions directed to shortening or removing an axis generally involve vegetative responses which are more or less strong in relation to location, intensity and when they are performed. Particular attention is required because strong negative or positive effects on the vegetative and reproductive equilibrium of the tree may arise. The negative effects regard mainly an excessive vegetative reaction but, if the pruning is carefully performed, the tree develops a species-specific fruiting structure more adequate to the economic goal of the orchard.

The detachment of fruits (thinning) performs a particular role in realizing a correct fruit-to-leaf ratio in the tree where the crop load is too heavy in relation to the leaves of the canopy.

Changing the position or the growth direction of the axes in the space (rectilinear, slanted, curved) generally decreases the growth rate and vigour of shoots and branches, improving the formation of reproductive structures. Therefore this type of manipulation assume a great importance in training the fruit trees.

Some pruning techniques, which tend to modify sap transport (incision above or below a bud, bark ringing, strangulation or girdling, shoot twisting and crashing, etc.), influence the relationships among sinks and the source-sink and thus they may stimulate or limit the development of an organ.

Whatever the manipulations of the above-ground part of the tree, root functioning is modified, but taking into account tree homeostasis, any modification to the root system affects the performance of the canopy. Therefore root pruning may be very useful for controlling tree vigour or improving root growth in adult trees.

All pruning manipulations mentioned involve variations in plant growth, size and geometry, thus modifying the architecture and functioning of the tree and affecting its productive life.

The timing of pruning manipulations is of great importance since the effects on the tree may be very different. In recent years summer pruning tends to prevail over winter pruning in most fruit tree species (Bargioni, 1988; Sansavini and Corelli, 1990; Costa, 1997; Sansavini et al., 1999; Neri and Sansavini, 2004). This tendency is mainly based on two reasons: to form small-sized trees and to follow the natural species-specific behaviour of the tree. Under the same cultivation conditions winter pruning tends to stimulate the vegetative reaction, whereas summer pruning generally has positive effects on reproductive activity. This may be due to the more powerful action of summer manipulations on source-sink relationships, and among sinks. Summer pruning, however, may reduce leaf area surface or the ratio between young, mature and old leaves and this may have some consequence on the photosynthetic performance of the canopy, which can be of some importance when light availability is limited. The timing of summer manipulation of the canopy is critical: if performed when vegetation is growing very fast. In this case the responses of tree may be too strong and consequently a consistent amount of resources are invested in the edification of new

vegetative structures or the density of the canopy may be increased. The timing of root pruning is as important as the time of canopy pruning since it has positive effects in the spring when it controls tree vigour, whereas it acts negatively if performed in late summer when storage of reserve materials is needed for the next year.

In the last few decades summer pruning (mainly pinching) has been extended to nurseries to train trees of some fruit species (apple, peach, etc.) carrying some feathers which speed up the construction of the tree crown in the orchard. In this way is possible the shortening of the unproductive period or to have young trees more suited for high density orchards or some particular training system (Sansavini and Corelli, 1990; Vigl, 1999; Neri and Sansavini, 2004).

In the 1990s some attempts were made to reduce production costs by omitting pruning during the training of trees and thereafter applying very simplified and superficial pruning, relying on thinning to equilibrate fruit load and leaf area surface. The performance of this technique, called 'no-pruning', was quite disappointing because of the serious drawbacks on fruit quality, such as variability in size and ripening of the fruits. Even in high density planting, without an appropriate adaptation of the training system, pruning was not able to overcome the excessive tree competition that determines premature aging of the fruiting structures, excessive shading, crop alternation and poor fruit quality (Sansavini, 1999). Therefore it may be concluded that pruning will always be an unavoidable operation, taking into account the economical goal of the orchards.

In conclusion, the best pruning derives from a clear production target and from precise planning while considering tree general physiology, the peculiar characteristics of the fruit species, cultivars, clones, scion-rootstock combinations, and the local environmental and cultivation conditions. Finally, it is important to remember that pruning represents only one of the many manipulations which can be performed in the orchard yet it cannot overcome basic mistakes made in designing the system.

References

ABBOT D.L., 1984 - *The apple tree - Physiology and Management*. - Grower Books, London, UK, pp. 90.

BAILEY L.H., 1916 - *The Pruning Manual. Being the eighteenth edition, revised and reset, of The pruning-book, which was first published in 1898* - Macmillian Company, New York, USA, pp. 407.

BALDINI E., SCARAMUZZI F., 1962 - *Glossario dei termini usati nella potatura degli alberi da frutto a foglia caduca*. - Tipocolor, Firenze, Italy, pp. 24.

BARGIONI G., 1988 - *Forme di allevamento e tecniche di potatura: come cambieranno?* - Frutticoltura, L(1-2): 97-103.

BARGIONI G., 1992 - *Potatura degli alberi da frutto*, pp. 393-494. - In: BALDONI L., G. BARGIONI, M. DEVREUX, O. FAILLA, C. FIDEGHELLI, G. FON-TANZZA, F. GORINI, R. JONA, F. LALATTA, G. MARACCHI, R. PAGLIETTA, G. RAPPARINI, C. XILOY-ANNIS, and A. ZOCCA. *Frutticoltura generale*. REDA, Roma, Italy, pp. 644.

BARTHÉLÉMY D., CARAGLIO Y., 2007 - *Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny*. - Ann. Bot., 99: 375-407.

BRANZANTI C.E., RICCI A., 2001 - *Manuale di Frutticoltura*. - Edagricole, Bologna, pp. 103-141.

CANNEL M.G.R., 1983 - *Plant management in agroforestry: manipulation of tree, population densities and mixture of trees and herbaceous crops*, pp. 455. - In: HUXLEY P.A. (ed.) *Plant Research and Agroforestry*. International Council for Research in Agroforestry, Nairobi, Kenya, pp. 617.

CANNEL M.G.R., 1985 - *Dry matter partitioning in tree crops*, pp. 160. - In: CANNEL M.G.R., and J.E. JACKSON (eds.) *Attributes of trees as crop plants*. Institute of Terrestrial Ecology Publisher, pp. 592.

CASELLA D., 1949 - *Mezzi per attenuare la cascola delle gemme, dei fiori e dei frutticini nelle specie legnose fruttifere*. - Atti III Conv. Naz. di Frutticoltura, Ferrara, Italy, pp. 200-212.

CHALMERS D.J., VAN DEN ENDE B., 1975 - *Productivity of peach trees: Factors affecting dry-weight distribution during tree growth*. - Ann. Bot., 39: 423-432.

CONNOR D.J., 1983 - *Plant stress factors and their influence on production of agroforestry plant associations*, pp. 401. - In: HUXLEY P.A. (ed.) *Plant Research and Agroforestry*. International Council for Research in Agroforestry, Nairobi, Kenya, pp. 617.

COSTA G., 1997 - *Potatura di produzione e diradamento dei frutti negli impianti di pianura*. - Proceeding Symposium Melicoltura di Pianura: quale futuro, Verona, Italy, 12 April.

COSTES E., LAURI P.E., REGNARD J.L., 2006 - *Analyzing fruit tree architecture: implications for tree management and fruit production*. - Horticultural Reviews, 32: 1-61.

DOTTI F., 1949 - *Recenti vedute sulla potatura dei fruttiferi*. - Atti III Conv. Naz. di Frutticoltura, Ferrara, pp. 213-230.

GIULIVO C., 1990, - *Basi fisiologiche della potatura degli alberi da frutto*. - Proceedings "La Potatura degli Alberi da Frutto negli Anni 90", Verona, Italy, 27 April.

GIULIVO C., RAMINA A., 1974 - *Osservazioni sulla formazione dei germogli anticipati nel pesco. II contributo*. - Riv. Ortoflorofrutt. It., 3: 170-176.

GIULIVO C., RAMINA A., 1975 - *Competizione tra germogli e giovani frutti di pesco*. - Riv. Ortoflorofrutt. It., 4: 273-280.

GIULIVO C., RAMINA A., COSTA G., 1981 b - *Il contributo del sottoprogetto 5 alle conoscenze dei processi di abscissione e maturazione dei frutti* - Proceedings I Fitoregolatori nel Controllo Chimico della Produzione degli Alberi da Frutto, Ferrara, Italy, 26-27 March.

GIULIVO C., RAMINA A., SCRITTORE G., 1981 a - *Accrescimento e sviluppo riproduttivo in cultivar di pesco con diversa epoca di maturazione dei frutti*. - Proceedings I Fitoregolatori nel Controllo Chimico della Produzione degli Alberi da Frutto, Ferrara, Italy, 26-27 March.

GRISVARD P., 1957 - *La taille des arbres fruitiers*. - La Maison Rustique, Paris, Frances, pp. 160.

HILKENBÄUMER F., 1953 - *Obstbau*. - Paul Parey, Berlin und Hamburg.

INGLES C., GEISEL P.M., UNRUH C.L., 2002 - *Fruit trees: training and pruning deciduous trees*. - ANR, Publication 8057, UCD, Davis, CA, USA, pp. 7.

LIEBSTER G., PESSERL G., 1982 - *Fachausdrücke des Obstbaumschnittes - Lexikon in deutscher, Wörterbuch in englischer, französicher, italienischer und niederländischer Sprache*. - Mitteilungen Klosterneuburg, 32: 50-100.

MORETTINI A., 1963 - *Frutticoltura Generale e Speciale*. - REDA, Roma, Italy, pp. 612.

NERI D., SANSAVINI S., 2004 - *Attualità della potatura nella frutticoltura intensiva*. - Frutticoltura, LXVI(1): 14-23.

PITACCO A., GIULIVO C., 1992 - *Dinamica della crescita dei germogli e dei frutti in cultivar di pesco a diversa epoca di maturazione*. - Giornate scientifiche S.O.I., Ravello, Italy, 8-10 April.

PROCTOR J.T.A., 1978 - *Apple photosynthesis: microclimate of the tree and orchard*. - Hort. Sci., 6: 641-643.

RAMINA A., 1981 - *La dinamica della cascola ed alcuni aspetti fisiologici dell'abscissione nel diradamento chimico dei frutti di pesco (*Prunus persica, *L. Batsch)*. - Conv. I Fitoregolatori nel Controllo Chimico della Produzione degli Alberi da Frutto, Ferrara, 26-27 March.

RICHARDS D., ROWE R.N., 1971 - *Effects of root restriction, root pruning and 6-benzilaminopurine on the growth of peach seedlings*. - Ann. Bot., 41: 729-740.

SANSAVINI S., 1999 - *Potatura in libertà*. - Frutticoltura, LXI(3). 5-6.

SANSAVINI S., CORELLI GRAPPADELLI L., COSTA G., LUGLI S., MARANGONI B., TAGLIAVINI M., VENTURA M., 1999 - *Ricostituzione degli impianti e revisione degli indirizzi produttivi della peschicoltura romagnola*. - Frutticoltura, LXI(3): 8-20.

SANSAVINI S., CORELLI L., 1990 - *La potatura e le forme di allevamento del melo*. - Proceedings La Potatura degli Alberi da Frutto negli Anni '90. Verona, Italy, 27 April, pp. 65-99.

SANSAVINI S., ERRANI A., 1998 - *Frutticoltura ad Alta Densità, Impianti, Forme di Allevamento e Tecniche di Potatura*. - Edagricole, Bologna, Italy, pp. 593.

SANSAVINI S., MUSACCHI S., 1992 - *Modelli di impianto, architettura e potatura nei moderni pereti*. - Frutticoltura, LVI(2): 7-18.

SCHULTZE E.D., 1982 - *Plant life forms and their carbon, water and nutrient relations*, pp. 615-676. - In: LANGE O.L., P.S. NOBEL, C.B. OSMOND, and H. ZIEGLER (eds.) *Physiological Plant Ecology, II. Encyclopedia of plant physiology*. Springer Verlag, Berlin, Germany.

SIMON S., SAUPHANOR B., LAURI P.E., 2007 - *Control of fruit tree pests through manipulation of tree architecture*. - Pest Technology, 1(1): 33-37.

VIGL J., 1999 - *L'allevamento del melo a "spindle"*. - Frutticoltura, LXI(3): 29-32.

WILLIAMSON J.G., COSTON D.C., 1989 - *The relationship among root growth, shoot growth, and fruit growth of peach*. - J. Amer. Soc. Hort. Sci., 2: 180-183.