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INVITED REVIEW

Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny

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• *Background and Aims* The architecture of a plant depends on the nature and relative arrangement of each of its parts; it is, at any given time, the expression of an equilibrium between endogenous growth processes and exogenous constraints exerted by the environment. The aim of architectural analysis is, by means of observation and sometimes experimentation, to identify and understand these endogenous processes and to separate them from the plasticity of their expression resulting from external influences.
• *Scope* Using the identification of several morphological criteria and considering the plant as a whole, from germination to death, architectural analysis is essentially a detailed, multilevel, comprehensive and dynamic approach to plant development. Despite their recent origin, architectural concepts and analysis methods provide a powerful tool for studying plant form and ontogeny. Completed by precise morphological observations and appropriated quantitative methods of analysis, recent researches in this field have greatly increased our understanding of plant structure and development and have led to the establishment of a real conceptual and methodological framework for plant form and structure analysis and representation. This paper is a summarized update of current knowledge on plant architecture and morphology; its implication and possible role in various aspects of modern plant biology is also discussed.

Key words: Plant morphology, plant architecture, level of organization, growth, branching, differentiation, morphogenetic gradients, physiological age, meristem, annual shoot, phenotypic plasticity, ontogeny, phase change.

INTRODUCTION

Progress in our understanding of plants has increased dramatically in recent decades and research in this domain has given rise to analytical, methodological and theoretical innovations on various aspects of plant science (Sattler and Rutishauser, 1997; Hedden *et al.*, 2002; Turnbull, 2005).

Plant form, development and evolution have been analysed under the functional view of biomechanics (Niklas, 1992, 2005; Rowe and Speck, 2005) and pollination ecology or population biology (White, 1979; Harper, 1985; Diggle, 2003; Friedman and Harder, 2004, 2005). The importance of phenotypic plasticity, phenology and crown architecture in evolutionary plant ecology or in the understanding of community and stand structure, functioning and production has been stressed by several authors (Givnish, 1984; King, 1998; Diggle, 1999, 2002; Huber *et al.*, 1999; Alpert and Simms, 2002; Novoplansky, 2002; Wright *et al.*, 2002; Oborny, 2004; Sachs, 2004; Damascos *et al.*, 2005; de Kroon *et al.*, 2005; Pearcy *et al.*, 2005; Wolfe and Mazer, 2005).

Since its introduction and definition by von Goethe (1790), plant morphology has had a successful history and it is commonly accepted that plants are modular organisms that develop by the repetition of elementary botanical entities whose morphological, dimensional, functional and anatomical features change during ontogeny and according to several processes variously called heteroblasty, phase change, life stages, maturation, ageing, age states or morphogenetic progression (Goebel, 1900; Troll and Rauh, 1950; Robbins, 1957; Wareing, 1959, 1961; Nozeran *et al.*, 1971, 1982; Nozeran, 1978, 1984; Gatsuk *et al.*, 1980; Greenwood, 1987, 1995; Poethig, 1990; Jones, 1999, 2001; Claßen-Bockoff, 2001; Kaplan, 2001). As plant morphology deals with plant form and/or structure and with their temporal and/or topological changes during ontogeny and even phylogeny, it is therefore relevant to practically all the disciplines of modern plant biology cited above (Sattler, 1978; Roloff, 1988; Sattler and Rutishauser, 1997; Gleißner, 1998; Claßen-Bockhoff, 2000, 2005; Kaplan 2001; Scotland *et al.*, 2003; Wiens, 2004; Mueller, 2006).

The study of plant architecture emerged as a new scientific discipline some 30 years ago, and derived, in several ways, from earlier works on plant morphology (Hallé and Oldeman, 1970; Oldeman, 1974; Hallé *et al.*, 1978). An original feature of architectural studies is that they were initiated in tropical regions and were, at first, concerned with the analysis of the aerial vegetative structure of tropical trees (Hallé and Oldeman, 1970). Since their definition, architectural concepts have provided powerful tools for studying plant form or even tropical forest structure and the understanding of its dynamics (Oldeman, 1974, 1983, 1990; Hallé *et al.*, 1978; Vester, 1997). Investigations based on these concepts quickly spread to temperate species (Edelin, 1981; Caraglio and Edelin,

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1990; Gleißner, 1998; Nicolini, 1998; Grosfeld *et al.*, 1999; Millet *et al.*, 1999; Sabatier and Barthélémy, 1999; Claßen-Bockhoff, 2000; Stecconi *et al.*, 2000), herbs (Jeannoda-Robinson, 1977; Blanc, 1978; de Castro e Santos, 1981; Gay, 1993; Cremers and Edelin, 1995; Rua and Gróttola, 1997; Perreta *et al.*, 2000), lianas (Cremers, 1973; Coudurier, 1992; Caballé, 1998) and root systems (Atger and Edelin, 1994*a*, *b*; Jourdan and Rey,1997*a*, *b*). The architecture of a plant depends on the nature and on the relative arrangement of each of its parts; it is, at any given time, the expression of an equilibrium between endogenous growth processes and exogenous constraints exerted by the environment. The aim of architectural analysis is to identify these endogenous processes and to separate them from the plasticity of their expression resulting from external influences by means of observation and sometimes experimentation. Considering the plant as a whole, from germination to death, architectural analysis is essentially a global, multilevel and dynamic approach to plant development. For each species, at each stage of development and in each environmental condition, careful qualitative and quantitative morphological or even anatomical observations are made on varying numbers of individuals, depending on the complexity of the architecture. Small plants can be analysed, observed and manipulated directly but this is hardly possible when plants reach several metres high. For the highest and biggest trees, some qualitative observations can be carried out from ground level (Barthélémy *et al.*, 1989, 1991; Millet *et al.*,1998*b*; Nicolini, 1998) but the use and practice of destructive methods are most generally necessary for more precise analysis and data collection (Heuret *et al.*, 2000, 2002; Passo *et al.*, 2002). Results of field observations are summarized in a series of diagrams that symbolize successive growth stages or developmental steps, whereas quantitative analyses are grouped and made according to this qualitative knowledge. The validity of these diagrams and analyses is then checked by comparing them with reality and they must apply to the architecture of any individual of the same species encountered in the field for the study to be considered as complete.

Applicable to any kind of plant, architectural analysis has proved to be one of the most efficient means currently available for the study of the organization of complex arborescent plants. Architectural concepts appear to be of particular interest for the understanding of crown construction in trees. Completed by precise morphological observations and innovative computational aspects, recent research in this field has greatly increased our understanding of plant structure and development and has led to the establishment of a real conceptual and methodological framework for plant form analysis and understanding (Barthélémy *et al.*,1997*a*; Bouchon *et al.*, 1997; Caraglio and Barthélémy, 1997; de Reffye and Houllier, 1997; Godin and Caraglio, 1998; de Reffye *et al.*, 1998; Guédon *et al.*, 2001, 2003; Hu and Jaeger, 2003; Yan *et al.*, 2004).

The present paper describes major concepts and notions that are currently used in plant architecture and morphology description. It aims to provide a summarized update of our knowledge in this field. The possible applications, implications and roles of plant architecture in modern and current plant research are discussed.

MORPHOLOGICAL BASES AND CRITERIA FOR PLANT ARCHITECTURE DESCRIPTION AND ANALYSIS

Plant morphology, in its historical and broader sense and as a synthetic discipline (see, for example, Sattler, 1978; Claßen-Bockoff, 2001; Kaplan, 2001; Mueller, 2006), may be considered as one of the main 'inspiring soul' of plant architecture studies. In this section, however, we will only illustrate the main morphological traits that are commonly used in plant architectural analysis (for a more comprehensive and general illustration and survey of other morphological traits we refer the reader to Troll, 1937 or Bell, 1991). These traits are well documented in previous synthetic works (Hallé and Oldeman, 1970; Hallé *et al.*, 1978) and they may be grouped according to four major categories: (1) growth process, (2) branching process, (3) the morphological differentiation of axes and (4) the position (lateral vs. terminal) of reproductive structures. Although they correspond to basic morphological concepts, their associated terminology proved to be sometimes confused and led to incorrect interpetations. They were thus recently discussed and sometimes redefined (Caraglio and Barthélémy, 1997, and see below).

Growth process

The primary growth of a plant is the result of several processes that can be grouped into two distinct, but co-ordinated morphogenetic events: organogenesis and extension (Champagnat *et al.*, 1986). The inception of new organs (organogenesis) results from the functioning of undifferentiated cells constituting the apical meristem (Fig. 1A). Located at the tip of a stem, this meristem forms, when in an active phase, small cell masses with

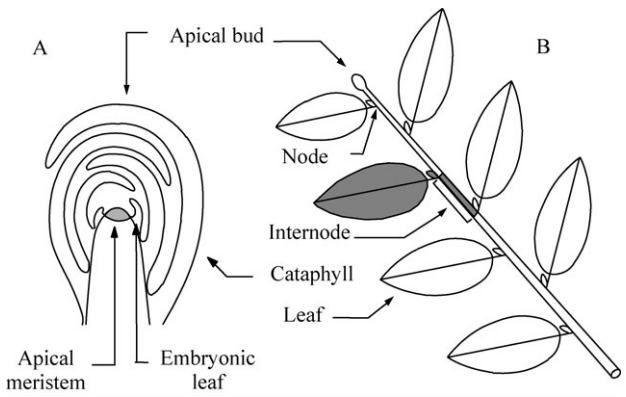


FIG. 1. Shoot apex (A) and stem (B) organization. Each leafy axis (B) ends in an apical meristem frequently protected in an apical bud (A). Each stem comprises a succession of metamers, i.e. the set composed by (1) one internode, (2) the node (i.e. insertion point of the leaves on a stem) located at its tip and (3) the corresponding one or several leaves and associated lateral buds (in grey on A; White, 1979; Caraglio and Barthélémy, 1997).

different potentialities (Lyndon, 1988; Nougarède, 2001); these masses develop into embryonic leaves, then leaves on elongated stems. The insertion zone of a leaf on the stem is referred to as a node and the stem portion which separates two successive nodes is called the internode. According to species and phyllotaxis, one, two or more leaves may be inserted at one node and one to several, named supernumerary, buds (see Fig. 8) may develop at the axil of each individual leaf. A stem can thus be considered as a succession of internodes and the entity formed by a node, associated with its leaf (or leaves) and axillary bud(s) plus the subtending internode, represents the basic structural unit of the plant body commonly called the metamer or phytomer (White, 1979; Barlow, 1989). During growth, the superposition and repetition of this elementary entity builds up the leafy axis (Fig. 1B).

Plant growth may be considered in several ways according to the kind of organ and/or level of organization concerned (growth of a leaf, a stem, a fruit, the whole plant, etc.). As we are dealing here with the topological edification of the stem and macroscopic aspects of plant growth, we will focus mainly on the extension process of the leafy axis or shoot and will neither detail organogenesis processes nor consider secondary (*sensu* Fahn, 1967) or radial growth.

Determinate vs. indeterminate growth (Fig. 2). In many plant species, the apex may abscise or abort after some period of functioning (Garrison and Wetmore, 1961; Millington, 1963; Puntieri *et al.*, 1998, 1999) or it may transform into a specialized structure (flower, inflorescence, spine, tendril, parenchymatous cells, etc.) lacking further extension capacity. In these cases, the axis is considered to have a determinate growth (Fig. 2A–C; Hallé *et al.*, 1978; 'definite extension', Bell, 1991). By contrast, indeterminate growth (Hallé *et al.*, 1978) or indefinite extension (Bell, 1991) refers to an axis on which apical meristem indefinitely maintains its growth potential (Fig. 2D). As the indefinite functioning of an apex is always limited at least by the limited life span of the plant it belongs to, this ultimate term is somewhat 'theoretical' and a misuse of the language (Guinochet, 1965). Nonetheless, this notion is useful and justified by the necessity to describe and name this phenomenon.

Rhythmic vs. continuous growth. Hallé *et al.* (1978) distinguished shoots which have no marked endogenous cessation of extension (continuous growth) from shoots which have marked endogenous periodicity and cessation of extension (rhythmic growth; Hallé and Martin, 1968). Although organogenesis may be considered or known, these two growth patterns are generally more concerned with extension.

Continuous extension (Fig. 3A, B) is quite a rare phenomenon in the field and has generally been observed and described mostly in uniform equatorial climates or environments (mainly palm or mangrove trees; Venkatanarayana, 1957; Rees, 1964; Gill and Tomlinson, 1971) or for some herbs native to temperate (Bell, 1991) or tropical (Blanc, 2002) regions. In all these cases, plants

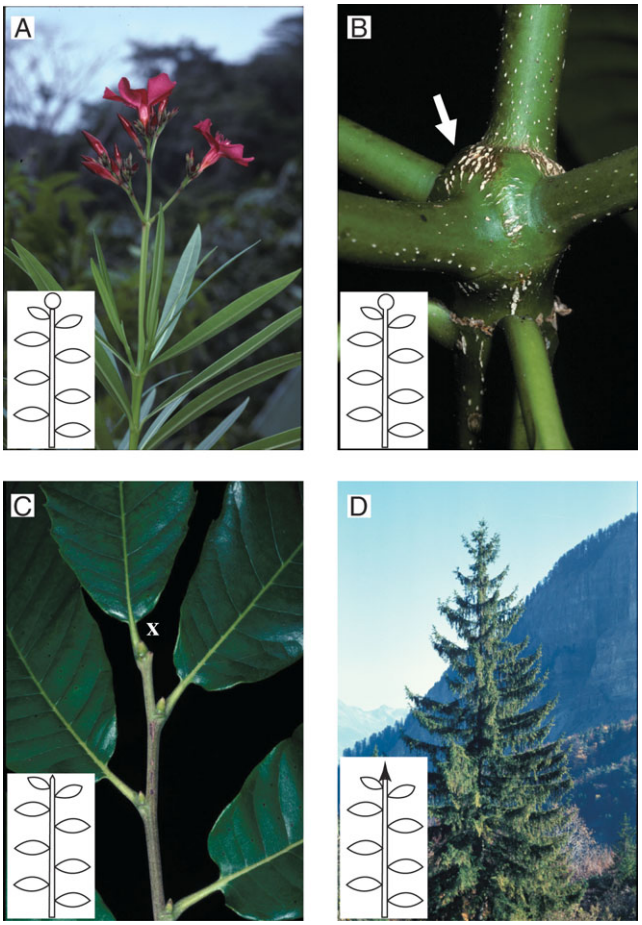


FIG. 2. Determinate growth corresponds to an irreversible transformation of the apical meristem, which can be due to (A) apical flowering as in *Nerium oleander*, (B) parenchymatization (arrow) of the apical meristem as in *Alstonia* sp. or (C) apical death or abscission ('X') as in *Castanea sativa*. Indeterminate growth corresponds to permanent apical meristem functioning, as illustrated by the main stem of *Picea excelsa* (D).

exhibit a more or less constant production of leaves and/or shoots throughout the year. For the mangrove trees *Rhizophora mangle* (Gill and Tomlinson, 1971), growing in the subtropical climate of Florida, it was shown that the extension of each axis may have a fluctuating rate according to the seasonal climatic conditions, without ever being interrupted completely (Fig. 3B). In some cases, the endogenous nature of continuous extension may be 'masked' by fluctuating environmental conditions in the field and can be revealed experimentally by growing plants in favourable and constant conditions, as was demonstrated for several temperate Cupressaceae from the Southern Hemisphere (Grosfeld and Barthélémy, 2004). It has been shown that plants with continuous extension may also present a continuous production of new embryonic leaves, i.e. organogenesis (Gill and Tomlinson, 1971). As far as it has been documented, when extension is continuous the resulting stem is generally quite homogeneous and successive metamers and their constitutive elements are more or less of the same type and size along the elongated axis (Fig. 3A, B, right; Tomlinson and Gill, 1973; Hallé *et al.*, 1978).

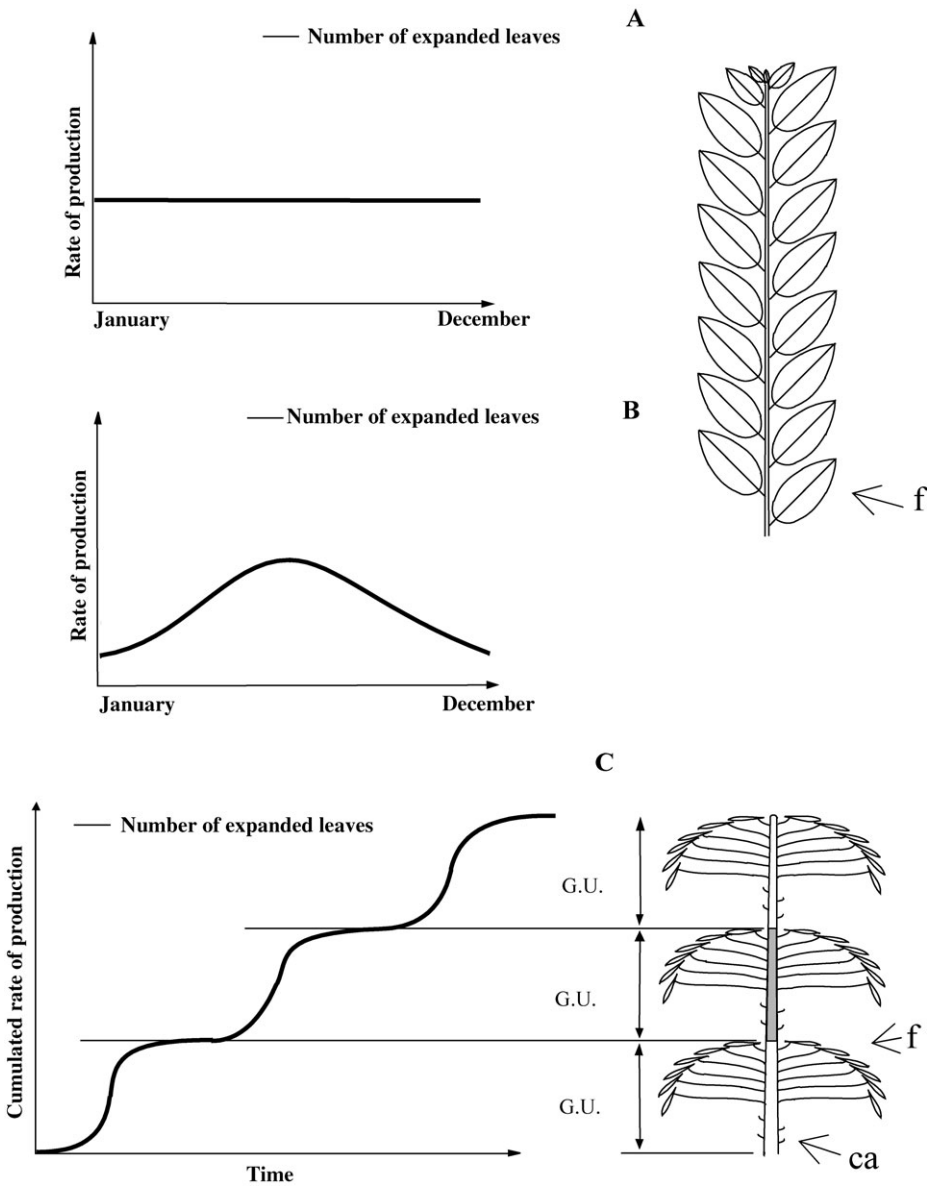


FIG. 3. Leaf extension rate in continuous (A and B) vs. rhythmic (C) growth and structure of the resulting stems (modified from Hallé *et al.*, 1978). (A) Constant leaf extension in a theoretical case (i.e. several palm trees) and (B) fluctuations in the leaf extension rate of *Rhizophora mangle* correlated with climatic fluctuations. (C) Rhythmic cumulative rate of leaf extension in *Hevea brasiliensis*. G.U., growth unit; f, leaf; ca, cataphyll.

Rhythmic extension of leafy axes is a far more frequent growth pattern in plants, regardless of their geographical origin, and is expressed by an alternation of periods of rest in meristem activity and periods of active shoot extension or 'growth flushes' (Fig. 3C). This rhythmic growth has been thoroughly studied by numerous authors (Alvim, 1964; Kozlowski, 1971; Hallé *et al.*, 1978; Puntieri *et al.*, 1998; Sabatier and Barthélémy, 1999). Hallé and Martin (1968), in their detailed study of the tropical tree *Hevea brasiliensis*, defined the 'growth unit' as the portion of an axis which develops during an uninterrupted period of extension. A growth unit is generally easy to identify on the elongated stem as the limit between two growth units is usually marked by a zone of short internodes and/or cataphylls (i.e. scale leaves) corresponding to the protective organs of the bud from which it derives (Fig. 4). Even if very common in rhythmically growing axes, this alternation of cataphylls and leaves (termed articulate growth by Tomlinson and Gill, 1973; Fig. 3C right, Fig. 4) may not be obvious in some species, and other morphological or macro-anatomical markers may sometimes be used in addition, for the *a posteriori* identification of a rhythmically elongating axis (Fig. 5).

As with continuous growth, the identification of the endogenous nature of rhythmic growth, for plants naturally growing in seasonal climates, requires experimental verification in controlled, constant and favourable environmental conditions (Greathouse *et al.*, 1971; Lavarenne, 1971; Payan, 1982; Parisot, 1985). Regardless, the rhythmic (or continuous) pattern of a shoot or axis growth must

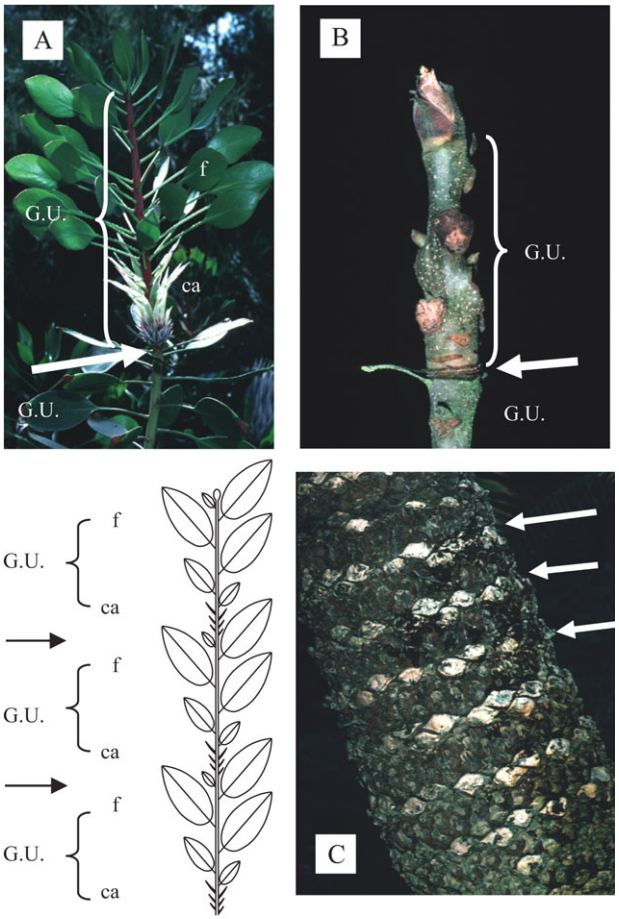


FIG. 4. Morphological markers of rhythmic extension. Growth cessation phases (arrows) and delimitation of successive growth units (G.U.) as revealed *a posteriori* by an alternation of cataphylls (ca) and photosynthetic leaves (f) in *Protea cynaroïdes* (A) or their scars (*Carya laciniosa*, B, or *Cycas pectinata*, C).

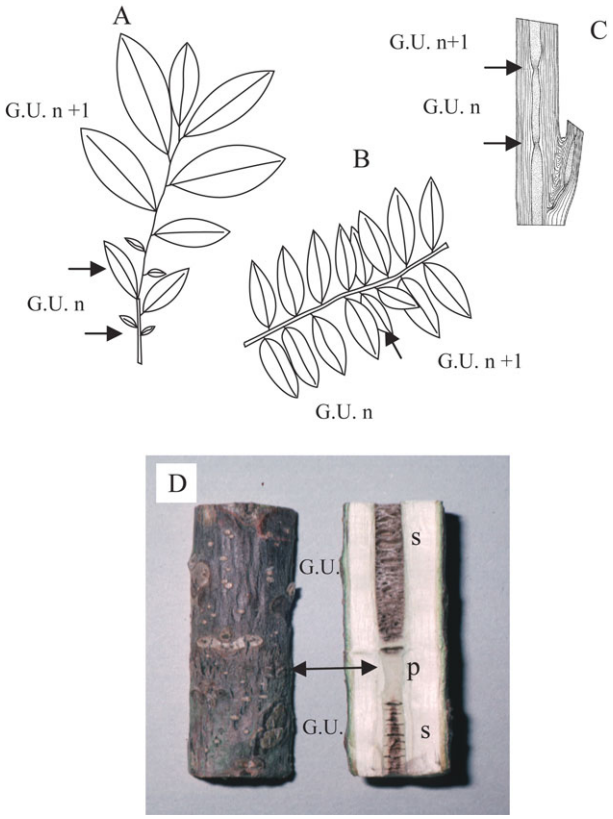


FIG. 5. Successive growth units may be delimited (arrows) only by more or less marked changes in leaf size (*Virola michelii*, A; *Virola surinamensis*, B; drawings from Edelin, 1993). In some cases the limit (arrow) between two growth units is indicated by a decrease in the pith diameter (*Carapa procera*, C; drawings from Edelin, 1993) and/or even by pith structure as in *Juglans* sp. (D). G.U., growth unit; 'n', 'n + 1', successive theoretical years of growth; p, plain pith; s, septate pith.

be checked by periodic measurement of its length. In practice, most often only the extension component of growth is known, such that some authors have proposed the use of the term 'unit of extension' (Gill and Tomlinson, 1971; Hallé *et al.*, 1978) rather than growth unit, even though the two terms are synonymous. When organogenesis is known, it has been shown that the rhythmic extension of the stem may be combined either with a continuous (Bond, 1942) or more frequently, a rhythmic (Hallé and Martin, 1968; Gill, 1971; Puntieri *et al.*, 2002*a*; Sabatier *et al.*, 2003*b*) organogenesis pattern. In the latter case, it has been proposed that the 'unit of morphogenesis' is the axis portion corresponding to an uninterrupted phase of organogenesis (Hallé and Martin, 1968). Despite its relevance for the understanding of growth patterns in plants, the nature of the unit of morphogenesis is unknown in most cases partly owing to the long and tedious experimental work needed for its identification.

Preformation and neoformation. In the case of rhythmic growth, all the metamers and organs of the future elongated shoot may be present at an embryonic stage in a bud before the elongation of the shoot deriving from it; in this case the shoot is referred to as 'preformed' and its constitutive organs as 'preformed organs' or 'preformation' (Hallé *et al.*, 1978; 'early leaves', Critchfield, 1960; 'fixed growth', Lanner, 1976). The duration of preformed organs at an embryonic stage in a bud may vary from several days or weeks (Hallé and Martin, 1968; Sabatier *et al.*, 1995) to several years (Aydelotte and Diggle, 1997; Diggle, 1997; Meloche and Diggle, 2001). In other cases, more organs than those included at an embryonic stage in the bud are elongated: these supplementary, non-preformed elements are referred to as 'neoformed organs' (i.e. 'neoformation' *sensu* Hallé *et al.*, 1978, or 'late leaves', Critchfield, 1960; 'free growth', Jablanczy, 1971; Lanner, 1976). As a consequence stems or shoots may comprise only preformed metamers (Critchfield, 1960; Rivals, 1965, 1966; Gill, 1971; Roloff, 1985; Sabatier *et al.*, 1995; Nicolini, 1998; Puntieri *et al.*, 2000, 2002*a*, *b*; Souza *et al.*, 2000) or, more rarely, may be entirely neoformed (Borchert, 1969; El-Morsy, 1991). In many cases, a preformed part can be followed by a neoformed part and thus give rise to a mixed shoot (Critchfield, 1960; Hallé and Martin, 1968; Kozlowski, 1971; Nitta and Ohsawa, 1998; Puntieri *et al.*,

2000, 2002*b*; Souza *et al.*, 2000; Seleznyova *et al.*, 2002; Costes *et al.*, 2003; Gordon *et al.*, 2006). As discussed in recent studies, the amount of preformation or the relative extent of preformation and neoformation in shoots may vary both between and within species according to external or internal parameters. For a number of tree species, preformation seems to be more relevant than neoformation in the mean number of organs developed by a shoot at a specific position within a tree's architecture (Remphrey and Davidson, 1994; Puntieri *et al.*, 2000, 2002*b*; Souza *et al.*, 2000). Neoformation responses within a specific position of a tree would be involved in the plastic response of trees to factors acting locally at the time of shoot extension (Remphrey and Powell, 1984; Gordon *et al.*, 2006; Guédon *et al.*, 2006).

Annual shoot (Fig. 6). In rubber trees growing in equatorial conditions (Hallé and Martin, 1968), an axis with indeterminate growth forms a new growth unit about every 45 d and these successive units are morphologically identical (cf. Fig. 3C) so that the growth unit level itself is pertinent to describe the infrastructure of an axis and its morphological heterogeneity. In other tropical species, however, the timing of rhythmic extension during a whole calendar year is more complex. In *Ryania speciosa* var. *subuliflora* (Comte, 1993), for instance, the annual growth pattern corresponds to the extension of two growth units in a relatively short time, followed by a long resting phase, which again is followed by the rapid emission of a succession of two growth units. In some temperate species, shoot extension may occur in one, two or more successive events in a same growing season giving rise to an 'annual shoot' made up of one or a succession of several growth units or growth cycles (respectively monocyclism vs. polycyclism, i.e. Bugnon and Bugnon, 1951 or Lanner 1976, and see Caraglio and Barthélémy, 1997, for a critical and historical revision of these terms) occurring in a vegetative cycle (period between two marked seasons or two winters, Lanner, 1976). When several successive growth units are formed in the same annual vegetative cycle these growth units most often present distinctive features (Fig. 6); spring shoots and summer or additional shoots are frequently distinguished (Späth, 1912; Kozlowski, 1971; Cannell *et al.*, 1976). In this situation, successive growth units produced in a same year are thus not identical and it is useful and pertinent to distinguish an annual-shoot level of organization.

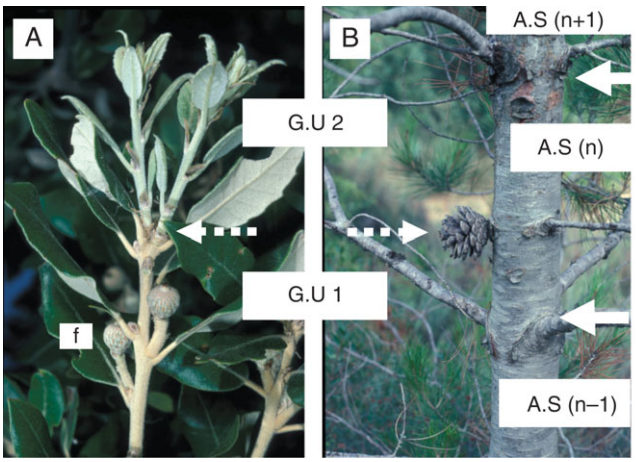


FIG. 6. Stem extension may occur more than once during a same calendar year. The set of growth units produced in one year is then called an annual shoot (A.S.). In *Quercus ilex* (A) or *Pinus halepensis* (B) bicyclic shoots, the first growth unit (G.U.1) may produce reproductive organs whereas the second (G.U.2) is vegetative. On old stems, the presence of female cones or fruits on the first growth unit and the major development of branches borne on the second growth unit of such bicyclic annual shoots distinguishes these first and second growth units, respectively, as the *a posteriori* delimitation of successive annual shoots (B). 'n-1', 'n', 'n + 1', successive theoretical years of growth; solid white arrow, limit of an annual shoot; dashed white arrow, limit of a growth unit.

According to the number of constitutive growth units of an annual shoot and according to the indeterminate vs. determinate nature and to the relative extent of preformation and neoformation in each of the constitutive growth units, several combinations may exist for different species or even for a single species, depending on external and/or internal conditions (Lanner, 1971, 1976; de Reffye *et al.*, 1991; Costes, 1993; Fontaine *et al.*, 1999; Heuret *et al.*, 2000, 2003, 2006; Puntieri *et al.*, 2000; Isik *et al.*, 2001).

Branching process

Although the architecture of some vascular plants consists only of a single vegetative axis during their whole life span, most display a more complex architecture consisting of several axes, one derived from another by a repetitive process known as branching.

Terminal vs. lateral branching. An apical meristem (McManus and Veit, 2002) or an initial apical cell (Gifford, 1983) can directly split and give rise to two or more new sibling axes, which results in dichotomy or polytomy, respectively (Emberger, 1960). Frequently encountered in ferns and mosses (Emberger, 1960), this terminal branching (Gatin, 1924) is rarely expressed in angiosperms (see for monocotyledons: Schoute, 1909; Tomlinson, 1971; Fisher, 1976; Tomlinson and Posluszny, 1977; and for dicotyledons: Nolan, 1969; Boke, 1976; Iwamoto *et al.*, 2005). It is important to mention that this phenomenon is, as far as we know, not encountered within gymnosperms.

In other cases, the branching process relies on the delimitation of a zone of embryonic cells just aside the initiated leaf, i.e. the axillary meristem. This lateral branching process is the most common one among angiosperms and gymnosperms. The resulting lateral branch is characterized by the presence of one or two (in respectively monocotyledons or dicotyledons) prophylls: the first foliar organs of the lateral axis (see Fig. 7A, B for their particular location).

In some plants, there are, at a single leaf axil, more than one axillary meristem, which are then called supernumerary or accessory buds (Sandt, 1925; Troll, 1937; Espagnac and Neuville, 1969; Altman and Goren, 1978; Bell, 1991; Fig. 8A, B). In this case, each individual lateral meristem may be identified by the position of its prophylls, which

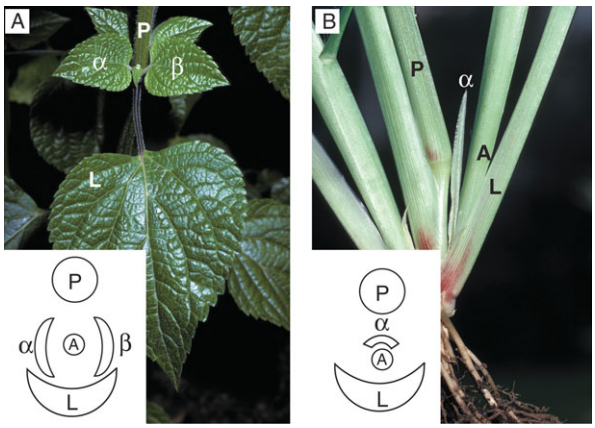


FIG. 7. The leaf, or leaves, of the first (proximal) node of a lateral shoot (A) are referred to as prophylls. In dicotyledons prophyll α and prophyll β are mainly in opposite and lateral position with respect to the plan formed by the axillary leaf (L) and the parent axis (P) (*Salvia guaranitica*, A). In monocotyledons, the first leaf (prophyll α) is often bicarinate and shows a particular arrangement (unidentified Poaceae, B): it is located in adaxial position between the lateral shoot (A) and its parent axis (P).

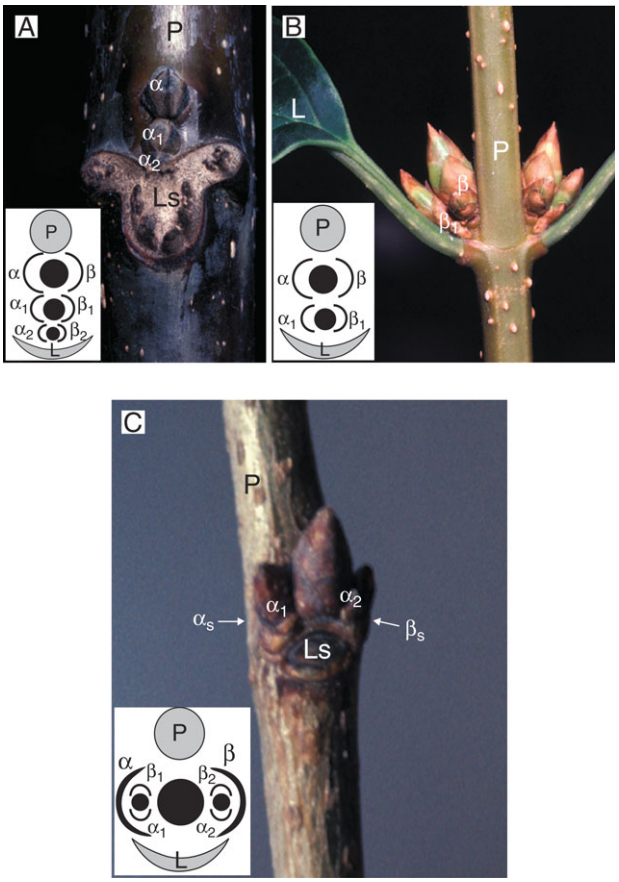


FIG. 8. Vertical succession of supernumerary (or accessory) buds in *Juglans regia* (A) and in *Forsythia vulgaris* (B). The arrangement of the prophylls (diagrams) distinguishes supernumerary buds from reduced branching systems as illustrated in *Zelkova serrata* (C). L, axillary leaf; Ls, leaf scar; P, parent axis; prophylls α and β or their scars, αs and βs, after abscission.

also allows the distinction between this situation and the development of condensed and more complex lateral branching systems (i.e. complexes of secondary buds, Hallé *et al.*, 1978), where second-order lateral buds may be present in the axils of main lateral bud's prophylls (Fig. 8C).

Immediate vs. delayed branching (Fig. 9). Once initiated, an axillary meristem may remain dormant or can develop into a lateral axis. A lateral axis may elongate immediately after lateral meristem initiation or after a phase during which the lateral meristem remains inactive and very often protected in a lateral bud. These branching patterns are referred to, respectively, as immediate (i.e. 'sylleptic' *sensu* Hallé *et al.*, 1978; Müller-Doblies and Weberling, 1984; Wu and Hinckley, 2001) or delayed ('proleptic' *sensu* Hallé *et al.*, 1978; 'prolepsis', Bell, 1991) branching. The terms immediate vs delayed branching should be preferred to the more traditional 'sylleptic' vs. 'proleptic' branching (*sensu* Hallé *et al.*, 1978) because of etymological and historical reasons, which have rendered the latter two terms ambiguous (see Caraglio and Barthélémy, 1997, for a critical review).

Morphologically, these two branching patterns may generally be identified *a posteriori* by the observation of the base of the lateral axis. Because of the immediate extension of lateral organs, branches with immediate development generally lack proximal cataphylls and present a relatively long most proximal internode termed a hypopodium (Fig. 9A; Tomlinson and Gill, 1973). Irrespective of the delay length, delayed branches present very short internodes and one or several cataphylls in their proximal portion, close to the point of insertion (Fig. 9B; Hallé *et al.*, 1978). Thorough observation of the proximal part of lateral axes and a periodic observation and measurement of lateral meristem or bud size normally leaves no doubt as to the immediate or delayed nature of branching. In some cases, however, because lateral resting buds may be 'hidden', during the resting phase, in the axils of persistent basal foliar organs of the terminal bud (Guédès, 1975, 1980) or because lateral axes in an embryonic stage may already exist inside a resting bud (Champagnat, 1965; Roloff, 1985), the interpretation may be complicated or may lead to a misuse of the terminology (Caraglio and Barthélémy, 1997). Finally, in delayed branching it has been shown that the duration of the delay may be of several weeks to a year (Sabatier *et al.*, 1995, 1998, 2003*b*; Puntieri *et al.*, 1998; Heuret *et al.*, 2003) and even several years (Fink, 1983; Nicolini *et al.*, 2001).

Monopodial vs. sympodial branching. Depending on the indeterminate or determinate growth pattern of an axis, its branching pattern may respectively be monopodial (Emberger, 1960; or 'monopodic', Sachs, 1874), or sympodial (Emberger, 1960; or 'sympodic', Sachs, 1874). In the latter case, one, two or more branches may develop after the death, abscission, abortion or transformation of the apex, and the resulting sympodial branching pattern be qualified respectively as mono-, di- or polychasial. In plant architecture, the concept of module ('article' in

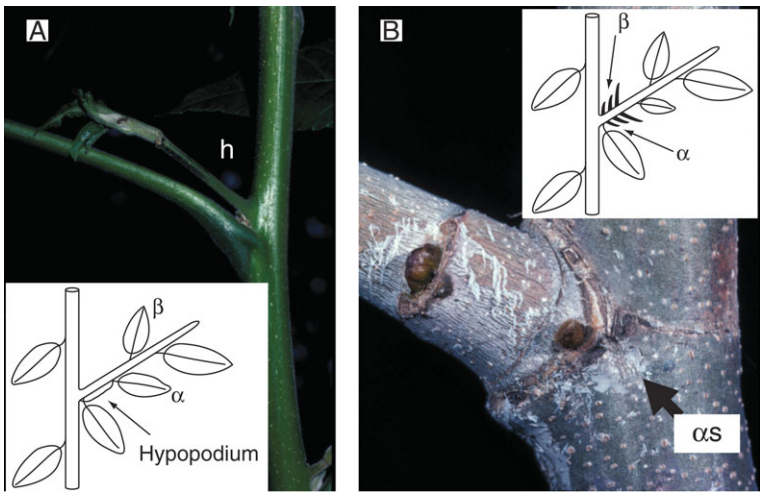


FIG. 9. In the case of immediate branching (*Juglans regia*, A), the first internode is generally long and termed the hypopodium (h). Delayed branching refers to a system where lateral branching follows a resting phase of the lateral meristem during which it is frequently included in a bud. When elongated, such delayed branching lateral shoots frequently show a short first internode and proximal scale leaves or bud scale scars when abscissed (*Platanus* sp., B). x, apical mortality; α, prophyll alpha; αs, scar of abscissed prophyll alpha.

French) was defined for the first time by Prévost (1967) in her study of tropical Apocynaceae and then applied to 'a leafy axis in which the entire sequence of differentiation is carried out from the initiation of the meristem that builds up the axis to the sexual differentiation of its apex' (Hallé, 1986). Because of the various causes of determinate growth (see above), this definition is, however, restrictive and the term 'module' increasingly refers to the portion of an axis edified by a single terminal meristem, which corresponds also to a 'sympodial unit' as used by Bell (1991).

Involving one or more lateral axes, a sympodial branching system is very often three dimensional. In some cases, however, a sympode may imply a linear succession of 'modules' or 'sympodial units' forming a so-called 'pseudomonopodium' as termed by German mophologists (Troll, 1937; Rauh, 1939). The resulting rectilinear structure mimics an axis edified by a single meristem with indeterminate growth and, if reproduced on all axes, may give rise to a totally sympodial branching system that resembles a monopodial one (Caraglio and Edelin, 1990; Bell, 1991). As a consequence, a rectilinear stem may thus 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 units or modules. In a broader sense and following Room *et al.* (1994), the term 'leafy axis' or 'axis' will identify not only a structure edified by a single meristem as initially considered by Hallé *et al.* (1978) but also a rectilinear stem, whatever its intrinsic mode of construction.

Branched system and branching order (Fig. 10). The description of a branched system implies the use of a precise topological terminology. In plant architecture analysis it is usual to use ordinal numbers and to consider the main stem arising from seed as the order 1 axis (Fig. 10A; Hallé *et al.*, 1978; Barthélémy *et al.*, 1989, 1991) whereas the axes it gives rise to are referred to

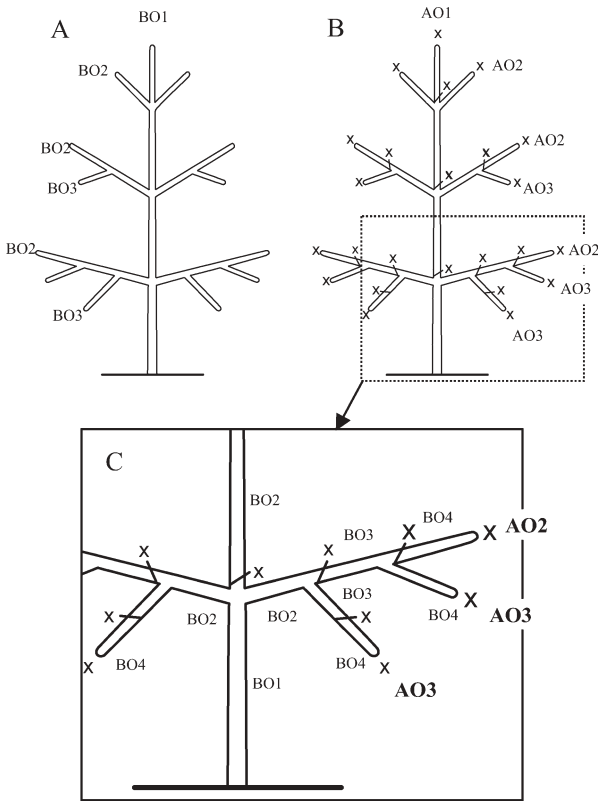


FIG. 10. As a result of branching, sibling axes succeed topologically from a parent axis. This spatial succession is referred to as 'branching order' (BO). The first axis (branching order one, BO1) bears a lateral one (branching order 2, BO2) and so on as illustrated diagrammatically for a monopodial branching system (A). In a sympodial branching system, the branching order may increase rapidly (C). When successive sympodial units (each resulting from the functioning of a single meristem) are more or less in a rectilinear disposition (B), it can be considered that the general spatial direction of such a succession constitutes an 'apparent branching order' (AO) as in a monopodial system (pseudomonopodium *sensu* Troll, 1937). x, apical mortality; AO*x*, 'apparent branching order' number *x*.

order 2 axes and so on. In a sympodial system, a rigorous use of this terminology will lead to the reference of the successive sympodial units as axis orders 1, 2, 3, etc. In order to be coherent with our broad axis definition (see above), each rectilinear succession of modules, even though not strictly edified by a single meristem, will be considered as an axis and will represent an 'apparent branching order' (Fig. 10A, C).

Rhythmic vs. continuous or diffuse branching. Defined and used for the first time for plant architecture description, these terms contribute to the characterization and definition of architectural models (Hallé and Oldeman, 1970; Hallé *et al.*, 1978) and take into account the topological distribution of sibling axes on a parent axis. Depending on whether all the axillary meristems of a stem develop into lateral axes, or whether lateral axes are grouped as distinct tiers with an obvious regular alternation of a succession of unbranched and branched nodes on the parent stem, branching is respectively referred to as continuous or rhythmic. In some cases, neither all nodes of a parent axis are associated with a lateral axis nor is there an obvious regular distribution of branches in tiers, and the branching pattern is then called 'diffuse'. As revealed in Cupressaceae by qualitative observations (Courtot and Baillaud, 1961; Baillaud, 1999) and, in recent years by sophisticated mathematical methods (Guédon *et al.*, 2001; Grosfeld, 2002; Heuret *et al.*, 2002), a diffuse branching pattern may not mean an unorganized distribution of sibling shoots on a parent shoot but may indicate a predictable, precise and subtle branching organization.

Acrotonic vs. mesotonic or basitonic branching (Fig. 11). In order to describe the positional preferential development of lateral axes on a vertical parent axis or shoot, Troll (1937) and Rauh (1939) distinguished three modalities that were grouped under the German expression 'longitudinale Symmetrie'. Acrotony (Fig. 11A, B) is the prevalent development of lateral axes in the distal part of a parent axis or shoot, and depending on whether branching is monopodial or sympodial, Rauh (1939) and Champagnat (1947) termed it, respectively, 'primary' or 'secondary' acrotony. In the initial definition of acrotony, the parent axis was always longer than the sibling ones, but Bell (1991) used the term 'acrotonic branching' for the distal position of the largest lateral branch, independent of its size relative to parent stem. Basitony (Fig. 12) was at first (Troll, 1937) considered as the preferential development of lateral axes in the basal part of a vertical stem. Bell (1991) used the term 'basitonic branching' when the proximal branches grow larger than the distal ones. Finally, mesotony (Fig. 11C, D) is used for a privileged development of branches in the median part of a shoot or axis.

Clearly included in the definition (Bell, 1991) or implicitly shown in the illustrations (Troll, 1937; Rauh, 1939), the topological lateral arrangement of branches along the parent axis is often associated with an increasing or decreasing gradient in length and/or vigour of the branches. As discussed by Caraglio and Barthélémy (1997), these two points must nevertheless be considered separately as the diversity of their expression in plants shows that there is neither automatic nor direct correlation between the privileged position and the relative vigour of lateral branches (compare Fig. 11A with Fig. 11B, or Fig. 11C with Fig. 11D). As all kinds of combinations may be found in the plant kingdom, we would prefer the terms acrotony, basitony and mesotony to be used only in reference to the privileged localization of branches on a

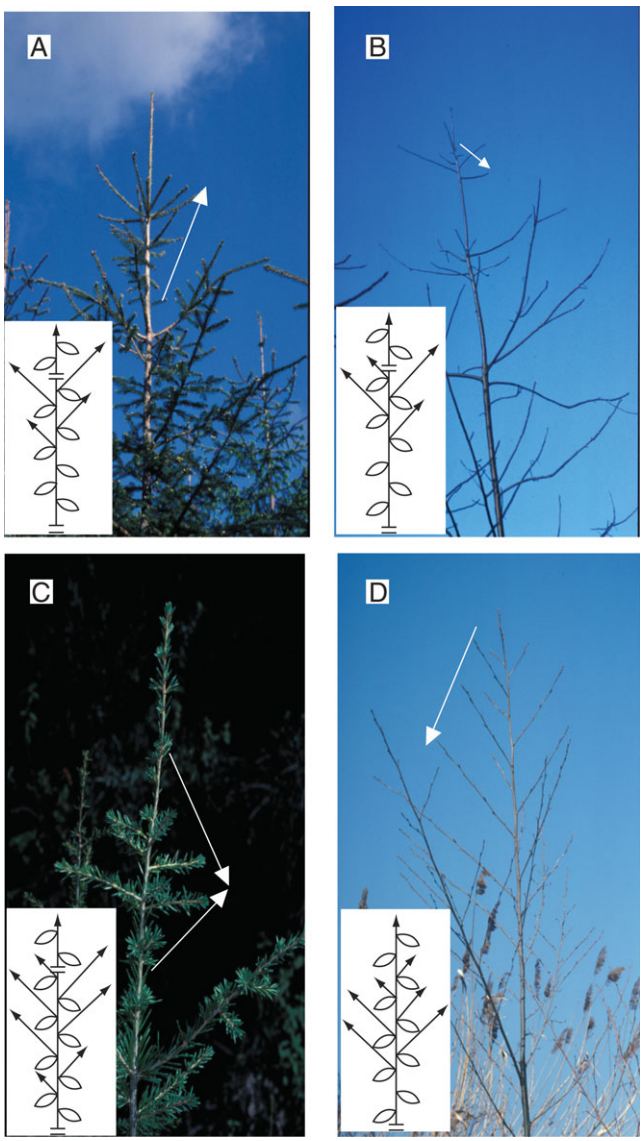


FIG. 11. Privileged repartition of sibling shoots on a vertical parent shoot or axis. Acrotony is the preferred development of lateral axes in the distal part of a parent axis or shoot (A and B). The topological lateral arrangement of branches along the parent axis may be associated with an increasing (*Abies* sp., A) or decreasing (*Juglans nigra*, B) gradient in length and/or vigour of the branches. Mesotony refers to a privileged development of branches in the median part of a shoot or axis. The topological lateral arrangement of branches along the parent axis may be associated with a distal to proximal increasing and then decreasing (*Cedrus atlantica*, C) or a decreasing (*Alnus glutinosa*, D) gradient in length and/or vigour of the branches. White arrows indicate the increasing gradient in length of branches. On the diagrams, the break represents the limit of an annual shoot.

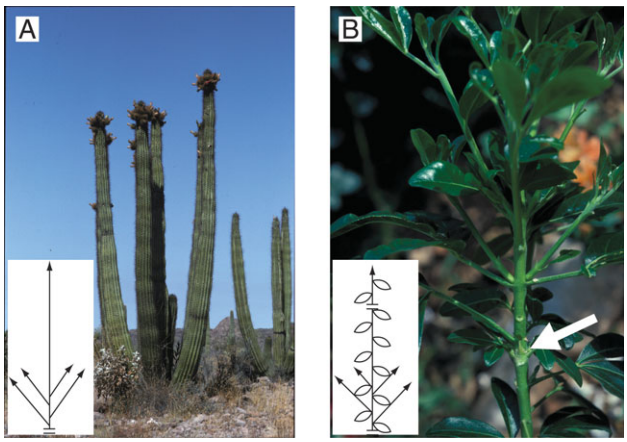


FIG. 12. Privileged repartition of sibling shoots on a vertical parent shoot or axis. Basitony is the privileged development of lateral axes in the basal part of a vertical stem or shoot. This may involve the whole plant level as for the shrubby plant *Stenocereus thurberi* (A) or the growth unit level only (*Choysia ternatea*, B). White arrow, limit of a growth unit. On the diagrams, the break is the limit of a growth unit.

parent shoot (respectively distal part, proximal part and median position) without reference to their relative vigour or length, which can be given in precise terms in addition.

Acrotony or basitony are frequently considered as two fundamental phenomena underlying, respectively, the 'arborescent' or 'bushy' growth habit (Troll, 1937; Rauh, 1939; Champagnat, 1947; Barnola and Crabbé, 1991). Nevertheless these authors refer mainly to the acrotonic branching of growth units or annual shoots in the arborescent case whereas they consider the proximal branching at the base of the whole individual when considering bushy plants. As discussed by Caraglio and Barthélémy (1997) either acrotonic or basitonic branching may characterize the growth units or shoots of either tree or bush, whereas basal sprouts may also be an adaptative strategy of some trees (Fig. 12). Therefore, these terms should be used only at the growth unit annual shoot or axis levels or, at least, the plant level of organization under consideration must be specified when using these terms.

Hypotony, epitony and amphitony (Fig. 13). In order to describe the privileged arrangement of lateral axes on a horizontal, curved or slanted parent axis, Troll (1937) defined three modalities of so-called 'laterale Symmetrie'.

According to this terminology the privileged development of branches on the upper, lateral or basal position of a parent axis is referred to, respectively, as epitony, amphitony or hypotony. Epitony is a very common process in many fruit trees (Costes *et al.*, 2006) and in plants belonging to such architectural models as those of Champagnat, Troll or Mangenot (Hallé *et al.*, 1978); it is also often associated with the survival of old branches in the canopy of old trees (Fig. 13C). Hypotony (Fig. 13A) is frequently marked by a privileged development of lateral axes in the curvature zone of a slanted branch whereas amphitony (Fig. 13B) is frequent on rectilinear horizontal or slightly slanted branches. Hypotony and amphitony may be combined in slanted and curved branches and their incidence in the expansion of lateral branch complexes is of the utmost importance in the crown architecture of many woody plants. Finally, it is noticeable that amphitony is a frequent feature in rectilinear branches whereas epitony and hypotony are characterized by the predominant development of lateral axes on the convex side of the curved, downwardly or upwardly orientated branches (Caraglio and Barthélémy, 1997; and compare Fig. 13A, B and C). As highly influenced by axis orientation, these phenomena are frequently combined with the previously described topological arrangement along axes (acrotony, basitony, mesotony) and these combinations have considerable relevance to bud fate according to their topological position and space orientation within a plant crown.

Morphological differentiation of axes

The general orientation of a leafy axis and the spatial disposition of its leaves are of major importance in the growth strategy of a plant. Within a single plant, some of these axes are essential in plant skeleton edification; some are aerials whereas others may grow underground; some are involved in space exploration whereas others are more related to reproductive dissemination activities or in environment exploitation via photosynthesis. This axis polymorphism is frequent in plants and represents a true morphological differentiation related to meristem expression and activity (Hallé and Oldeman, 1970).

Orthotropy, plagiotropy and mixed axes (Fig. 14). On most plants and more evidently in trees, two major types of axes may be distinguished according to their erect or horizontal general orientation. Orthotropy (Fig. 14A; Frank, 1868; Koriba, 1958) refers to axes whose general orientation is vertical and whose symmetry is radial, with leaves in a spiral, opposite or verticillate disposition, and associated lateral branches arranged in all spatial directions. Plagiotropic axes (Fig. 14B; Frank, 1868; Koriba, 1958) have a general horizontal to slanted orientation and a bilateral symmetry owing to leaves (distichous phyllotaxis) and branches being generally arranged in one plane.

Therefore, both kinds of axes are defined not just by their orientation but rather by a set or 'syndrome' of features (Edelin, 1984). In addition, some axes may have intermediate features and/or secondary orientation of axes may sometimes occur thus complicating their exact characterization. In many plants, a single meristem may give rise to an axis with mixed properties. Sometimes an axis may have an orthotropic proximal portion and a plagiotropic distal end; the superposition of such 'mixed axes' is a distinctive feature of the trunk edification in some plants (Mangenot's architectural model for instance; Hallé and Oldeman, 1970). Other mixed axes may present the reverse configuration, i.e. a proximal plagiotropic portion followed by a distal orthotropic end. In such cases, the modules are formed by successive hypotonic branching, giving rise to horizontal branched systems named plagiotropy by apposition (Fig. 14C; Hallé *et al.*, 1978; apposing growth of Koriba, 1958; apposition growth of Roux, 1968)

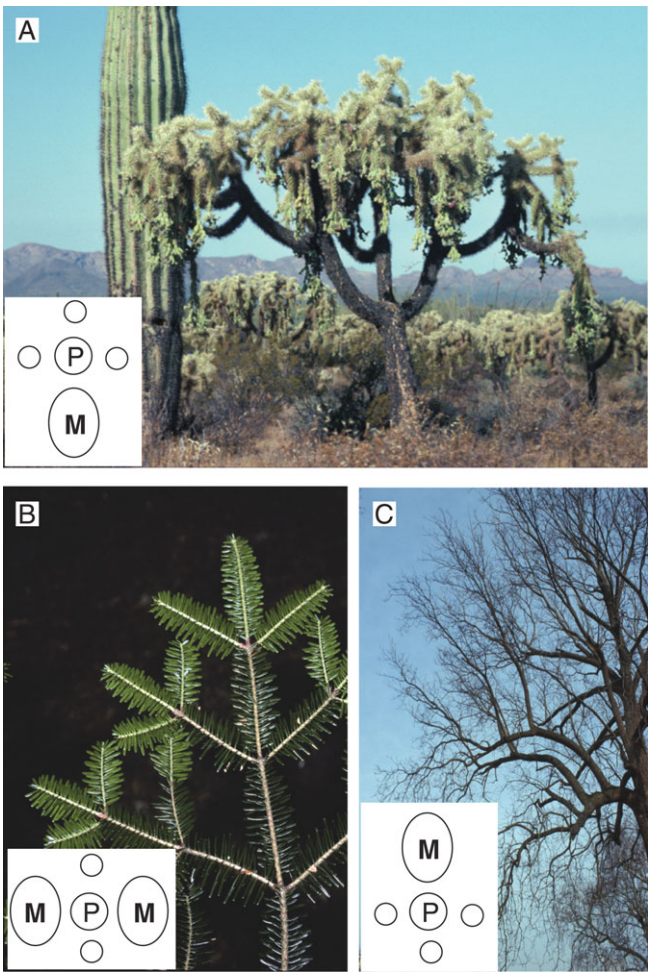


FIG. 13. Privileged repartition of sibling shoots on a slanted or horizontal parent shoot or axis. Hypotony refers to the privileged development of branches on a basal position on a parent axis (*Opuntia fulgida*, A). Mesotony refers to the privileged development of branches on a lateral position on a parent axis (branches of *Abies* sp. from above, B). Epitony refers to the privileged development of branches on upper positions on a parent axis (*Juglans nigra*, C). P, parent axis; M, privileged lateral branch.

or plagiotropy by substitution (Fig. 14D; Hallé *et al.*, 1978; substituting growth of Koriba, 1958) depending on whether modules are of, respectively, indeterminate or determinate growth.

For a given species, all axes may be of the same kind or several axis types may coexist on the same individual. Different axis types may even coexist at the same foliar axil. On the main stem of *Coffea* trees for instance, the more distal axillary meristem develops in an immediate plagiotropic branch whereas a more proximal reserve (supernumerary) bud (Varossieau, 1940; Moens, 1963) in the same leaf axil may develop as a delayed orthotropic axis. The coexistence of buds with different fates on the same node leads to many questions regarding the physiological control and genetic determinism of plagiotropy (Tomlinson, 1986, 1987) and more generally branching differentiation.

Short vs. long axes (Fig. 15). In the vegetative aerial part of most woody plants, orthotropy is generally associated with plant skeleton construction and the colonization or exploration of the vertical space, whereas plagiotropy is generally more concerned with exploration and exploitation of the horizontal space and reproductive functions (photosynthesis, flowering).

In many cases, axis differentiation is also related to axis size and very often long and short axes, respectively, specialized in environmental exploration and exploitation (Fig. 15A and B) may be identified in a plant species (Champagnat, 1965; Rivals, 1965, 1966; Kozlowski, 1971; Zimmerman and Brown, 1971). Here again the differentiation of axes and bud fate may be highly specialized and very different structures (i.e. flowers, inflorescences, spines, long axis, etc.) may be found in a single leaf axil and in a precise position, as is the case in several species (see Fig. 15C). In all these cases, however, differentiation of an axis may not be an irreversible process, and according to modifications of internal or external conditions or after architectural traumatism, reversion of axis differentiation is very often possible (see Fig. 15D–F), indicating that shoot differentiation and bud fate are controlled by a whole plant network of correlations (Champagnat, 1961;

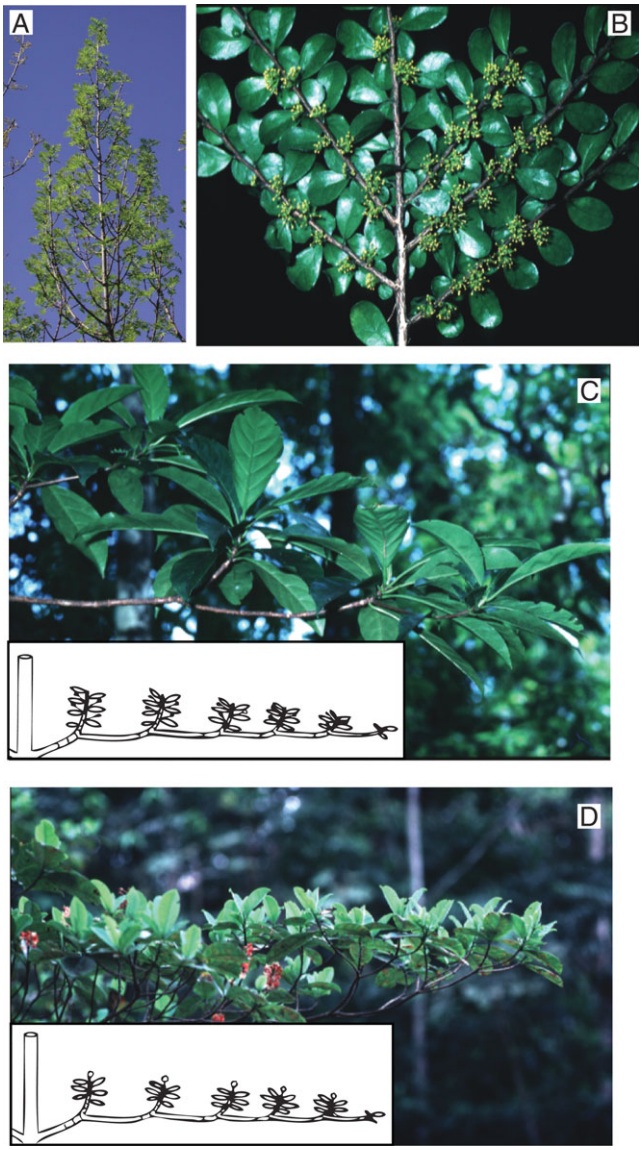


FIG. 14. Orthotropic axes are generally erect to vertical with a radial symmetry, bear large leaves and long lateral axes (*Fraxinus oxyphylla*, A). By contrast, horizontal axes tend to exhibit a bilateral symmetry frequently associated with a high reproductive and photosynthetic strategy: they represent plagiotropic axes (*Azara microphylla*, B). Particular kinds of plagiotropic axes correspond to an immediate hypotonic sympodial branching system of successive indeterminate (plagiotropy by apposition: unidentified Sapotaceae, C) or determinate (plagiotropy by substitution: *Byrsonima densa*, D) sympodial units.

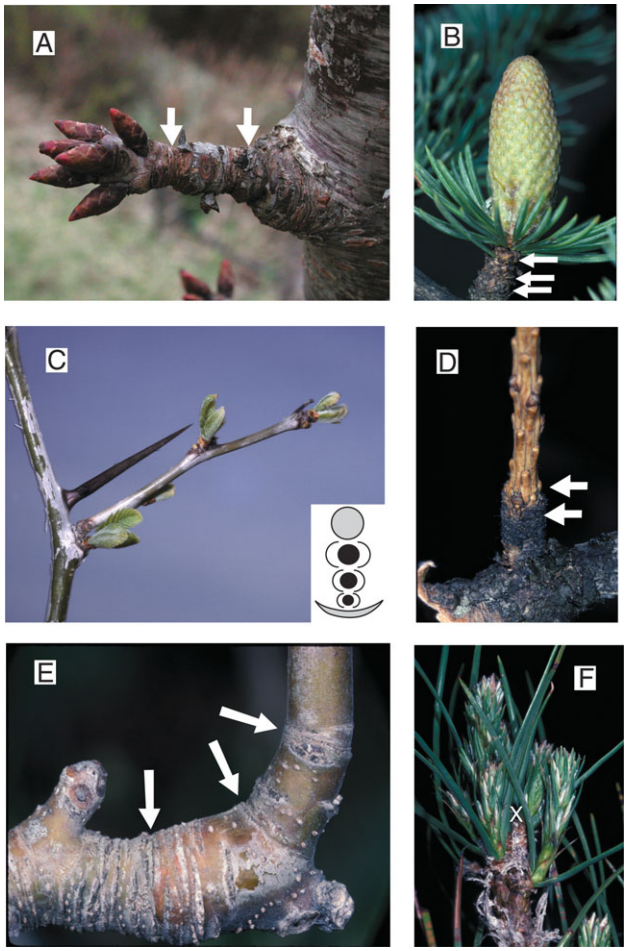


FIG. 15. Short shoots are characterized by short internodes and successive growth units (*Prunus avium*, A). They are frequently associated with lateral (A) or terminal (*Cedrus atlantica*, B) reproductive organs. Short shoot type may be linked to position in the leaf axil in the case of supernumerary buds (*Gleditsia triacanthos*, C). In some conditions a short shoot can dedifferentiate into a long shoot (*Larix decidua*, D; *Malus domestica*, E). Even the very specialized brachyblast of *Pinus* species (*P. nigra*, F) may transform into a long shoot after stem traumatism (white cross). White arrows indicate the transition between two successive growth units.

Nozeran *et al.*, 1984; Greenwood, 1987, 1995) and environmental conditions.

Position (terminal vs. lateral) of sexuality and reproductive organs

As architectural studies have historically focused mainly on the vegetative structure of the plant body, reproductive structures are considered as a whole and according to the impact they have on plant growth and branching. Because of their incidence on growth and branching, the lateral or terminal position of reproductive structures will be considered, i.e. whether they result from the transformation of a lateral or terminal meristem, respectively. Readers seeking more precise terminology and descriptions of the structure of reproductive organs or inflorescences in angiosperms should refer to more general (Bell, 1991) or dedicated synthetic works dealing with inflorescence typology or shoot typology according to the arrangement of reproductive or floral elements (Parkin, 1914; Pilger, 1921; Troll, 1957; Briggs and Johnson, 1979; Müller-Doblies and Weberling, 1984; Weberling, 1989; Claßen-Bockhoff, 2000, 2005).

THE CONCEPT OF ARCHITECTURAL MODEL

For a tree species the growth pattern which determines the successive architectural phases is called its architectural

model, or shorter, its model (Hallé and Oldeman, 1970). The architectural model is an inherent growth strategy that defines both the manner in which the plant elaborates its form and the resulting architecture. It expresses the nature and the sequence of activity of the endogenous morphogenetic processes of the organism, and corresponds to the fundamental growth programme on which the entire architecture is established. The identification of the architectural model of any given plant is based on the observation of the features belonging to the four major groups of simple morphological features presented above: (1) the growth pattern, i.e. determinate vs. indeterminate growth and rhythmic vs. continuous growth; (2) the branching pattern, i.e. terminal vs. lateral branching vs. no branching, monopodial vs. sympodial branching, rhythmic vs. continuous vs. diffuse branching, immediate vs. delayed branching; (3) the morphological differentiation of axes, i.e. orthotropic vs. plagiotropic vs. axes with mixed morphological and/or geometrical features (with plagiotropic and orthotropic portions); and (4) lateral vs. terminal flowering.

Each architectural model is defined by a particular combination of these simple morphological features and named after a well-known botanist (Fig. 16). Although the number of these combinations is theoretically very high, there are apparently only 23 architectural models found in nature. Each of these models applies equally to arborescent or herbaceous plants, from tropical or temperate regions, and which can belong to closely related or distant taxa.

The reader will find detailed information on each architectural model in Hallé and Oldeman (1970) and Hallé *et al.* (1978).

Growth patterns defined by the architectural models are genetically determined. Only under extreme ecological conditions is their expression affected by the environment (Hallé, 1978; Barthélémy, 1986; Barthélémy *et al.*, 1995, 1997*b*, 1999; Grosfeld *et al.*, 1999; Grosfeld, 2002; Stecconi, 2006). Different models can be represented by plants belonging to closely related species (Edelin, 1977; Temple, 1977; Edelin and Hallé, 1985; Vester, 1999; Hallé, 2004). Architectural analysis also shows that some plants frequently exhibit morphological features that are apparently related to two or three models (Hallé and Ng, 1981; Edelin, 1977, 1984; Veillon, 1978, 1980; Grosfeld *et al.*, 1999). These intermediate forms indicate that there is no real disjunction between the models. On the contrary, it must be considered that all architectures are theoretically possible and that there could be a gradual transition from one to another. Among this 'architectural continuum' (Edelin, 1977, 1981; Hallé *et al.*, 1978), the models themselves represent the forms that are the most stable and the most frequent, i.e. the most probable biologically. As an architectural model is defined by few and simple morphological features, it gives only an idea of the elementary developmental pattern of a species. Nonetheless, this level of representation of the plant could be well adapted to describe the evolutionary pattern or phylogenetic or taxonomic distribution of plant architecture (Johnson, 2003; Hallé, 2004) and may help to unravel the ecological importance of these patterns (Foresta, 1983; Vester, 1997, 1999).

THE ARCHITECTURAL UNIT

The architectural model represents the basic growth strategy of a plant, and this concept has allowed the definition of a typology of main plant growth strategies. Nevertheless, the characters used in its identification are far too general to describe the complete and precise architecture of a plant. For any given plant, the specific expression of its model has been called its 'architectural unit' (Barthélémy *et al.*, 1989, 1991; originally called 'diagramme architectural' in French: Edelin, 1977).

The architecture of a plant can be seen as a hierarchical branched system in which the axes can be grouped into categories according to their morphological, anatomical or functional distinctive features (Fig. 17).

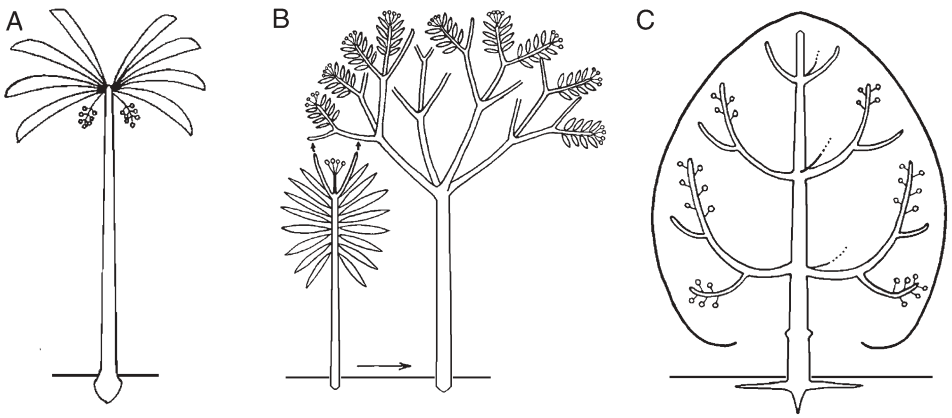
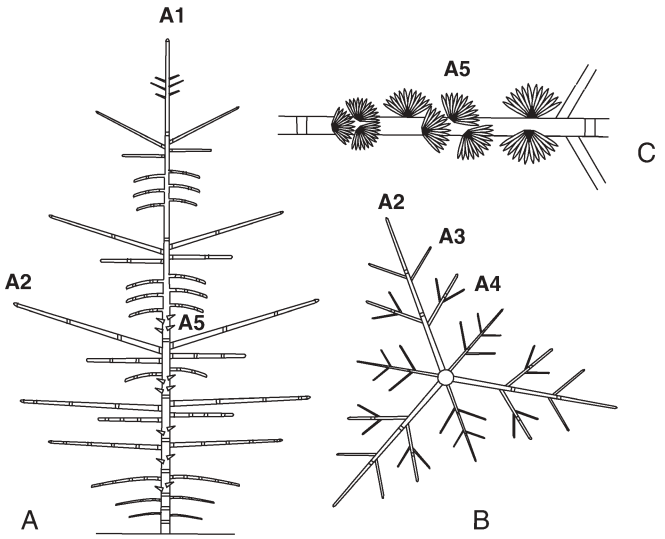


FIG. 16. Some architectural models. Corner's model (A) concerns unbranched plants with lateral inflorescences. Leeuwenberg's model (B) consists of a sympodial succession of equivalent sympodial units, each of which is orthotropic and determinate in its growth. Rauh's model (C) is represented by numerous woody plants where growth and branching are rhythmic, all axes are monopodial and sexuality is lateral. Illustrations after Hallé and Oldeman (1970), Hallé *et al.* (1978) and Barthélémy (1991).



Trunk (A1)	Branches (A2)	Branchlets (A3)	Twigs (A4)	Brachyblasts (A5)
Indeterminate growth	Long term determinate growth	Long term determinate growth	Medium term determinate growth	Short term determinate growth
Rhythmic growth	Rhythmic growth	Rhythmic growth	Rhythmic growth	Rhythmic growth
Vertical growth direction	Horizontal to slanted growth direction	Horizontal growth direction	No precise growth direction	No precise growth direction
Rhythmic delayed and immediate branching	Rhythmic delayed and immediate branching	Rhythmic delayed and immediate branching	Rhythmic delayed branching	Unbranched
No reproductive structures	No reproductive structures	No reproductive structures	No reproductive structures	Terminal male or female cones
Spiral phyllotaxis	Spiral phyllotaxis	Spiral phyllotaxis	Spiral phyllotaxis	Spiral phyllotaxis

FIG. 17. The architectural unit of *Cedrus atlantica* (Pinaceae) is composed of five axis categories (A1 to A5). (A) Diagrammatic representation of the tree (view in elevation) representing the relative position of main axis categories; (B) diagrammatic representation of a tier of branches (view from above); (C): diagram of a twig annual shoot bearing several short shoots. The break symbol indicates the limit between two successive annual shoots (from Sabatier and Barthélémy, 1999). The table summarizes the morphological features of all axis categories.

The structure and function of each category of axis may be described by a non-limitative series of features. For each of them, the observation of all the architectural characteristics previously described is necessary, but the observations have to be as exhaustive as possible and may concern any elementary level of organization (i.e. metamer, growth unit, annual shoot, module) and any kind of morphological feature (e.g. precise growth direction, phyllotaxis, pre- or neoformation, immediate or delayed branching, form and size of foliar organs, presence, absence and position of sexuality).

The results may be summed up in a table and diagrams that describe and define the specific elementary architecture of each plant, i.e. its architectural unit. Within the context of a general organization, the differences between architectural units are thus represented by the number of categories of axes, their functional and morphological features, and their relative positions.

For each species it has been shown that the number of categories of axes is finite (Edelin, 1977; Caraglio and Edelin, 1990; Caraglio, 1997; Grosfeld *et al.*, 1999; Sabatier, 1999; Grosfeld, 2002; Stecconi, 2006) and generally small (no more than five or six in some Cupressaceae according to the above cited studies). This indicates that the architecture of a fully established branched system, whatever its complexity, can be summarized in terms of a very simple sequence of axes which represents its fundamental organization. In this sequence, leading from axis 1 to the ultimate axis category, following the specific branching pattern, each branch is the expression of a

particular state of meristematic activity and the branch series as a whole can be considered to be tracking the overall activity. In this sense, the architectural unit represents the fundamental architectural and functional elementary unit of any given species.

For structurally complex woody plants in particular, strong axis specialization is frequent: for example, some axes have a more structural and/or exploration function (like the main axis and major branches), and others (short shoots, twigs, etc.) are more concerned with photosynthesis and reproduction. Depending on the species, the differentiation of axes may be strong or not. In some species, axes of different categories have similar features (e.g. ability to flower on all axis categories) whereas some other species have more specialized categories of axes, each presenting very distinctive and exclusive features. Similarly, the relative arrangement of the categories of axes may depend on the degree of differentiation among them, which, in turn, may be related to particular morphological processes such as acrotony. Thus, the categories of axes may or may not be superposed to the notion of branching order (Fig. 18).

According to a species' developmental pattern, the expression of the architectural unit may be different. Whereas the relative arrangement of categories of axes is generally clear in most woody plants and especially in trees, the total expression of the architectural unit in some herbs or sympodial plants may include the whole succession of modules (Fig. 19).

In a particular species the architectural unit is a very stable and endogenous feature, as shown for several species in which different environmental conditions affect the external form of individuals but change only

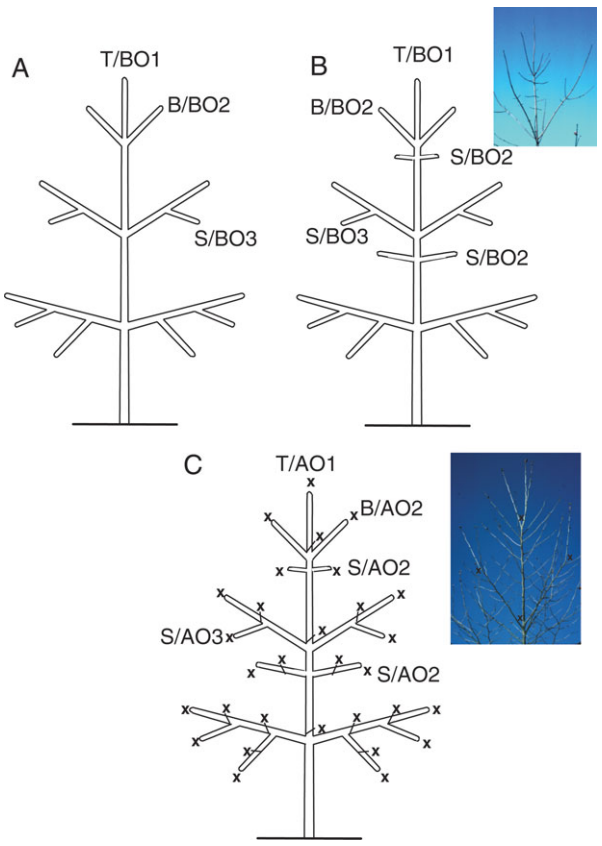


FIG. 18. Category of axis vs. branching order. The relative arrangement of categories of axes (T, trunk; B, branch; S, short shoot) may (A, i.e. *Araucaria araucana*) or may not (B and C) be superposed to the notion of branching order, in either monopodial (B, i.e. *Acer* sp.) or sympodial (C, i.e. *Platanus* sp.; Caraglio and Edelin, 1990) branching pattern. x, apical mortality; BO*n*, branching order *n*; AO*n*, apparent branching order *n*.

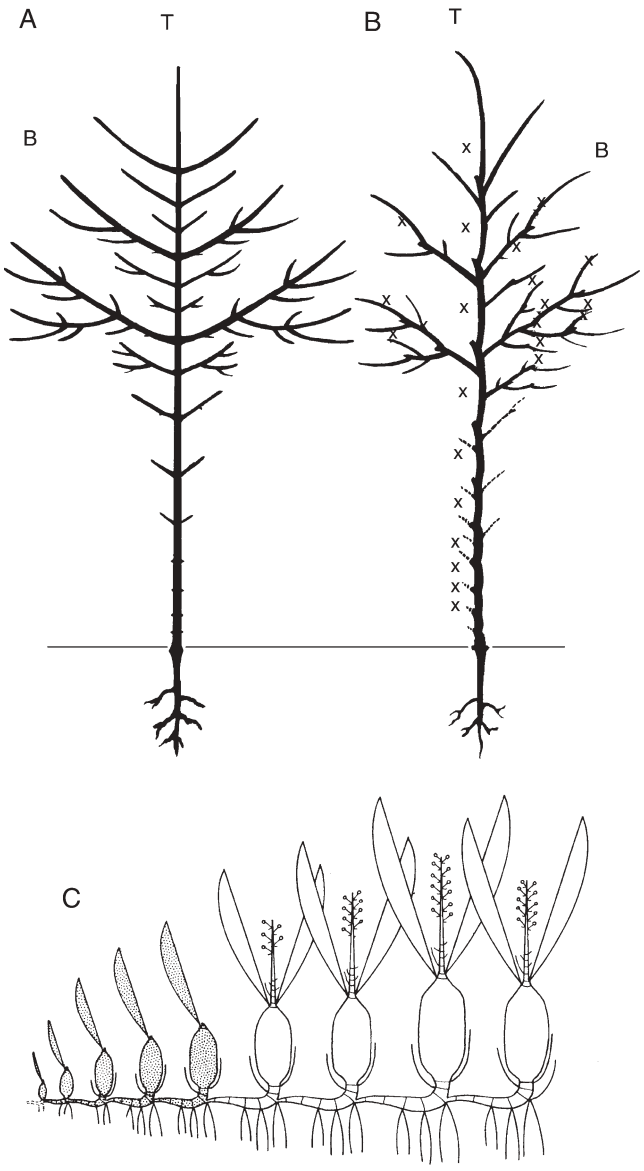


FIG. 19. Each category of axis (trunk, T; branch, B) results from the succession of shoots in a monopodial system (A, *Acer* sp., redrawn from Troll, 1937) or the succession of modules in sympodial trees (B, *Ulmus* sp., redrawn from Troll, 1937; dotted lines represent self shed branches; x, apical mortality) or herbs (C, *Encyclia vespa*, from Barthélémy, 1988; dotted sympodial units represent those that are naturally shed for the developmental stage diagrammatically represented).

quantitatively the expression of the species' endogenous morphogenetic sequence (Fig. 20; Grosfeld *et al.*, 1999).

Finally, for species such as *Cupressus sempervirens*, for which several 'forms' are traditionally well known by foresters and horticulturists (i.e. fastigiated, horizontal and intermediate), it was also shown that there were only minor qualitative differences between the elementary architecture or architectural sequence of these three forms. In this case, the observed phenotypic variability could be explained by the different expressions of several basic morphological and geometrical features such as (1) the relative main stem/branch length, (2) the straightness or gradual straightening-up status of the branches, (3) the insertion angle, (4) homogeneity or heterogeneity of branch types within a single tree and (5) the occurrence, early manifestation and importance of the reiteration process (Fig. 21; Barthélémy *et al.*,1999).

THE CONCEPT OF REITERATION

Although some plants conform to their architectural unit during their whole life span (Fig. 22), most plants repeat their architectural unit during their development, late in ontogeny, or under particular conditions. Oldeman, (1974) named this process 'reiteration' and defined it as a morphogenetic process through which the organism duplicates its own elementary architecture, i.e. its architectural unit. The result of this process is called a 'reiterated complex' (Hallé *et al.*, 1978; Barthélémy *et al.*, 1989, 1991) or a 'reiterate' (Millet *et al.*,1998*a*). Reiteration encompasses several aspects (sprouts, root-suckers, etc.) that have been known incidentally by botanists for a long time. The fundamental interest of this concept resides on it regrouping all these phenomena into a coherent whole, to bring out a common morphogenetic event. Oldeman, (1974) and others (Hallé *et al.*, 1978; Edelin, 1984; Nicolini, 1997; Vester, 1997) hypothesized about the factors triggering this process, and distinguished several types of reiteration.

As first stated by Oldeman, (1974) the reiteration process may involve the expression of the total architectural unit from axis 1 to the most differentiated axis category ('complete' or 'total' reiteration), or the expression of part of the developmental sequence duplicating only part of the species' architectural unit ('partial reiteration'): see Fig. 23A.

Reiterated complexes may originate from dormant meristems and reiteration in this case is called 'proleptic' or 'delayed'. By contrast, reiteration may result from a shift in the functioning of the apical meristem of a growing shoot that will finally produce a 'less differentiated structure', i.e. a branch apex that after some time of functioning gives rise to a 'supernumerary trunk'. In this case, the reiteration is described as 'sylleptic' (or better 'immediate') or 'reiteration by dedifferentiation' (Fig. 24). Either of these two types of reiterations may be qualified as total or partial.

Reiteration at first was considered as an opportunistic (non-automatic) process (Oldeman, 1974; Hallé *et al.*, 1978). 'Opportunistic reiteration' may today be considered as any kind of reiteration linked to the individual history of each tree and may have two main origins: (1) 'adaptive reiteration' is a response to an increase in resource levels whereas (2) 'traumatic reiteration' is a response of a plant after it has been damaged and lost a major part of its structure (Fig. 25). More recent investigations (de Castro e Santos, 1980; Edelin, 1984; Sanoja, 1992; Nicolini, 1997; Sabatier, 1999; Vester, 2001; Grosfeld, 2002; Stecconi, 2006), however, have

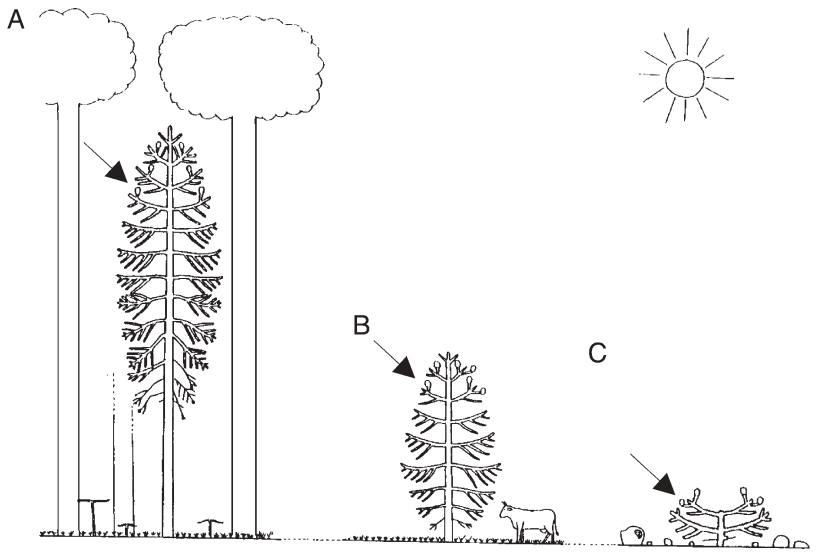


FIG. 20. Variation in crown physiognomy and architecture in relation to environmental conditions at the time of architectural unit expression in *Araucaria araucana*. (A) In forest stands, the mature tree expressing its architectural unit has a 15–20-m-high trunk which bears at its top a large conical crown composed of up to 20 tiers of living branches. (B) In full sun and with favourable soil and precipitation conditions, the tree has, at first cone production, a typical pyramidal crown. The trunk is 6–8 m high and most branches are alive. (C) In full sun and poor soil and precipitation conditions, the first production of cones may occur in a tree no more than 4 m high. The crown has a typical 'umbrella form' and most of the branches are alive (Grosfeld *et al.*, 1999). Black arrows indicate terminal female cones.

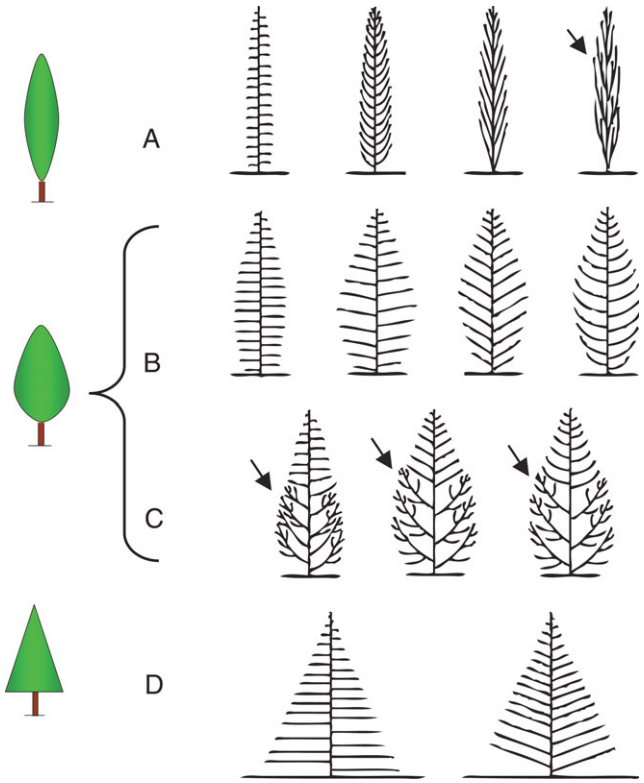


FIG. 21. Architectural types of *Cupressus sempervirens* observed in 'fastigiated' (A), 'intermediate' (B and C) and 'horizontal' (D) crown shape groups (from Barthélémy *et al.*,1999). Distinctive features of these architectural types are: the length of branches (compare A left and D), their straightness (A and B left) or straightening up (A and B right), their initial insertion angle (differences between D left and D right), homogeneity (A, B and D) or heterogeneity (C) of branch types within a single individual, the occurrence and importance of the reiteration process (A right and C). Black arrows indicate reiterated complexes.

demonstrated that, beside these cases of opportunistic reiteration, the same process of repetition may be involved in the inherent growth pattern of a species and occur automatically during plant development after a definite threshold of differentiation (Fig. 26). This latter case is a common feature of tree development and crown construction and is referred to as 'automatic' (Edelin, 1984) or 'sequential' reiteration (Nicolini, 1997).

As already noted, the development of a plant conforming to its model implies the notion of a differentiation sequence in the activity of the whole set of meristems of the plant (see also following sections). In the case of opportunistic reiteration (cf. Fig. 23) the occurrence of reiterated complexes seems to be a move backwards within the plant's developmental sequence, i.e. a real 'dedifferentiation'. A supernumerary trunk (or branch), resulting from the transformation of a growing branch (Fig. 24, 'immediate reiteration'), or from the development of a branch from a dormant meristem (Fig. 23, 'delayed reiteration'), implies that the plant expresses again the juvenile growth pattern of the organism developed from seed. This is well illustrated in cases of regeneration in which, when a trunk is cut, sprouts resembling young trunks are formed from the stump, whereas reiterated complexes that develop after a branch has been damaged have an architecture similar to that of this branch. More generally speaking, it has been demonstrated that, in this case, the real degree of dedifferentiation of a reiterated complex depends on the location of the reiterated complex in the whole plant architecture and on the ontogenetic stage of the plant at the moment reiteration occurs (Barthélémy, 1988; Fig. 23B, C).

'Automatic' or 'sequential' reiteration has been intensively studied in the last two decades (Edelin, 1984; Caraglio and Edelin, 1990; Barthélémy *et al.*, 1991;

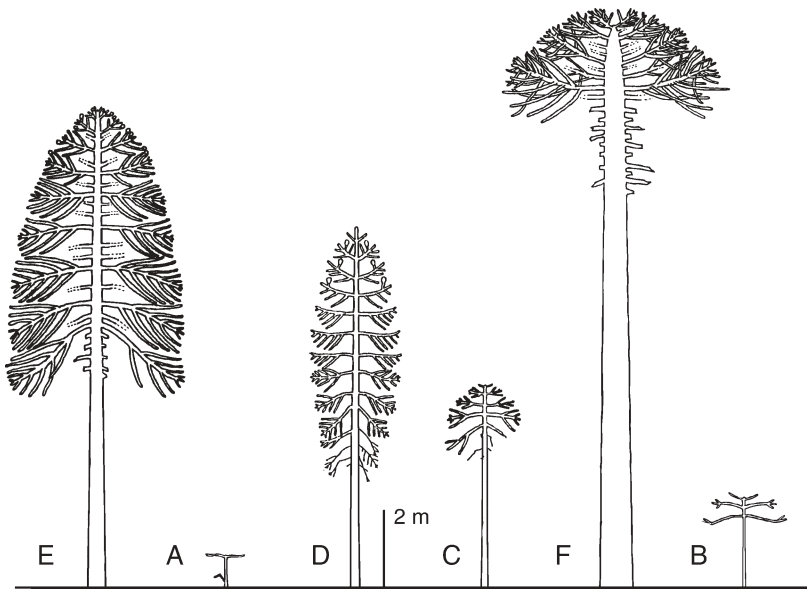


FIG. 22. Architectural sequence of development in *Araucaria araucana* (from Grosfeld, 2002). In this temperate South American species, the plant expresses step by step (A–D) its architectural unit composed of three axis categories (D). The following stages of development (E and F) are only marked by quantitative modifications, and the tree remains conform to its architectural unit, without any reiteration, up to the end of its life.

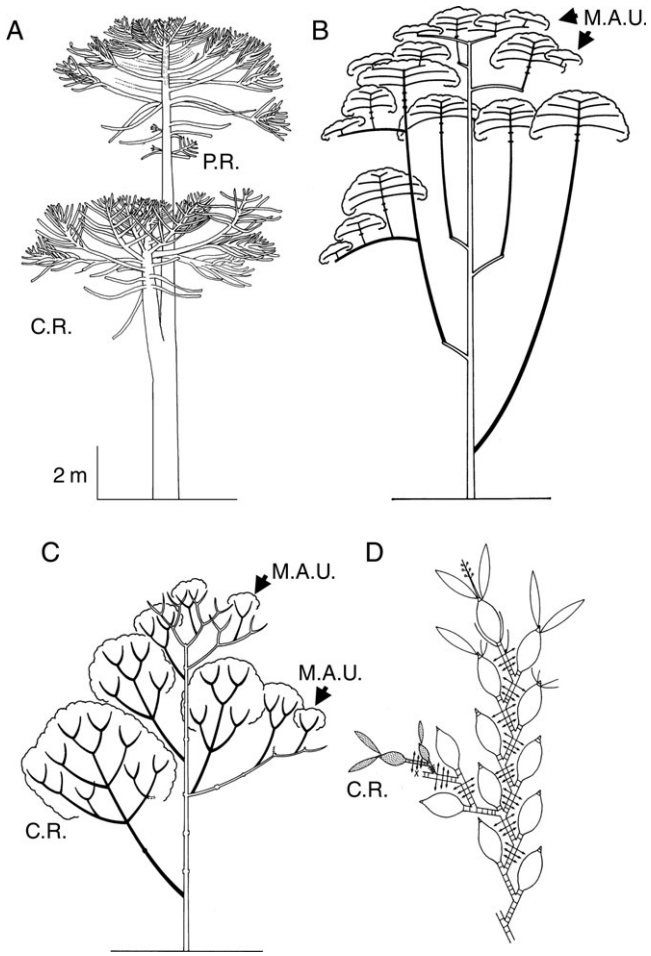


FIG. 23. Opportunistic reiteration and structure of the reiterated complexes. (A) Opportunistic, 'partial' (P.R.) and 'complete' (C.R.) reiteration in an individual of *Araucaria araucana* (Araucariaceae; from Grosfeld *et al.*, 1999). Diagrammatic representation of reiterated complexes (in black) according to their location on the tree in (B) *Symphonia globulifera* (from Barthélémy, 1988) and in (C) *Isertia coccinea* (from Barthélémy, 1988). All complete reiterated complexes result from the development of a previously dormant bud (delayed reiteration). They all duplicate the original sequence of differentiation of the original individual but the duplication is smaller and more 'pauperized' according to their insertion from the base of the trunk to the 'periphery' of the crown. At the top of the tree and in the most peripheral part of the crown, pauperization of the duplication is the highest and reiterated complexes all have a reduced and minimal specific structure (in the case of *Symphonia globulifera*, a small trunk bearing only one flowering tier of plagiotropic branches, and in the case of *Isertia coccinea*, a succession of small sympodial units only branched below the terminal inflorescence) named 'Minimal Architectural Unit' (M.A.U.) by Barthélémy (1988). (D) Opportunistic, 'complete' (C.R.) reiteration (dotted units) in old parts of a traumatically cut (x) sympodial herb (*Encyclia vespa*, Orchidaceae, from Barthélémy, 1988). Double arrows, roots.

Durand, 1997; Nicolini, 1997; Vester, 1997; Sabatier, 1999; Grosfeld, 2002; Stecconi, 2006) and proved to be a very common and major morphogenetic process underlying crown construction in most forest trees. In these studies, it was suggested that sequential reiteration must not be interpreted as a move backwards within the developmental sequence of the original organism, but rather as part of this sequence as illustrated by the continuous and gradual trends in morphological and/or anatomical parameters observed during the whole sequence of development (Fig. 27).

LEVELS OF ORGANIZATION, REPETITION PHENOMENA AND SEQUENCES OF DIFFERENTIATION

Since the pioneering work of von Goethe (1790), observations of many authors on numerous plant species (e.g. White, 1979; Barthélémy, 1986, 1991; Bell, 1991; Room *et al.*, 1994; Caraglio and Barthélémy, 1997; Gleißner, 1998) have confirmed that plants are modular organisms developing by the repetition of elementary botanical entities or construction units. In seed plants, considering their huge species diversity, the number of these entities is actually relatively small. They correspond, in increasing order of complexity or integration, to: metamer, growth unit, sympodial unit, annual shoot, axis, architectural unit, and whole reiterated organism (Barthélémy, 1991; Barthélémy *et al.*,1997*a*; Caraglio and Barthélémy, 1997). From the most elementary to the most global and integrative, these units represent as many nested 'levels of organization'. During ontogeny, they progressively derive from one another by three main and fundamental morphogenetic processes or 'repetition phenomena', namely growth, branching and reiteration, involving the repetition of respectively more complex and integrative elementary entities (Fig. 28).

As stated earlier, the development of a plant may be seen as the expression of a precise and ordered sequence of morphogenetic events underlying a strong differentiation process. Whatever the botanical entity concerned, all the above cited studies and others (Goebel, 1900; Troll and Rauh, 1950; Poethig, 1990; Gleißner, 1998; Claßen-Bockhoff, 2000, 2001; Kaplan, 2001) show that its repetition, by one or another repetition phenomenon (i.e. growth, branching, reiteration), always induces either abrupt or progressive changes in its morphological features (Barthélémy *et al.*,1997*a*; Caraglio and Barthélémy, 1997). Whatever their qualitative or quantitative nature these variations always lead to a 'differentiation' of the different repeated botanical entities. For each level of organization, this differentiation is most often related to an ordered and precise series of transformations that represent a real 'sequence of differentiation', the morphological expression of which may be observable at any organizational level, from the most elementary, i.e. the metamer, to the most global, i.e. the whole reiterated individual (Barthélémy, 1988; Barthélémy *et al.*,1997*a*; Fig. 29, but see also Figs 23 and 27).

Owing to the widespread effect of differentiation at each level of organization, the specific and exact structure of a particular botanical entity in a given location within the architecture of a plant may be seen as the result of the concomitant influence of several ontogenetic and morphogenetic factors that affect all levels of organization of the organism, at each stage of its development and during its whole life span. Although

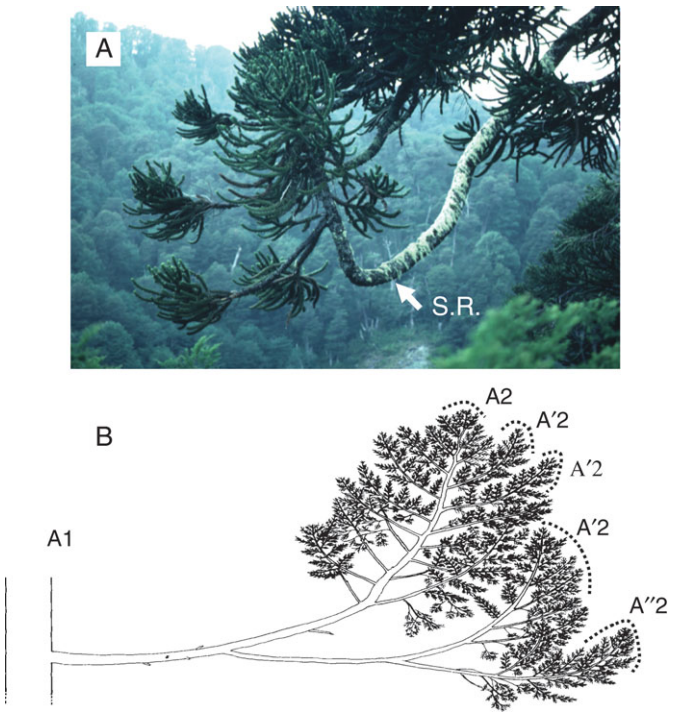


FIG. 24. (A) Total immediate reiteration (S.R.) expressed on the distal part of a branch of *Araucaria araucana*. (B) Successive immediate and partial reiterated complexes on a branch of *Austrocedrus chilensis* (from Grosfeld, 2002). A1, main stem; A'2, first order of reiteration of A2 category of axis; A''2, second order of reiteration.

environmental factors may 'modulate' these sequences of differentiation (Fig. 20), it was shown (Barthélémy *et al.*, 1995, 1997*a*, *b*; Nicolini 1997; Sabatier, 1999; Claßen-Bockhoff, 2000; Heuret *et al.*, 2000; Guérard *et al.*, 2001) that they almost never (except probably in extreme conditions) modify the inherent morphogenetic and ontogenetic constructional rules of plant organization.

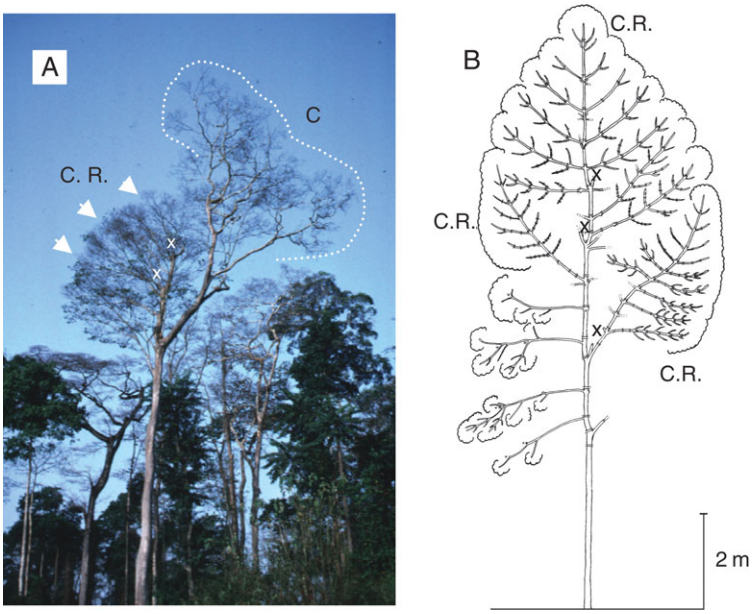


FIG. 25. (A) Damaged tree crown of an unidentified tropical tree comprising a part of the initial crown (C) and a set of reiterated complexes (C.R.) on the broken part (x). (B) Adaptive reiterated complexes (C.R.) can occur following local structural changes in the crown of an individual of *Fraxinus excelsior* (Barthélémy *et al.*,1997*a*) as caused by traumatism along the main stem (x); compare with Fig. 26.

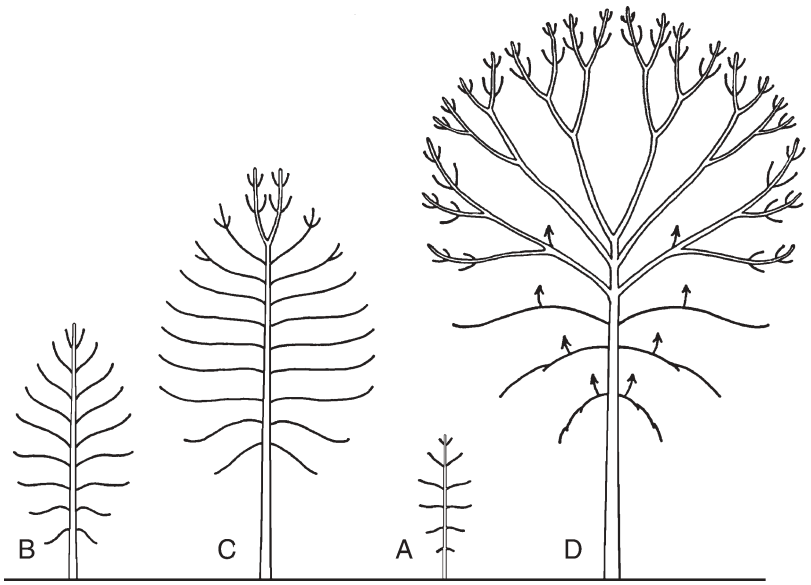


FIG. 26. Diagrammatic representation of the architectural sequence of development in *Fraxinus excelsior* (from Barthélémy *et al.*,1997*a*; highest category axes are not represented). The young plant expresses step by step (A and B) its architectural unit (in B) and then duplicates it automatically in the following stages of development (C and D) finally to give rise to a complex mature crown made of a succession of reiterated complexes (D).

THE NOTION OF 'MORPHOGENETIC GRADIENTS'

In the last two decades, coupled with precise morphological observations, architectural analyses of several plant species (Caraglio and Edelin, 1990; Barthélémy *et al.*, 1992, 1995; Drénou, 1994; Nicolini and Caraglio, 1995; Caraglio and Barthélémy, 1997; Nicolini, 1997, 1998, 2000; Gleißner, 1998; Puntieri *et al.*, 1998, 1999, 2000, 2001, 2002*a*, *b*; Genoyer *et al.*, 1999; Nicolini and Chanson, 1999; Sabatier and Barthélémy, 1999, 2001*a*, *b*; Sabatier *et al.*, 1999, 2003*a*, *b*; Claßen-Bockhoff, 2000; Heuret *et al.*, 2000; Nicolini *et al.*, 2000; Souza *et al.*, 2000; Stecconi *et al.*, 2000; Guérard *et al.*, 2001; Passo *et al.*, 2002) revealed that, under given environmental conditions, the structure and features of a particular elementary botanical entity (metamer, growth unit, annual shoot) are predictable and strongly dependent on both (1) its topological location in the comprehensive architecture of a plant and (2) the ontogenetic stage of the organism.

At the level of the whole plant, the 'morphogenetic gradients' notion was defined (Barthélémy *et al.*,1997*a*) in order to take into account the intrinsic organization rules of plant structure and was shown to be a powerful concept (Prusinkiewicz *et al.*, 2001) to explain the observed structure and series of modifications of botanical entities during the ontogeny of any plant species (Fig. 30).

These morphogenetic gradients reflect the various processes of differentiation related to morphogenetic repetition phenomena that can be identified in plant construction (see previous paragraph). Their observable number in a plant largely depends on its specific structural complexity and on the number of levels of organization it is able to express. It is at a minimum for a monocaulous continuously growing plant in which morphogenetic gradients will only concern the successive metamers (and their individual constitutive parts) whereas it will be at a maximum in a polycyclic, branched and reiterated, rhythmically and sympodially growing plant where these gradients will reflect, at several levels, the complex topological and geometrical structural nested organization.

Some of these gradients are very widespread in the plant kingdom and have a very comprehensive and general expression during the development as a whole as they are associated with either the first successive steps of the ontogeny or the ageing of axes or plants. These gradients were respectively called 'base effect', or 'drift' (Barthélémy *et al.*,1997*a*) and take into account the respective ontogenetic increase or decrease in several parameters along the main stem of any plant, or even along lateral axes of branched plants. They encompass several phenomena that have been known and described for a long time but that very often were considered or defined independently or separately according to the observer's interest (plant structural edification for botanists, main stem height and radial growth for foresters) and the phylogenetic status (seed plant or not, actual or fossil plant, monocotyledons or dicotyledons, etc.) or the particular growth pattern of the plant, or plant group (i.e. monopodial or sympodial, herbaceous annual or woody perennial plants) under study. According to the specific complexity and/or growth pattern, these gradients may be described using different parameters. Among these parameters are the size, nature, and/or internal and external structure of the successive metamers, growth units, annual shoots or modules in sympodial plants or even appendages and sibling lateral axes if any (Fig. 31), but also on the growth rate and the various portions of the sigmoidal growth curve of all

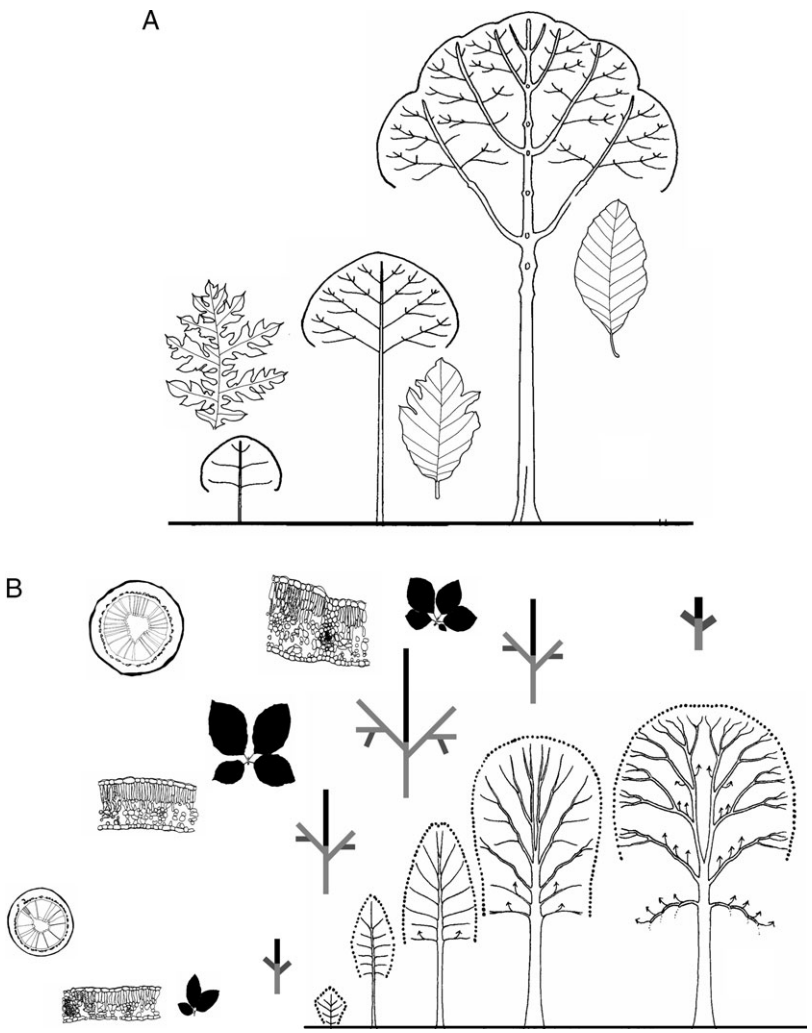


FIG. 27. Sequential ('automatic') reiteration and gradual trends in architectural, morphological and anatomical features according to stages of development. (A) Trends in leaf size and form for the main axis during the ontogeny of *Artocarpus elasticus* (from Edelin, 1984). (B) From left to right: trends in stem and leaf anatomy, in leaf and short shoot size and structure, in a main stem branching complexity (branching grade) and size (length of the latest G.U. in black and position of short shoots in dark grey on maximum expanded branching system in grey) and in architecture according to successive stages of development in *Fagus sylvatica* (after Nicolini, 1997; Nicolini and Chanson, 1999).

plants and axes (Pressler, 1865; Pardé and Bouchon, 1988) or even on the 'rhythms of primary thickening growth' (Kaplan, 2001) described by various authors ('Erstarkungswachstum' of Troll and Rauh, 1950; 'establishment growth' of Tomlinson and Zimmerman, 1966; Tomlinson and Esler, 1973; 'epidogenesis' and 'apoxogenesis' of Eggert, 1961, 1962; Daviero *et al.*, 1996; Soria and Meyer-Berthaud, 2004). These rhythms are often associated with the obconic shape of primary structures (Martinez and De La Sota, 2001; Hueber and Galtier, 2002; Isnard *et al.*, 2005) during the first stages of shoot (or even plant) ontogeny and/or with the diameter of the shoot apex (Steeves and Sussex, 1989). Whatever their specific and particular expression and because of their very wide occurrence in any actual or fossil plant, these gradients or 'rhythms of primary thickening growth' may be considered as one of the few fundamental principles of plant shoot organization (Kaplan, 2001).

'Base effect' and 'drift' are commonly expressed at the axis level and thus affect the main axis of any plant and all the lateral axes of branched ones. According to these gradients, the exact structure of a lateral axis depends on its topological and ontogenetic position on the parent axis (Fig. 30). The effect of 'branching order' may be superimposed on these previous gradients at a whole plant level. In general terms, the higher the branching order of an axis, the higher its degree of differentiation. At a more local scale in the architecture of a branched plant or system and according to the expression of the specific branching pattern, gradients, linked to shoot structure and precise branching pattern (acrotony, basitony, mesotony) or linked to shoot spatial orientation and/or geometry (hypotony, epitony, amphitony), may be superimposed on previous ones, which explains the observed heterogeneity of axes or shoots in close topological positions.

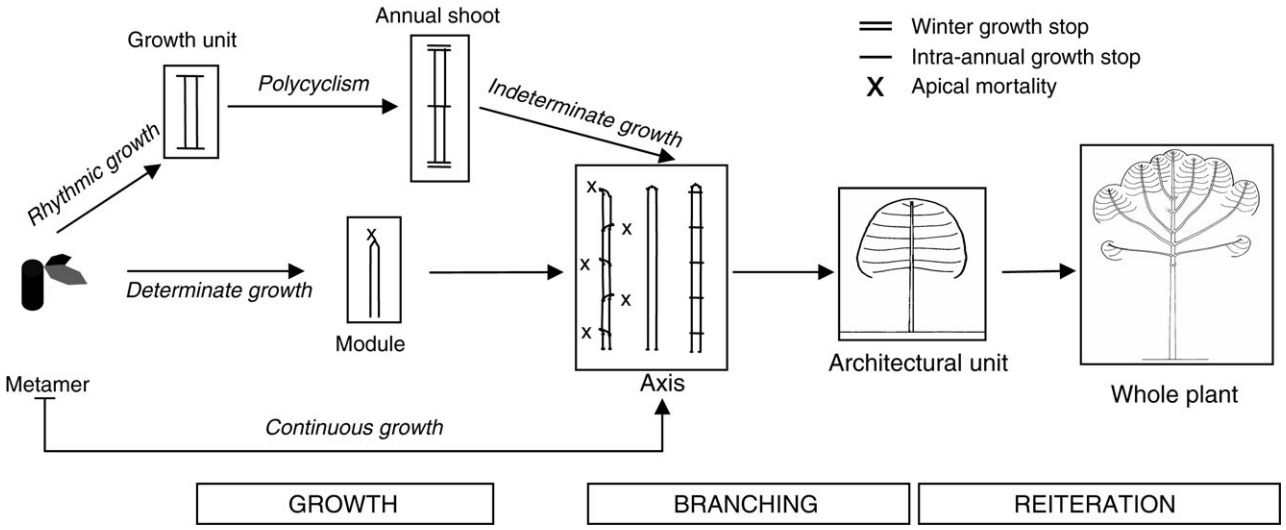


FIG. 28. Diagrammatic representation of main levels of organization (construction units) and repetition phenomena (in italics or terms in boxes) in seed plants (synthesis from Barthélémy, 1991; Barthélémy *et al.*,1997*a*; Caraglio and Barthélémy, 1997). x, apical mortality.

Because of its duplicative and repetitive nature, the reiteration process reproduces the morphogenetic gradients of the non-reiterated parent plant (Fig. 30) and the structure of the reiterated complexes resembles that of the whole plant (Fig. 23B, C; Barthélémy, 1988).

As previously stated, all these morphogenetic gradients have a strong intrinsic basis and allow in a given environmental condition the prediction of the precise structure of a particular elementary entity according to its precise architectural position and to the developmental stage of the plant. Their expression, however, may be modulated by environmental or technical factors. Where constant but different conditions prevail during the whole ontogeny, this may lead to very different final structures as development in each condition may be related to a particular 'reading' of the intrinsic sequence of differentiation or in other words a particular ontogenic trajectory (Fig. 17). In fluctuating conditions, in case of a trauma or according to localized and temporally limited perturbations resulting from environmental or technical causes, knowledge of these gradients and the possible *a posteriori* identification of their local or partial alteration or modification and the induced local perturbation of the sequence of differentiation may also serve as a basis for a very precise diagnosis of a plant's particular history (Fig. 25B).

THE NOTION OF 'PHYSIOLOGICAL AGE OF A MERISTEM'

The notion of morphogenetic gradients illustrates and takes into account the commonly observed situations where, for a given plant species or even individual, (1) at a given time and/or for a given stage of development, homologous botanical entities with very different features (or 'states of differentiation') coexist on the same individual (e.g. short vs. long shoots or reproductive vs. vegetative shoots; for instance see Figs 19, 21, 23 and 27) whereas, by contrast, (2) similar elementary botanical entities with the same morphological features (e.g. short floriferous shoots for instance; e.g. see Figs 15 and 29) may be encountered for very different plant ages or stages of development.

These observations complemented by others led to the definition of 'physiological age of a meristem' (Barthélémy *et al.*,1997*a*) that may generally be characterized and defined by a particular combination of several morphological, anatomical and/or functional attributes of a given botanical entity derived from this meristem (Fig. 32).

This physiological age of a meristem is thus determined, *a posteriori*, by the morphological analysis of the elementary botanical entity it produces, and may not be an intrinsic property of this meristem itself but the result of all morphogenetic interactions between plant parts that are related to differentiation processes and result in the expression of morphogenetic gradients.

As previously discussed, the physiological age of a meristem (or elementary botanical entity) depends on its precise location in the plant architecture and on the stage of development of the organism, and its expression may be modulated by environmental factors. The functioning of a meristem, or the elementary botanical entities it produces, can thus be characterized by three different ages (Barthélémy *et al.*,1997*a*; Fig. 33):

(1) the calendar or chronological age corresponds to the period (i.e. year, month, week or day of formation for instance) in which the elementary botanical entity has been edified (metamer, growth unit or annual shoot according to specific and relevant growth pattern and plant complexity);
(2) the ontogenetical age refers to the elapsed time after seed germination (the ontogenetic time unit considered may be a year, a day or a growth cycle according to

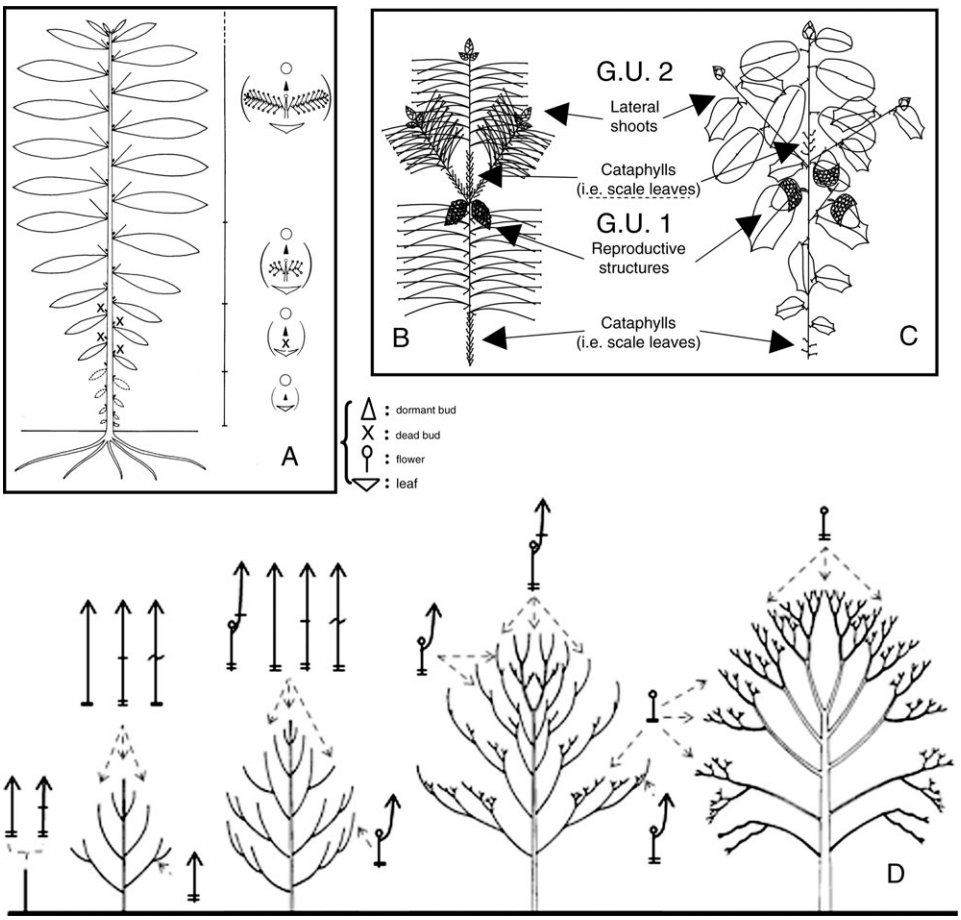


FIG. 29. Differentiation processes and levels of organization in seed plants. (A) Coordinate and related trends in leaf and internode structure and in size and nature of foliar axil products along the unique axis of a herbaceous tropical plant native to French Guyana: *Noisettia longifolia* (after Barthélémy, 1988). (B and C) Differentiation at the level of the growth unit (G.U.) and annual bicyclic shoot in the Mediterranean trees *Pinus halepensis* (B) and *Quercus ilex* (C, after Caraglio and Barthélémy, 1997, see also Fig. 6). In both cases, differentiation at the level of each growth unit is marked by the nature of foliar organs (cataphylls vs. photosynthetic leaves) or axillary products (dormant bud vs. lateral shoot or vs. reproductive organs) for G.U.1. For both species, at the bicyclic annual shoot level, differentiation between the two successive G.U.s (i.e. G.U.1 vs. G.U.2) is revealed by the presence of reproductive structures and lateral shoots on G.U.1 only and by differences in leaf size and structure according to their bearing G.U., i.e. G.U.1 vs. G.U.2. (D) Differentiation at the comprehensive level of the whole ontogeny of a plant is illustrated in the case of common walnut (*Juglans regia*, after Sabatier, 1999) by the architectural trend from young to mature tree (left to right) and by the associated annual shoot structure trends (diagrammatically represented here at each stage for the main stem and some lateral branches). Break symbol (=), winter growth stop; – or ~, intra-annual growth stop or decrease in growth speed; o, terminal female flower.

the specific complexity and growth pattern of the species);

(3) the physiological age of a meristem relates to the degree of differentiation of the structures it produced. It may be estimated *a posteriori* by a non-limitative series of qualitative and quantitative criteria. For example, the short axes of many trees are typical features of 'physiologically aged' structures: growth units are short, bear flowers and have a short lifetime. These highly differentiated axes may be considered as 'physiologically old' whatever their moment of appearance. By contrast, main axes consisting of vigorous growth units and/or annual shoots may be considered as 'physiologically young' products and generally appear only in the young tree.

The identification for a botanical entity of these three ages is fundamental in order to understand the comprehensive architecture of a plant or even its plasticity, i.e. the effects of the environment on its development and structure. It permits the precise characterization of all elementary levels of organization within the more integrative individual architecture and allows a precise multilevel description of plant architecture and organization.

CONCLUSIONS

Any plant may be recognized by its general form, but this physiognomy is always the result of a very precise structure that underlies the existence of a strong inherent organizational pattern in plant architecture construction.

Architectural studies that have been carried out for some 30 years have led to the definition of several concepts and notions that provide powerful tools for studying plant form and intrinsic morphogenetic and ontogenetic

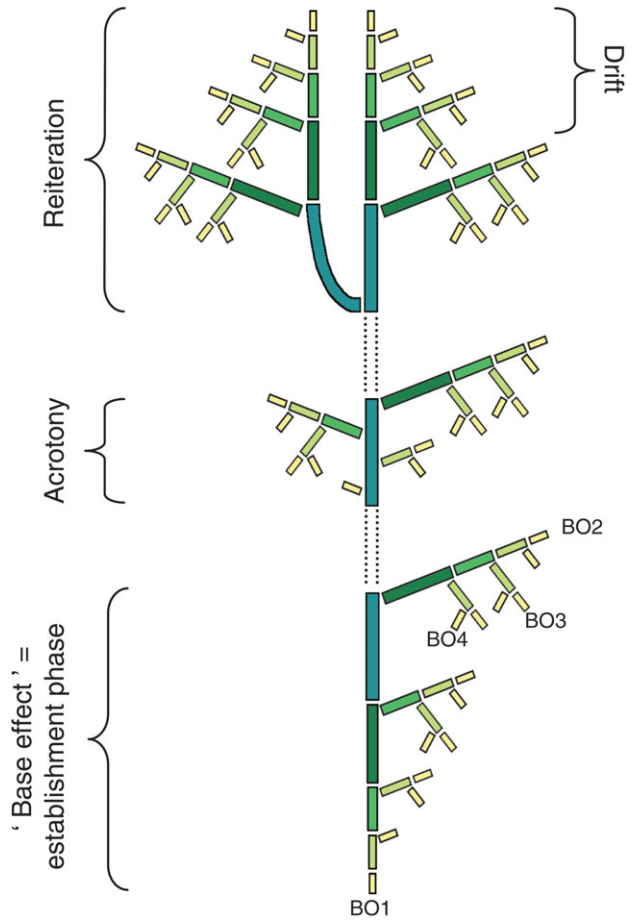


FIG. 30. Morphogenetic gradients and physiological age of meristems (after Barthélémy *et al.*,1997*a*). Theoretical and diagrammatic representation of the distribution of elementary botanical entities with similar characteristics (i.e. presenting the same 'physiological age' and represented by the same size and colour rectangle on the diagram) according to some main morphogenetic gradients very commonly observed in seed plants: for the initial structure and reiterated complexes four 'branching orders' (BO1–BO4), BO1 representing the main axis; 'base effect' is a gradient linked to the 'establishment growth phase' of any plant grown from seed; 'acrotony', with increasing acropetal gradient of vigour of lateral axes, is a common feature of the annual shoots and growth units of most rhythmically growing trees; 'drift' is a general feature linked with axis ageing; sequential 'reiteration', in this case, represented by the automatic duplication of the sequence of development and associated gradients of the main axis by another axis.

rules. Combined with architectural concepts, the recognition and definition of the notions of 'levels of organization', 'repetition phenomena', 'sequence of differentiation', 'morphogenetic gradients' and 'physiological age of meristems' provide a general and robust framework for the understanding and interpretation of plant morphogenesis. This framework has applications in agronomy, botany, forestry and plant or landscape management, owing to its contribution in the study of: the diagnosis of the physiological status of a plant (Barthélémy *et al.*, 1992; Millet *et al.*, 1998*a*, *b*, 1999; Génoyer *et al.*, 1999; Nicolini *et al.*, 2003), the effect of environmental factors and architectural plasticity (Grosfeld *et al.*, 1999; Nicolini *et al.*, 2000; Guérard *et al.*, 2001; Stecconi, 2006), technical practices (Caraglio *et al.*, 2000; Sabatier *et al.*, 2000; Leroy and Caraglio, 2003), architectural and genetic variation, plant breeding and selection (Barthélémy *et al.*,1999; Corradini *et al.*, 2002; Sabatier *et al.*, 2003*a*) and landscape management (Auclair *et al.*, 2001), among other issues.

Based on this botanical background and with the development of high-power computers, a concomitant and complementary computational and numerical approach to the modelling and computer visualization of plant architecture has gained importance in recent decades. Mathematical models of growth, branching and architecture have been developed on the basis of qualitative botanical knowledge, e.g. models and quantitative data on the demography, size and positions of plant components (Godin *et al.*, 1997, 1999; Godin and Caraglio, 1998; Ferraro and Godin, 2000, 2003; Godin, 2000; Guédon *et al.*, 2001; Costes and Guédon, 2002; Heuret *et al.*, 2002, 2003; Costes *et al.*, 2003; Durand *et al.*, 2005; Ferraro *et al.*, 2005; Godin *et al.*, 2005). This new multidisciplinary approach offers new possibilities to understand or quantify the genetic basis or regulation of plant architecture (Barbier de Reuille *et al.*, 2005, 2006; McSteen and Leyser, 2005; Mündermann *et al.*, 2005; Wang and Li, 2005) and will probably renew various aspects of developmental biology studies (Turnbull, 2005).

Results of these mathematical models are used to simulate plant development and architecture (de Reffye and Houllier, 1997). In these simulations much emphasis has been given to the changes in the physiological age of plant components and in the three-dimensional structure during plant development (Bouchon *et al.*, 1997; Yan *et al.*, 2003; Zhao *et al.*, 2003). This methodology may be used for any kind of plant (Barczi *et al.*, 1997) and has also been successfully used to simulate root systems (Jourdan and Rey,1997*a*, *b*, *c*; Danjon *et al.*,1999*a*, *b*, 2005; Dupuy *et al.*, 2005*a*, *b*, *c*, 2006). It can also be used to evaluate developmental changes such as growth responses to controlled environments, aerial biomass, volume prospected in soil by roots, radiant energy transfer, retrodiffusion of the canopy for calibrating remote-sensing techniques, and the mechanical status of a tree (de Reffye and Houllier, 1997; Castel *et al.*, 2002; Hu and Jaeger, 2003; Soler *et al.*, 2003; Picard *et al.*, 2004; Chenu *et al.*, 2005; Sellier *et al.*, 2006). Finally, the models may be linked to eco-physiological models, leading to structural functional models (Godin and Sinoquet, 2005) or process-based architectural models, i.e. morphogenetic models of tree architecture directly driven by eco-physiological processes, with possible applications in environmental and genetic control of morphogenesis in crops and phenotypic plasticity modelling and simulation (de Reffye *et al.*, 1997; Yan *et al.*, 2004; Dingkuhn *et al.*, 2005; Guo *et al.*, 2006).

Because of its economic importance for agronomic production, plant reproduction or vegetative propagation, acquisition of reproductive capacities during ontogeny has been extensively studied (Goebel, 1900; Passecker, 1944, 1958; Chouard, 1950; Rémy, 1951; Stokes and Verkerk,

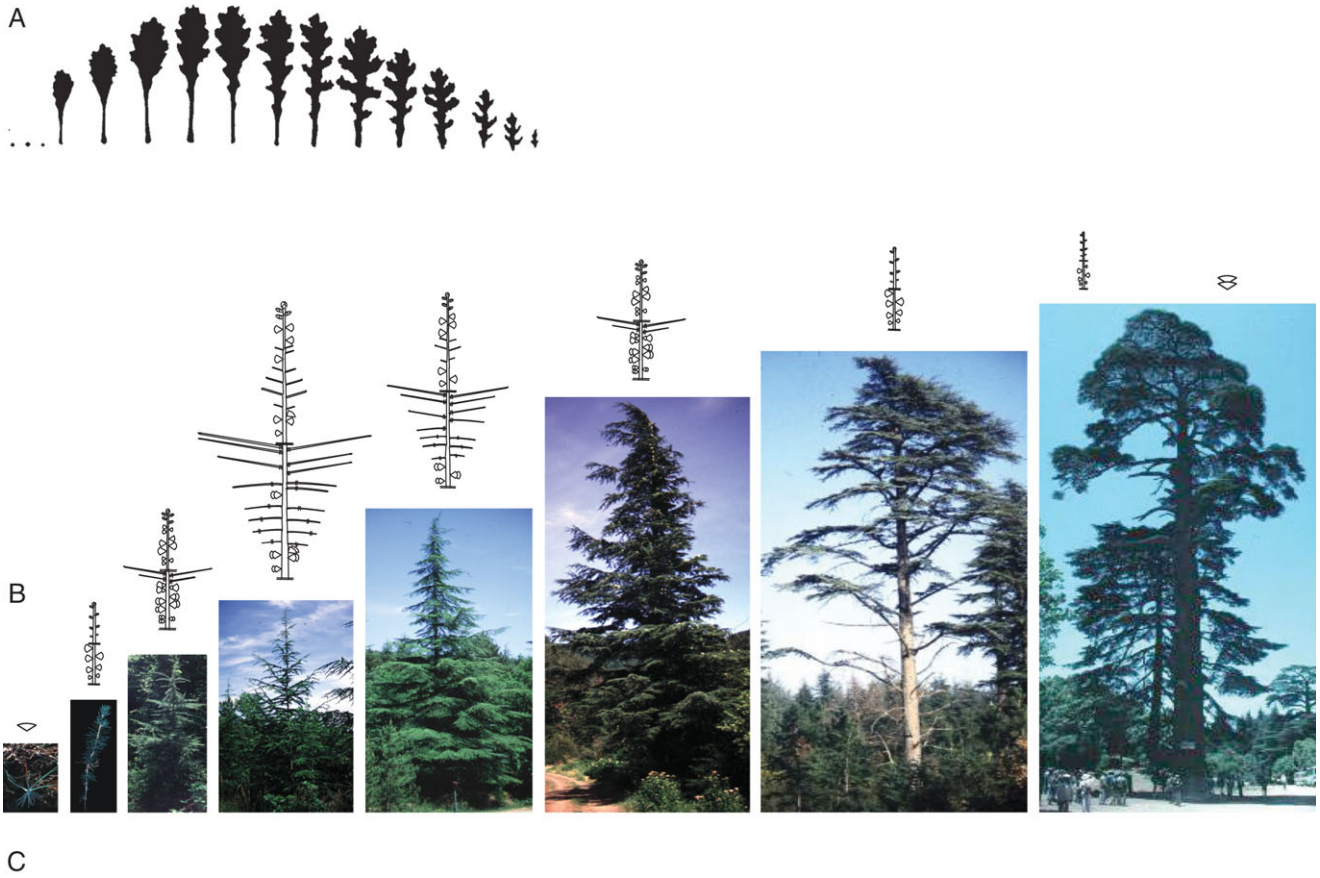


FIG. 31. (A) Shape and size of successive leaves along a stem of a herbaceous *Senecio* sp. (redrawn from Baillaud and Courtot, 1955). (B) Organization of the two last successive annual shoots of the main stem of *Cedrus atlantica* during its life and (C) the corresponding global tree structure (from Sabatier and Barthélémy, 1995).

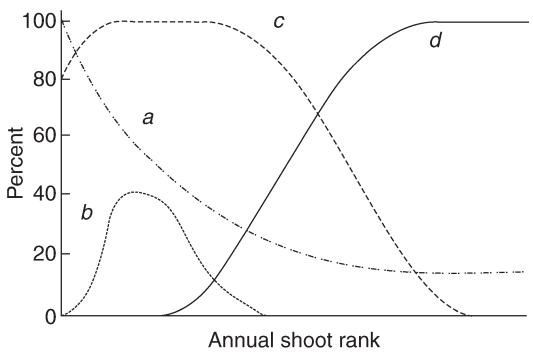


FIG. 32. Diagrammatic representation of trends in the value of some morphological parameters according to annual shoot rank of successive annual shoots of branches borne on the same ontogenetical age parent shoots of the main stem of a set of 22-year-old dominant to co-dominant *Pinus pinaster* individuals grown on a same stand in the south-west of France (unpublished data; Coudurier *et al.*, 1995; Heuret *et al.*, 2006), where *a* is the mean annual shoot length (in percentage of maximum length), *b* is the percentage of polycyclic shoots, *c* is the percentage of branched shoots, and *d* is the percentage of shoots with male cones. For each shoot rank the particular combination of the value of the morphological parameters allows a strict characterization of the physiological age of meristem activity that produced it.

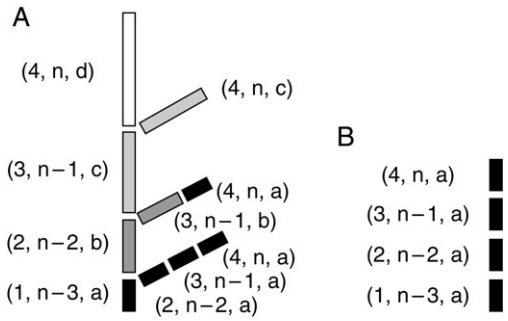


FIG. 33. Diagrammatic representation of a theoretical plant whose elementary botanical entities produced by the meristems (for instance annual shoots, represented by rectangles) may encompass four different physiological ages (a–d). The 'plant' grows from seed in four steps (possible ontogenetic ages 1–4), each step corresponding to one year of growth (n – 3 to n). It is hypothetically represented as growing in 'good' environmental conditions (where the main stem expresses the four possible physiological ages successively and in relation to successive four ontogenetic ages and where branches fully express morphogenetic gradients as shown in Fig. 30: case 'A'), or in suppressed condition (as for the growth of *Araucaria araucana* in Fig. 20; case 'B'). Each entity is characterized by a trinom – where the first element represents ontogenetic age (1–4), the second element represents calendar age (n – 3 to n) and the third element represents physiological age (a–d) – that allows us to understand the structure of each entity in the whole architecture of the plant (represented in A and B 4 years after germination).

1951; Doorenbos, 1954; Robbins, 1957, 1961; Wareing, 1959, 1961; Zeevaart, 1962; Stoutmeyer, 1964; Visser, 1964; Doorenbos, 1965; Picard, 1965; Visser and De Vries, 1970; Zimmerman, 1972; Borchert, 1976; Schwabé, 1976; Greenwood, 1995). With regard to this potential, four main phases of plant development have been proposed: the embryonic phase, in which the shoot and root meristem are established; the juvenile phase, in which there is no sexual reproduction; the adult vegetative phase, in which reproductive capacity is established; and finally the adult reproductive phase (Greenwood, 1995; Poethig, 2003). The transition between these phases is currently referred to as phase change (Jones, 1999). In addition to reproductive function, ontogenetic changes in several other parameters and morphological, anatomical and/or functional features has long been described in plants (Koch, 1873; Carrière, 1880; Hochtetter, 1880; Beissner, 1888; Cockayne, 1912; Frost, 1938; Webber and Batchelor, 1948; Ashby, 1949; Doorenbos, 1954; Schaffalitzky de Muckadell, 1954, 1959; Brink, 1962; Trippi, 1963; Wardle, 1963; Greenwood and Atkinson, 1977; Poethig, 1990, 2003; Jones, 1999; Kaplan, 2001) and these changes may be simultaneous with the appearance of reproductive capacity during development. At the whole individual level, plant development may thus be viewed as a succession of phases, each characterized by a set of several features or parameters. Under given conditions, the duration of these phases may be more or less fixed for a species (Wareing, 1959; Zimmerman, 1972; Hackett, 1985) and it is thus possible to identify a mean specific age in which a plant will be able or unable to express a particular feature. According to plant species, this 'chronological' (Ritterbusch, 1990) or 'calendar' (Gatsuk *et al.*, 1980) age may be expressed in days or years after germination and it is known that it may be strongly modified by environmental factors (Doorenbos, 1954; Zimmerman, 1972; Gatsuk *et al.*, 1980). At a given moment, a plant may thus be characterized not only by its 'chronological' or 'calendar' age but also by a set of biological criteria that indicates its 'stage' of development variously referred to as 'biological age' (Levin, 1966; Roloff, 1989; Gleißner, 1998), 'physiological age' (Robbins, 1957; Schaffalitzky de Muckadell, 1959; Grubb, 1977), 'ontogenic age' (Passecker, 1977) or 'age state' (Uranov, 1975; Gatsuk *et al.*, 1980). The 'physiological age' of the individual may merge with the metamer level and may be defined or even quantified by the features or parameters of the successive constitutive metamers or leaves in small, herbaceous monocaulous continuously growing plants, as variously demonstrated (Ashby, 1949; Baillaud and Courtot, 1955; Poethig, 2003; Fig. 31A), because the whole plant structure corresponds to an elementary botanical entity. In more complex plants with several nested levels of organization we have demonstrated that metamer level is not sufficient to take into account the complete heterogeneity of plant parts either at a given stage or during the whole ontogeny. In the latter cases, the idea of a 'physiological age' better corresponds to the growth unit and/or sympodial unit and/or annual shoot levels (Fig. 31B). The general description of plant parts heterogeneity thus implies the use of this notion at the meristem level and the pertinent elementary levels it produces in order to take into account plant architecture diversity. Coupled with the description of 'morphogenetic gradients', the notion of physiological age of a meristem (as applied to the pertinent level of organization) may allow a generic description of the multiple and diverse expressions of 'ontogenetic contingency' (Diggle, 1994, 1997) observed in the plant kingdom (Kaplan, 2001). Furthermore, as these notions allow a multilevel description of the influence of the environment on several features and their expression along ontogeny and according to architectural position, they may provide a powerful tool to separate ontogenetic variations from environmental plasticity or to separate traits or ontogenetic trajectories plasticity (Wu and Stettler, 1998; Huber *et al.*, 1999; Wu and Hinckley, 2001; Alpert and Simms, 2002; Diggle, 2002; Novoplansky, 2002; Wright *et al.*, 2002; Sachs, 2004; de Kroon *et al.*, 2005; Wolfe and Mazer, 2005).

Despite the frequently stressed importance of considering plant morphology and/or architecture to understand their phylogeny, very few studies actually describe the link between phylogeny and architecture (Sanoja, 1992; Johnson, 2003; Hallé, 2004) and here also we probably require more data and a multilevel consideration of plant structure.

Finally, the dynamic, multilevel and comprehensive approach of plant form and ontogeny have proved to be fruitful but the number of questions raised shows that some of the answers will also, we hope, come from a multidisciplinary approach and by the combination of different approaches to the same plant object.

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LITERATURE CITED

Alpert P, Simms EL. 2002. The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology* **16**: 285–297.

Altman A, Goren R. 1978. Development of *Citrus* bud explants in culture. *Journal of the American Society for Horticultural Science* **103**: 120–123.

Alvim P de T. 1964. Tree growth periodicity in tropical climates. In: Zimmermann MH ed. *Formation of wood in forest trees.* New York: Academic Press, 479–495.

Ashby E. 1949. De la forme des feuilles et de leur rapport avec l'âge physiologique des plantes. *Endeavour* **T 8** (**29**): 18–25.

Atger C, Edelin C. 1994*a*. Premières données sur l'architecture comparée des systèmes racinaires et caulinaires. *Canadian Journal of Botany* **72**: 963–975.

Atger C, Edelin C. 1994*b*. Stratégies d'occupation du milieu souterrain par les systèmes racinaires des arbres. *Revue d'Ecologie (Terre Vie)* **49**: 343–356.

Auclair D, Barczi J-F, Borne F, Etienne M. 2001. Assessing the visual impact of agroforestry management with landscape design software. *Landscape Research* **26**: 397–406.

Aydelotte AR, Diggle PK. 1997. Analysis of developmental preformation in the alpine herb *Caltha leptosepala* (Ranunculaceae). *American Journal of Botany* **84**: 1646–1657.

Baillaud L. 1999. Structures répétitives spatiales et spatio-temporelles des plantes. *Phytomorphology* **49**: 377–404.

Baillaud L, Courtot Y. 1955. Temps et rythmes chez les végétaux. *Annales Françaises de Chronométrie* **9**: 87–102.

Barbier de Reuille P, Bohn-Courseau I, Godin C, Traas J. 2005. A protocol to analyse cellular dynamics during plant development. *Plant Journal* **44**: 1045–1053.

Barbier de Reuille P, Bohn-Courseau I, Ljung K, Morin H, Carraro N, Godin C, Traas J. 2006. Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in Arabidopsis. *Proceedings of the National Academy of Science* **103**: 1627–1632.

Barczi JF, de Reffye P, Caraglio Y. 1997. Essai sur l'identification et la mise en oeuvre des paramètres nécessaires à la simulation d'une architecture végétale: le logiciel AMAPsim. In: Bouchon J, de Reffye P, Barthélémy D eds. *Modélisation et Simulation de l'Architecture Des Végétaux*. Science Update. Paris: INRA Editions, 205–254.

Barlow PW. 1989. Meristems, metamers and modules and the development of shoot and root systems. *Botanical Journal of the Linnean Society* **100**: 255–279.

Barnola P, Crabbé J. 1991. La basitonie chez les végétaux ligneux. Déterminisme et variabilité d'expression. *Comptes rendus du 2ème Colloque International sur l'Arbre, Montpellier, 10–15 Septembre 1990, Naturalia Monspeliensia, No. Hors Série*: 381–396.

Barthélémy D. 1986. Establishment of modular growth in a tropical tree: *Isertia coccinea* Vahl. (Rubiaceae). In: Harper JL, Rosen BR, White J eds. *The growth and form of modular organisms. Philosophical Transactions of the Royal Society of London, sér*. B, **313**: 89–94.

Barthélémy D. 1988. *Architecture et sexualité chez quelques plantes tropicales: le concept de floraison automatique*. PhD thesis, University Montpellier 2.

Barthélémy D. 1991. Levels of organization and repetition phenomena in seeds plants. *Acta Biotheoretica* **39**: 309–323.

Barthélémy D, Edelin C, Hallé F. 1989. Architectural concepts for tropical trees. In: Holm-Nielsen LB, Balslev H eds. *Tropical forests: botanical dynamics, speciation and diversity*. London: Academic Press, 89–100.

Barthélémy D, Edelin C, Hallé F. 1991. Canopy architecture. In: Raghavendra AS ed. *Physiology of trees*. Chichester: John Wiley and Sons, 1–20.

Barthélémy D, Caraglio Y, Drénou C, Figureau C. 1992. Architecture et sénescence des arbres. *Forêt Entreprise* **83**: 15–35.

Barthélémy D, Sabatier S, Pascal O. 1995. Le développement architectural du Noyer commun *Juglans regia* L. (Juglandaceae). *Forêt Entreprise* **103**: 61–68.

Barthélémy D, Caraglio Y, Costes E. 1997*a*. Architecture, gradients morphogénétiques et âge physiologique chez les végétaux. In: Bouchon J, de Reffye P, Barthélémy D eds. *Modélisation et simulation de l'architecture des végétaux*. Sciences Update. Paris: Editions INRA, 89–136.

Barthélémy D, Sabatier S, Pascal O. 1997*b*. Le développement architectural du Noyer noir *Juglans nigra* L. (Juglandaceae). *Forêt Entreprise* **115**: 40–47.

Barthélémy D, Grosfeld J, Bouroulet-Hallard F, Ducatillion C. 1999. Biology, growth and development. In: Teissier du Cros E ed. *Cypress: a practical handbook*. Florence: Studio Leonardo, 26–33.

Beissner L. 1888. Über Jugendformen von Pflanzen. speciell Coniferen. *Berichte der Deutschen Botanischen Gesellschaft* **6**: 83–86.

Bell A. 1991. *Plant form an illustrated guide to flowering plant morphology*. Oxford: Oxford University Press.

Blanc P. 1978. *Aspects de la ramification chez des aracées tropicales*. PhD thesis, University Paris VI.

Blanc P. 2002. *Etre plante à l'ombre des forêts tropicales*. Paris: editions Nathan.

Boke N. 1976. Dichotomous branching in *Mammillaria* (Cactaceae). *American Journal of Botany* **63**: 1380–1384.

Bond TET. 1942. Studies in the vegetative growth and anatomy of the Tea plant (*Camellia thea* Link.) with special reference to the phloem. I. The flush shoot. *Annals of Botany* **9**: 183–216.

Borchert R. 1969. Unusual shoot growth pattern in a tropical tree, *Oreopanax* (Araliaceae). *American Journal of Botany* **56**: 1033–1041.

Borchert R. 1976. The concept of juvenility in woody plants. *Acta Horticulturae* **56**: 21–33.

Bouchon J, de Reffye P, Barthélémy D. 1997. *Modélisation et simulation de l'architecture des végétaux*. Sciences Update, Inra Editeur.

Briggs B, Johnson L. 1979. Evolution in the Myrtaceae – evidence from inflorescence structure. *Proceedings of the Linnean Society of New South Wales* **192**: 157–272.

Brink RA. 1962. Phase change in higher plants and somatic cell heredity. *Quarterly Review of Biology* **37**: 1–22.

Bugnon P, Bugnon F. 1951. Feuilles juvéniles et pousses multinodales chez le Pin maritime. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **86**: 18–23.

Caballé G. 1998. Le port autoportant des lianes tropicales: une synthèse des stratégies de croissance. *Canadian Journal of Botany* **76**: 1703–1716.

Cannell MGR, Thompson S, Lines R. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. In: Cannell MGR, Last FT eds. *Tree physiology and yield improvement*. New York: Academic Press, 223–243.

Caraglio Y. 1997. Le développement architectural. In: Le Merisier B, Boulet-Gercourt eds. *Les guides du sylviculteur*. Paris: IDF, 19–23.

Caraglio Y, Barthélémy D. 1997. Revue critique des termes relatifs à la croissance et à la ramification des tiges des végétaux vasculaires. In: Bouchon J, de Reffye Ph, Barthélémy D eds. *Modélisation et simulation de l'Architecture des végétaux*. Sciences Update, Editions Inra, 11–88.

Caraglio Y, Edelin C. 1990. Architecture et dynamique de la croissance du platane, *Platanus hybrida* Brot. (Platanaceae) {syn. *Platanus acerifolia* (Aiton) Willd.}. *Bulletin de la Société Botanique de France, Lettres Botaniques* **137**: 279–291.

Caraglio Y, Becquey J, Gallois F, Vidal C. 2000. Réaction de jeunes merisiers à deux modalités de taille. *Forêt Entreprise* **132**: 25–29.

Carrière EA. 1880. *Revue du genre* Retinospora. Paris.

Castel T, Guerra F, Caraglio Y, Houllier F. 2002. Retrieval biomass of a large Venezuelan pine plantation using JERS-1 SAR data. Analysis of forest structure impact on radar signature. *Remote Sensing of Environment* **79**: 30–41.

de Castro e Santos A. 1980. Essai de classification des arbres tropicaux selon leur capacité de réitération. *Biotropica* **12**: 187–194.

de Castro e Santos A. 1981. *L'appareil végétatif des monocotylédones. Un essai de synthèse*. PhD thesis, University Montpellier 2.

Champagnat P. 1947. Les principes généraux de la ramification des végétaux ligneux. *Revue Horticole* **2143**: 335–341.

Champagnat P. 1961. Dominance apicale. Tropisme. Epinastie. In: Rühland W ed. *Encyclopedia of plant physiology*, Vol. 14. Berlin: Springer Verlag, 872–908.

Champagnat P. 1965. Physiologie de la croissance et de l'inhibition des bourgeons: dominance apicale et phénomènes analogues. In: Rühland W ed. *Encyclopedia of plant physiology*, Volume 15 (1). Berlin: Springer-Verlag, 1106–1171.

Champagnat P, Barnola P, Lavarenne S. 1986. Quelques modalités de la croissance rythmique endogène des tiges chez les végétaux ligneux. *Comptes rendus du Colloque International sur l'Arbre, Montpellier, 9–14 Septembre 1985, Naturalia Monspeliensia, No. Hors Série*: 279–302.

Chenu K, Franck N, Dauzat J, Barczi JF, Rey H, Lecoeur J. 2005. Integrated response for rosette organogenesis, morphogenesis and architecture to reduced incident light in *Arabidopsis thaliana* results in higher efficiency of light interception. *Functional Plant Biology* **32**: 1123–1134.

Chouard P. 1950. Pourquoi fleurissent les plantes. *Conférence faite au Palais de la Découverte*, 29 October **1949**. University of Paris

Claßen-Bockhoff R. 2000. Inflorescences in Bruniaceae. With general comments on inflorescences in woody plants. *Opera Botanica Belgica* **12**: 5–310.

Claßen-Bockhoff R. 2001. Plant morphology: the historic concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber. *Annals of Botany* **88**: 1153–1172.

Claßen-Bockhoff R. 2005. Aspekte, Typifikationsverfahren und Asussagen der Pflanzenmorphologie. In: Harlan V eds. *Wert und Grenzen des Typus in der Botanischen Morphologie*. Galunder: Nümbrecht, 31–52.

Cockayne L. 1912. Observations concerning evolution, derived from ecological studies in New Zealand. *Transactions and Proceedings of the New Zealand Institute* **44**: 1–50.

Comte L. 1993. *Rythmes de croissance et structures spatiales périodiques d'arbres tropicaux. Exemple de cinq espèces de forêt équatoriale*. PhD thesis, University Montpellier 2.

Corradini P, Edelin C, Bruneau A, Bouchard A. 2002. Architectural and genotypic variation in the clonal shrub *Taxus canadensis* as determined from random amplified polymorphic DNA and amplified fragment length polymorphism. *Canadian Journal of Botany* **80**: 205–219.

Costes E. 1993. Architecture aérienne de l'Abricotier en développement libre. *Acta Botanica Gallica* **140**: 249–261.

Costes E, Guédon Y. 2002. Modelling branching patterns on one-year-old trunks of apple cultivars. *Annals of Botany* **89**: 513–523.

Costes E, Sinoquet H, Kelner JJ, Godin C. 2003. Exploring within tree architectural development of two apple tree cultivars over 6 years. *Annals of Botany* **91**: 91–104.

Costes E, Lauri PE, Regnard JL. 2006. Analyzing fruit tree architecture: implications for tree management and fruit production. In: Janick J, ed. *Horticultural reviews*, Vol. 32. New York: John Wiley and Sons, 1–61.

Coudurier T. 1992. *Sur la place des lianes dans la forêt guyanaise. Une approche qui utilise l'architecture végétale*. PhD thesis, University Montpellier 2.

Coudurier T, Barthélémy D, Chanson B, Courdier F, Loup C. 1995. Modélisation de l'architecture du Pin maritime *Pinus pinaster* Ait. (Pinaceae): premiers résultats. In: Bouchon J ed. *Architecture des Arbres Fruitiers et Forestiers, Montpellier (FRA), 23–25 Novembre 1993*, Les Colloques no. 74, INRA editions, 305–321.

Courtot Y, Baillaud L. 1961. Sur la ramification d'un *Cupressus*. *Annales des Sciences de l'Université de Besançon*. *Botanique* **17**: 69–72.

Cremers G. 1973. Architecture de quelques lianes d'Afrique tropicale. *Candollea* **28**: 249–280.

Cremers G, Edelin C. 1995. Study on aerial architecture of some tropical plants with basitone branching – for a revision of the Tomlinson model. *Canadian Journal of Botany* **73**: 1490–1503.

Critchfield WB. 1960. Leaf dimorphism in *Populus trichocarpa*. *American Journal of Botany* **47**: 699–711.

Damascos MA, Prado CH, Ronquim CC. 2005. Bud composition, branching patterns and leaf phenology in cerrado woody species. *Annals of Botany* **96**: 1075–1084.

Danjon F, Bert D, Godin C, Trichet P. 1999*a*. Structural root architecture of 5-year-old *Pinus pinaster* measured by 3D digitising and analysed with AMAPmod. *Plant and Soil* **217**: 49–63.

Danjon F, Sinoquet Y, Godin C, Colin F, Drexhage M. 1999*b*. Characterisation of structural tree root architecture using 3D digitising and AMAPmod software. *Plant and Soil* **211**: 241–258.

Danjon F, Fourcaud T, Bert D. 2005. Root architecture and windfirmness of mature *Pinus pinaster* Aït. *New Phytologist* **168**: 387–400.

Daviero V, Meyer-Berthaud B, Lecoustre R. 1996. A morphometric approach to the architecture and ontogeny of the extant sphenopsid *Equisetum telmateia* Ehrh. *International Journal of Plant Science* **157**: 567–581.

Diggle P. 1994. The expression of andromonoecy in *Solanum hirtum* (Solanaceae): phenotypic plasticity and ontogenetic contingency. *American Journal of Botany* **81**: 1354–1365.

Diggle PK. 1997. Extreme preformation in Alpine *Polygonum viviparum*: an architectural and developmental analysis. *American Journal of Botany* **84**: 154–169.

Diggle PK. 1999. Heteroblasty and the evolution of flowering phenologies. *International Journal of Plant Sciences* **160**: S123–S134.

Diggle PK. 2002. A developmental morphologist's perspective on plasticity. *Evolutionary Ecology* **16**: 267–283.

Diggle PK. 2003. Architectural effects on floral form and function: a review. In: Stuessy T, Hörandl E, Mayer V eds. *Deep morphology: toward a renaissance of morphology in plant systematics*. Königstein: Koeltz, 000–000.

Dingkuhn M, Luquet D, Quilot B, de Reffye Ph. 2005. Environmental and genetic control of morphogenesis in crops: towards models simulating phenotypic plasticity. *Australian Journal of Agricultural Research* **56**: 1–14.

Doorenbos J. 1954. Rejuvenation of *Hedera helix* in grafts combinations. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen. Sér C* **57**: 99–102.

Doorenbos J. 1965. Juvenile and adult phases in woody plants. In: Rühland W ed. *Handbuch der Pflanzenphysiologie*, Vol. **15**(**1**). Berlin: Springer-Verlag, 1222–1235.

Drénou C. 1994. *Approche architecturale de la sénescence des arbres. Le cas de quelques angiospermes tempérées et tropicales*. PhD thesis, University Montpellier 2.

Dupuy L, Fourcaud T, Stokes A. 2005*a*. A numerical investigation into factors affecting the anchorage of roots in tension. *European Journal of Soil Science* **56**: 319–327.

Dupuy L, Fourcaud T, Stokes A. 2005*b*. A numerical investigation into the influence of soil type and root architecture on tree anchorage. *Plant and Soil* **278**: 119–134.

Dupuy L, Fourcaud T, Stokes A, Danjon F. 2005*c*. A density based approach for the modelling of root architecture: application to Maritime pine (*Pinus pinaster* Ait) root systems. *Journal of Theoretical Biology* **236**: 323–334.

Durand M. 1997. Architecture and growth strategy of two evergreen species of the Western Ghats (South Inda) *Knema attenuata* (Myristicaceae) and *Vateria indica* (Dipterocarpaceae). *Pondy Papers in Ecology*, 3. Pondichery: IFP.

Durand JB, Guédon Y, Caraglio Y, Costes E. 2005. Analysis of the plant architecture via tree-structured statistical models: the hidden Markov tree models. *New Phytologist* **166**: 813–825.

Edelin C. 1977. *Images de l'architecture des conifères*. PhD thesis, University Montpellier 2.

Edelin C. 1981. Quelques aspects de l'architecture végétative des Conifères. *Bulletin de la Société Botanique de France, Lettres Botaniques* **128**: 177–188.

Edelin C. 1984. *L'architecture monopodiale: l'exemple de quelques arbres d'Asie Tropicale*. Thesis Doct. Etat, University Montpellier 2.

Edelin C. 1993. *Aspects morphologiques de la croissance rythmique chez les arbres tropicaux. Compte Rendu du Séminaire du groupe d'Etude de l'Arbre: le rythme de croissance, base de l'organisation temporelle de l'arbre*. Angers, 25–26 Mars **1993**: 13–23.

Edelin C, Hallé F. 1985. Architecture et évolution chez deux genres d'arbres tropicaux: *Diospyros* et *Cordia. Actes du 110^e^ Congrès National des Sociétés Savantes. Montpellier Sciences* **II**: 255–265.

Eggert DA. 1961. The ontogeny of carboniferous arborescent *Lycopsida*. *Paleontographica (Part B)* **108**: 43–92.

Eggert DA. 1962. The ontogeny of Carboniferous arborescent Sphenopsida. *Palaeontographica, (Part B)* **110**: 99–127.

El-Morsy AA. 1991. *Croissance rythmique et micropropagation in vitro chez le bigaradier (Citrus aurantium) et le mandarinier (Citrus deliciosa)*. PhD thesis, University Franche-Comté, Besançon.

Emberger L. 1960. *Les Végétaux Vasculaires. Tome II du Traité de Botanique Systématique, Chadefaud M. & Emberger L.* Paris: Masson.

Espagnac H, Neuville P. 1969. Feuilles et aisselles doubles chez *Olea europaea* L. *Bulletin de la Société Botanique de France* **116**: 57–70.

Fahn A. 1967. *Plant anatomy*. Oxford: Pergamon Press.

Ferraro P, Godin C. 2000. A distance measure between plant architectures. *Annals of Forest Science* **57**: 445–461.

Ferraro P, Godin C. 2003. An edit distance between quotiented trees. *Algorithmica* **36**: 1–39.

Ferraro P, Godin C, Prusinkiewicz P. 2005. Toward a quantification of self-similarity in plants. *Fractals* **13**: 91–109.

Fink S. 1983. The occurrence of adventitious and preventitious buds within the bark of some temperate and tropical trees. *American Journal of Botany* **70**: 532–542.

Fisher JB. 1976. Development of dichotomous branching and axillary buds in *Strelitzia* (Monocotyledonae). *Canadian Journal of Botany* **54**: 578–592.

Fontaine F, Chaar H, Colin F, Clément Ch, Burrus M, Druelle J-L. 1999. Preformation and neoformation of growth units on 3-year-old seedlings of *Quercus petraea*. *Canadian Journal of Botany* **77**: 1623–1631.

de Foresta H. 1983. Le spectre architectural: application à l'étude des relations entre architecture des arbres et écologie forestière. *Bulletin du Muséum National d'Histoire Naturelle* **5**: 295–302.

Franck AB. 1868. Über die Einwirkung der Gravitation auf das Wachsthum einiger Pflanzentheile. *Botanik Zeitung* **26**: 873–882.

Friedman J, Harder LD. 2004. Inflorescence architecture and wind pollination in six grass species. *Functional Ecology* **18**: 851–860.

Friedman J, Harder LD. 2005. Functional associations of floret and inflorescence traits among grass species. *American Journal of Botany* **92**: 1862–1870.

Frost HB. 1938. Nucellar embryony and juvenile characters in clonal varieties of Citrus. *Journal of Heredity* **29**: 423–432.

Garrison R, Wetmore RH. 1961. Studies in shoot-tip abortion: *Syringa vulgaris*. *American Journal of Botany* **48**: 789–795.

Gatin C-L. 1924. *Dictionnaire de fotanique*. Paris: Lechevalier.

Gatsuk LE, Smirnova OV, Vorontzova LI, Zaugolnova LB, Zhukova LA. 1980. Age states of plants of various growth forms: a review. *Journal of Ecology* **68**: 675–696.

Gay H. 1993. The architecture of a dimorphic clonal fern, *Lomagramma guianensis* (Aublet) Ching (Dryopteridaceae). *Botanical Journal of the Linnean Society* **111**: 343–358.

Genoyer P, Atger C, Edelin C, Caraglio Y. 1999. Some architectural markers of plane tree development (*Platanus x acerifolia* (Aiton) Willd.): contribution to the establishment of an ontogenic based diagnosis. *Acta Horticulturae* **496**: 209–220.

Gifford EM. 1983. Concept of apical cells in Bryophytes and Pteridophytes. *Annual Review of Plant Physiology* **34**: 419–440.

Gill AM. 1971. The formation, growth and fate of buds of *Fraxinus americana* L. in Central Massachusetts. *Harvard Forest Paper* **20**: 1–16.

Gill AM, Tomlinson PB. 1971. Studies on the growth of Red Mangrove (*Rhizophora mangle* L.). 3. Phenology of the shoot. *Biotropica* **3**: 109–124.

Givnish TJ. 1984. Leaf and canopy adaptations in tropical trees. In: Medina E, Mooney HA, Vazquez-Yanes C eds. *Physiological ecology of plants of the wet tropics*. The Hague: Dr W. Junk, 51–84.

Gleißner P. 1998. Das Verzweigungsmuster ausgewählter Laubbaumarten und seine Veränderung durch nicht-pathogene Schädigungen. *Palmarum Hortus Francofurtensis* **6**: 3–132.

Godin C. 2000. Representing and encoding plant architecture: a review. *Annals of Forest Science* **57**: 413–438.

Godin C, Caraglio Y. 1998. A multiscale model of plant topological structures. *Journal of Theoretical Biology* **191**: 1–46.

Godin C, Sinoquet H. 2005. Functional–structural plant modelling. *New Phytologist* **166**: 705–708.

Godin C, Costes E, Caraglio Y. 1997. Exploring plant topology structure with the AMAPmod software: an outline. *Silva Fennica* **31**: 355–366.

Godin C, Costes E, Sinoquet H. 1999. A method for describing plant architecture which integrates topology and geometry. *Annals of Botany* **84**: 343–357.

Godin C, Costes E, Sinoquet H. 2005. Plant architecture modelling – virtual plants, dynamic and complex systems. In: Turnbull C ed. *Plant architecture and its manipulation. Annual plant reviews*, Vol. 17. Oxford: Blackwell Publishing, 238–287.

Goebel K. 1900. *Organography of plants. Part I. General organography (translated by IB Balfour)*. Oxford: The Clarendon Press.

von Goethe JW. 1790. *Lamétamorphose des plantes. Traduction de Bideau H. 1975*. Paris: Editions Triades.

Greathouse DC, Laetsch WM, Phinney BO. 1971. The shoot growth rhythm of a tropical tree, *Theobroma cacao*. *American Journal of Botany* **58**: 281–299.

Greenwood MS. 1987. Rejuvenation of forest trees. *Plant Growth Regulation* **6**: 1–12.

Greenwood MS. 1995. Juvenility and maturation in conifers: current concepts. *Tree Physiology* **15**: 433–438.

Greenwood RM, Atkinson IAE. 1977. Evolution of divaricating plants in New Zealand, in relation to moa browsing. *Proceedings of the New Zealand Ecological Society* **24**: 21–33.

Grosfeld J. 2002. *Análisis de la variabilidad morfológica y arquitectural de Austrocedrus chilensis (D. Don) Florin y Boutleje, Fitzroya cupressoides (Mol.) Johnson, Pilgerodendron uviferum (D. Don) y Cupressus sempervirens. L (Cupressaceae)*. PhD thesis, University Nacional del Comahue, Bariloche.

Grosfeld J, Barthélémy D. 2004. Primary growth and morphological markers of intra-annual growth limits in Cupressaceae from Patagonia. *Botanical Journal of the Linnean Society* **146**: 285–293.

Grosfeld J, Barthélémy D, Brion C. 1999. Architectural variations of *Araucaria araucana* (Molina) K. Koch (Araucariaceae) in its natural habitat. In: Kurmann MH, Hemsley AR eds. *The evolution of plant architecture*. Kew: Royal Botanic Gardens, 109–122.

Grubb PJ. 1977. Maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**: 107–145.

Guédès M. 1975. Modalités du développement sympodial chez quelques végétaux ligneux tempérés. *Comptes Rendus de l'Académie des Sciences, Paris* **281**: 527–530.

Guédès M. 1980. Endorhythmic development in *Choisya ternata* Kunth (Rutaceae), with a further elucidation of lammas shoots, as well as sylleptic and proleptic shoots. *Botanical Journal of the Linnean Society* **7**: 109–155.

Guédon Y, Barthélémy D, Caraglio Y, Costes E. 2001. Pattern analysis in branching and axillary flowering sequences. *Journal of Theoretical Biology* **212**: 481–520.

Guédon Y, Heuret P, Costes E. 2003. Comparison methods for branching and axillary flowering sequences. *Journal of Theoretical Biology* **225**: 301–325.

Guédon Y, Puntieri J, Sabatier S, Barthélémy D. 2006. Relative extents of preformation and neoformation in tree shoots: analysis by a deconvolution method. *Annals of Botany* **98**: 835–844.

Guérard N, Barthélémy D, Cabanettes A, Courdier F, Trichet P, Willm J. 2001. Influence de la compétition herbacée sur la croissance et le développement de jeunes Chênes rouges d'Amérique (*Quercus rubra* L., Fagaceae) en plantation. *Annals of Forest Sciences* **58**: 395–410.

Guinochet M. 1965. *Notions fondamentales de botanique générale*. Paris: Masson.

Guo Y, Ma Y, Zhan Z, Li B, Dingkuhn M, Luquet D, de Reffye P. 2006. Parameter optimization and field validation of the functional–structural model GREENLAB for maize. *Annals of Botany* **97**: 217–230.

Hackett TWP. 1985. Juvenility, maturation, and rejuvenation in woody plants. *Horticultural Reviews* **7**: 109–155.

Hallé F. 1978. Architectural variation at specific level of tropical trees. In: Tomlinson PB, Zimmermann MH eds. *Tropical trees as living systems*. Cambridge: Cambridge University Press, 209–221.

Hallé F. 1986. Modular growth in seed plants. In: Harper JL, Rosen BR, White J eds. *The growth and form of modular organisms. Philosophical Transactions of the Royal Society of London, Series B* **313**: 77–87.

Hallé F. 2004. *Eloge de la plante. Pour une nouvelle biologie*. Paris: Editions du Seuil.

Hallé F, Martin R. 1968. Etude de la croissance rythmique chez *Hevea brasiliensis* Müll. Arg (Euphorbiaceae – Crotonoïdées). *Adansonia, Série 2* **8**: 475–503.

Hallé F, Ng FSP. 1981. Crown construction in mature Dipterocarp trees. *Malaysian Forester* **44**: 222–223.

Hallé F, Oldeman RAA. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Paris: Masson.

Hallé F, Oldeman RAA, Tomlinson PB. 1978. *Tropical trees and forests*. Berlin: Springer-Verlag.

Harper JL. 1985. Modules, branches, and the capture of resources. In: *Population biology and evolution of clonal organisms*. New Haven, CT: Yale University Press, 1–33.

Hedden P, Phillips AL, Rojas MC, Carrera E, Tudzynski B. 2002. Gibberellin biosynthesis in plants and fungi: a case for convergent evolution? *Journal of Plant Growth Regulators* **20**: 319–331.

Heuret P, Barthélémy D, Nicolini E, Atger C. 2000. Analyse des composantes de la croissance en hauteur et de la formation du tronc chez le chêne sessile (*Quercus petraea* (Matt.) Liebl., Fagaceae) en sylviculture dynamique. *Canadian Journal of Botany* **78**: 361–373.

Heuret P, Barthélémy D, Guédon Y, Coulmier X, Tangre J. 2002. Synchronism in growth, branching and flowering processes on the individual and stand level in the South American tropical tree *Cecropia obtusa* Trécul (Cecropiaceae). *American Journal of Botany* **89**: 1180–1187.

Heuret P, Guédon Y, Guérard N, Barthélémy D. 2003. Analysing branching pattern in plantations of young red oak trees (*Quercus rubra* L., Fagaceae). *Annals of Botany* **91**: 479–492.

Heuret P, Meredieu C, Coudurier T, Courdier F, Barthélémy D. 2006. Ontogenetic trends in the morphological features of main stem annual shoots of *Pinus pinaster* Ait. (*Pinaceae*). *American Journal of Botany* **93**: 1577–1587.

Hochtetter W. 1880. Die sogenannten Retinospora-Arten der Gärten. *Regels Gartenflora* **29**: 362.

Hu B-G, Jaeger M. 2003. *Plant growth modelling and applications (PMA03). Proceedings of the 2003 International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications*, Beijing, Chine, 13–16 October 2003. Beijing: Tsinghua University Press, Springer.

Huber H, Lukács S, Watson MA. 1999. Spatial structure of stoloniferous herbs: an interplay between architectural blue-print, ontogeny and phenotypic plasticity. *Plant Ecology* **141**: 107–115.

Hueber FM, Galtier J. 2002. *Symplocopteris wyattii* n. gen. et n. sp. A zygopterid fern with a false trunk from the Tournaisian (Lower Carboniferous) of Queensland, Australia. *Review of Palaeobotany and Palynology* **119**: 241–273.

Isik F, Isik K, Yildrim T, Li B. 2001. Annual shoot growth components related to growth of *Pinus brutia*. *Tree Physiology* **22**: 51–58.

Isnard S, Speck T, Rowe N. 2005. Biomechanics and development of the climbing habit in two species of the South American palm genus *Desmoncus* (Arecaceae). *American Journal of Botany* **92**: 1444–1456.

Iwamoto A, Matsumura Y, Ohba H, Murata J, Imaichi R. 2005. Development and structure of trichotomous branching in *Edgeworthia chrysantha* (Thymeleaceae). *American Journal of Botany* **92**: 1350–1358.

Jablanczy A. 1971. Changes due to age in apical development in spruce and fir. *Canadian Forest Services, Bi-Monthly Results Notes* **27**: 10.

Jeannoda-Robinson V. 1977. *Contribution à l'étude de l'architecture des herbes*. PhD thesis, University Montpellier 2.

Johnson DM. 2003. Phylogenetic significance of spiral and distichous architecture in the Annonaceae. *Systematic Botany* **28**: 503–511.

Jones CS. 1999. An essay on juvenility, phase change and heteroblasty in seed plants. *International Journal of Plant Science* **160**: S105–S111.

Jones CS. 2001. The functional correlates of heteroblastic variation in leaves: changes in form and ecophysiology with whole plant ontogeny. *Boletin de la Sociedad Argentina de Botanica* **36**: 171–184.

Jourdan C, Rey H. 1997*a*. Architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. *Plant and Soil* **189**: 33–48.

Jourdan C, Rey H. 1997*b*. Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. I. The model. *Plant and Soil* **190**: 217–233.

Jourdan C, Rey H. 1997*c*. Modelling and simulation of the architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. II. Estimation of root parameters using the RACINES post-processor. *Plant and Soil* **190**: 235–246.

Kaplan DR. 2001. The science of plant morphology: definition, history and role in modern biology. *American Journal of Botany* **88**: 1711–1741.

Koch K. 1873. *Dendrologie*. Erlangen.

Koriba K. 1958. On the periodicity of tree growth in the tropics, with reference to the mode of branching, the leaf-fall, and the formation of the resting bud. *Garden's Bulletin, Singapore* **17**: 11–81.

King DA. 1998. Influence of leaf size on tree architecture: first branch height and crown dimensions in tropical rain forest trees. *Trees* **12**: 438–445.

Kozlowski TT. 1971. *Growth and development in trees, vol. 1: seed germination, ontogeny, and shoot growth, vol. 2: cambial growth, root growth, and reproductive growth*. New York: Academic Press.

de Kroon H, Huber H, Stuefer JF, van Groenendael JM. 2005. A modular concept of phenotypic plasticity in plants. *New Phytologist* **166**: 73–82.

Lanner RM. 1976. Patterns of shoot development in *Pinus* and their relation to growth potential. In: Cannell MGR, Last FT eds. *Tree physiology and yield improvement*. New York: Academic Press, 223–243.

Lavarenne S, Champagnat P, Barnola P. 1971. Croissance rythmique de quelques végétaux ligneux de régions tempérées cultivés en chambres climatisées à température élevée et constante et sous diverses photopériodes. *Bulletin de la Société Française de Physiologie Végétale* **118**: 131–162.

Leroy C, Caraglio Y. 2003. Effects of tube shelters on the growth of young Turkish pines (*Pinus brutia* Ten., Pinaceae). *Annals of Forest Science* **60**: 539–547.

Levin GG. 1966. Age changes in plants. *Botanicheskij Zhurnal S.S.S.R.* **51**: 1774–1795.

Lyndon RF. 1988. *The shoot apical meristem. Its growth and development*. Cambridge: Cambridge University Press.

Martinez OG, De La Sota ER. 2001. La obconidad caulinar de *Megalastrum pulverulentum* (Pteridophyta-Dryopteridaceae). *Boletin de la Sociedad Argentina de Botanica* **36**: 105–109.

McManus MT, Veit BE. 2002. *Meristematic tissues in plant growth and development* Sheffield Biological series. Sheffield: Academic Press.

McSteen P, Leyser O. 2005. Shoot branching. *Annual Review of Plant Biology* **56**: 353–374.

Meloche CG, Diggle PK. 2001. Preformation, architectural complexity, and developmental flexibility in *Acomastylis rossii* (Rosaceae). *American Journal of Botany* **88**: 980–991.

Millet J, Bouchard A, Edelin C. 1998*a*. Plagiotropic architectural development and successional status of four tree species of the temperate forest. *Canadian Journal of Botany* **76**: 2100–2118.

Millet J, Bouchard A, Edelin C. 1998*b*. Plant succession and tree architecture an attempt at reconciling two scales of analysis of vegetation dynamics. *Acta Biotheoretica* **46**: 1–22.

Millet P, Bouchard A, Edelin C. 1999. Architecture and successional status of trees in a temperate deciduous forest. *Ecoscience* **6**: 187–203.

Millington WF. 1963. Shoot tip abortion in *Ulmus americana*. *American Journal of Botany* **50**: 371–378.

Moens P. 1963. Les bourgeons végétatifs et génératifs de *Coffea canephora* Pierre. *La Cellule* **63**: 165–244.

Mueller RJ. 2006. Ask the plant: investigating and teaching plant structure. *Botanical Journal of the Linnean Society* **150**: 73–78.

Müller-Doblies D, Weberling F. 1984. Über Prolepsis und verwandte Begriffe. *Beitrage zur Biologie der Pflanzen* **59**: 121–144.

Mündermann L, Erasmus Y, Lane B, Coen E, Prusinkiewicz P. 2005. Quantitative modeling of *Arabidopsis* development. *Plant Physiology* **139**: 960–968.

Nicolini E. 1997. *Approche morphologique du développement du hêtre (Fagus sylvatica L.)*. PhD thesis, University Montpellier 2.

Nicolini E. 1998. Architecture et gradients morphogénétiques chez de jeunes hêtres (*Fagus sylvatica* L. Fagaceae) en milieu forestier. *Canadian Journal of Botany* **76**: 1232–1244.

Nicolini E. 2000. Nouvelles observations sur la morphologie des unités de croissance du hêtre (*Fagus sylvatica* L.). Symétrie des pousses, reflets de la vigueur des arbres. *Canadian Journal of Botany* **78**: 77–87.

Nicolini E, Caraglio Y. 1995. L'influence de divers caractères architecturaux sur l'apparition de la fourche chez le *Fagus sylvatica*, en fonction de l'absence ou de la présence d'un couvert. *Canadian Journal of Botany* **72**: 1723–1734.

Nicolini E, Chanson B. 1999. La pousse courte feuillée, un indicateur du degré de différenciation chez le Hêtre (*Fagus sylvatica* L.). *Canadian Journal of Botany* **77**: 1539–1550.

Nicolini E, Barthélémy D, Heuret P. 2000. Influence de l'intensité du couvert forestier sur le développement de jeunes chênes sessiles *Quercus petraea* (Matt.) Liebl. *Canadian Journal of Botany* **78**: 1531–1544.

Nicolini E, Chanson B, Bonne F. 2001. Stem growth and epicormic branch formation in understorey Beech trees (*Fagus sylvatica* L.). *Annals of Botany* **87**: 737–750.

Nicolini E, Caraglio Y, Pélissier R, Leroy C, Roggy JC. 2003. Epicormic branches: a growth indicator for the tropical forest tree, *Dicorynia guianensis* Amshoff (Caesalpiniaceae). *Annals of Botany* **92**: 97–105.

Niklas KJ. 1992. *Plant biomechanics*. Chicago: University of Chicago Press.

Niklas KJ. 2005. Modelling below- and above-ground biomass for non-woody and woody plants. *Annals of Botany* **95**: 315–321.

Nitta I, Ohsawa M. 1998. Bud structure and shoot architecture of canopy and understorey evergreen broad-leaved trees at their northern limit in East Asia. *Annals of Botany* **81**: 115–129.

Nolan JR. 1969. Bifurcation of the stem apex in *Asclepias syriaca*. *American Journal of Botany* **56**: 603–609.

Nougarède A. 2001. Le méristème caulinaire des Angiospermes: nouveaux outils, nouvelles interpretations. *Acta Botanica Gallica* **148**: 3–77.

Novoplansky A. 2002. Developmental plasticity in plants: implications of non-cognitive behaviour. *Evolutionary Ecology* **16**: 177–188.

Nozeran R. 1978. Réflexions sur les enchaînements de fonctionnements au cours du cycle des végétaux supérieurs. *Bulletin de la Société Botanique de France* **125**: 263–280.

Nozeran R. 1984. Integration of organismal development. In: Barlow PW, Carr DJ eds. *Positional control in plant development*. Cambridge: Cambridge University Press, 375–401.

Nozeran R, Bancilhon L, Neuville P. 1971. Intervention of internal correlations in morphogenesis of higher plants. *Advances in Morphogenesis* **9**: 1–66.

Nozeran R, Ducreux G, Rossignol-Bancilhon L. 1982. Réflexions sur les problèmes de rajeunissements chez les végétaux. *Bulletin de la Société Botanique de France, Lettres Botanique* **129**: 107–130.

Nozeran R, Rossignol-Bancilhon L, Mangenot G. 1984. Les recherches sur le genre *Phyllanthus* (Euphorbiaceae): acquis et perspectives. *Botanica Helvetica* **94**: 199–233.

Oborny B. 2004. External and internal control in plant development. *Complexity* **9**: 22–28.

Oldeman RAA. 1974. *L'architecture de la forêt guyanaise*. Mémoire no., 73. Paris: O.R.S.T.O.M.

Oldeman RAA. 1983. Tropical rain forest, architecture, silvigenesis and diversity. In: Sutton SL, Whitmore TC, Chadwick AC eds. *Tropical rain forest: ecology and management*. Oxford: Blackwell, 139–150.

Oldeman RAA. 1990. *Forests: elements of silvology*. Berlin: Springer-Verlag.

Pardé J, Bouchon J. 1988. *Dendrométrie*, 2ième édition. Nancy: Ecole Nationale du Génie Rural, des Eaux et des Forêts.

Parisot E. 1985. *Etude de la croissance rythmique chez les jeunes Manguiers (Mangifera indica)*. PhD thesis, University Clermont-Ferrand 2.

Parkin J. 1914. The evolution of the inflorescence. *Linnean Society of Botany of London* **42**: 511–563.

Passecker F. 1944. Jugend und Altersformen bei den Obstgehölzen. *Gartenbauwissenschaft* **18**: 219–230.

Passecker F. 1958. Zur Frage des 'primären' und 'fertilen' Stadiums bei Apfelsämlingen. *Mitteilungen Klosterneuburg, Series B* **8**: 116–117.

Passecker F. 1977. Theorie der ontogenetischen Evolution und Alterung holziger Gewächse. *Bodenkultur* **28**: 277–294.

Passo A, Puntieri J, Barthélémy D. 2002. Trunk and main-branch development in *Nothofagus pumilio* (Nothofagaceae): a retrospective analysis of tree growth based on the size and structure of its annual shoots. *Canadian Journal of Botany* **80**: 763–772.

Payan E. 1982. *Contribution à l'étude de la croissance rythmique chez de jeunes Chênes pédonculés (Quercus pedunculata Ehrh.)*. PhD thesis, University Clermont-Ferrand 2.

Pearcy RW, Muraoka H, Valladares F. 2005. Crown architecture in sun and shade environments: assessing function and tradeoffs with a 3-D simulation model. *New Phytologist* **166**: 791–800.

Perreta MG, Tivano JC, Vegetti AC. 2000. Forma de crecimiento en *Leptochloa chloridiformis* (Poaceae). *Darwiniana* **38**: 219–226.

Picard C. 1965. Contribution à la connaissance de la vernalisation, de ses particularités et de sa signification chez *Oenothera biennis* var. *sulfura* De Vries. *Annales des Sciences Naturelles, Botanique* **12**: 197–314.

Picard G, Le Toan T, Quegan S, Caraglio Y, Castel T. 2004. Radiative transfer modeling of cross-polarized backscatter from a pine forest using the discrete ordinate and eigenvalue method. *IEEE Transactions on Geoscience and Remote Sensing* **42**: 1720–1730.

Pilger R. 1921. Bemerkungen zur phylogenetischen Entwicklung der Blütenstände. *Bericht der Freien Vereinigung für Pflanzen Geographyraphie und Systematische Botanik für das Jahr* **1919**: 69–77.

Poethig RS. 1990. Phase change and the regulation of shoot morphogenesis in plants. *Science* **250**: 923–930.

Poethig RS. 2003. Phase change and the regulation of developmental timing in plants. *Science* **301**: 334–336.

Pressler R. 1865. *Das Gesetz der Stammbildung*. Leipzig: Arnloldische Buchhandlung.

Prévost MF. 1967. Architecture de quelques Apocynacées ligneuses. *Bulletin de la Société Botanique de France. Lettres Botaniques* **114**: 24–36.

Prusinkiewicz P, Muendermann L, Karkowski R, Lane B. 2001. The use of positional information in the modelling of plants. *Proceedings of SIGGRAPH*: 289–300.

Puntieri J, Barthélémy D, Martinez P, Raffaele E, Brion C. 1998. Annual–shoot growth and branching patterns in *Nothofagus dombeyi* (Fagaceae). *Canadian Journal of Botany* **76**: 673–685.

Puntieri J, Raffaele E, Martinez P, Barthélémy D, Brion C. 1999. Morphological and architectural features of young *Nothofagus pumilio* (Poepp. et Endl.) Krasser (Fagaceae) plants. *Botanical Journal of the Linnean Society* **130**: 395–410.

Puntieri J, Souza MS, Barthélémy D, Brion C, Nuñez M, Mazzini C. 2000. Preformation, neoformation and shoot structure in *Nothofagus dombeyi* (Mirb.) Blume (Nothofagaceae). *Canadian Journal of Botany* **78**: 1044–1054.

Puntieri J, Brion C, Barthélémy D, Souza MS. 2001. Variaciones en el tamaño y la composición de las yemas de *Nothofagus pumilio* y *N. dombeyi* (Fagaceae). *Darwiniana* **39**: 1–10.

Puntieri J, Barthélémy D, Mazzini C, Brion C. 2002*a*. Periods of organogenesis in shoots of *Nothofagus dombeyi* (Mirb.) Oersted (Nothofagaceae). *Annals of Botany* **89**: 115–124.

Puntieri J, Stecconi M, Barthélémy D. 2002*b*. Preformation and neoformation in shoots of *Nothofagus antarctica* (G. Forster) Oerst. (Nothofagaceae) shrubs from northern Patagonia. *Annals of Botany* **89**: 665–673.

Rauh W. 1939. Über die Gesetzmässigkeit der Verzweigung und deren Bedeutung für die Wuchsformen der Pflanzen. *Mitteilungen Deutsche Dendrologische Gesellschaft* **52**: 86–111.

Rees AR. 1964. The apical organization and phyllotaxis of the Oil Palm. *Annals of Botany (N.S.)* **28**: 209–269.

de Reffye P, Houllier F. 1997. Modelling plant growth and architecture: some recent advances and applications to agronomy and forestry. *Current Science* **73**: 984–992.

de Reffye P, Hu B-G. 2003. Relevant qualitative and quantitative choices for building an efficient dynamic plant growth model: GreenLab case. In: Hu B, Jaeger M eds. *Plant Growth Modelling and Applications (PMA03). Proceedings of the 2003 International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications*, Beijing, China, 13–16 October 2003. Beijing: Tsinghua University Press, Springer, 87–107.

de Reffye Ph, Dinouard P, Barthélémy D. 1991. Modélisation et simulation de l'architecture de l'Orme du Japon *Zelkova serrata* (Thunb.) Makino (Ulmaceae): la notion d'axe de référence. *Comptes Rendus du 2ème Colloque International Sur l'Arbre, Montpellier, 10–15 Septembre 1990, Naturalia Monspeliensia, No. Hors Série*: 251–266.

de Reffye P, Fourcaud T, Blaise F, Barthélémy D, Houllier F. 1997. A functional model of tree growth and tree architecture. *Silva Fennica* **31**: 297–311.

de Reffye P, Houllier F, Blaise F. 1998. Modelling plant growth and architecture: some recent advances and applications to agronomy and forestry. In: Marcelis LFM ed. *2nd International Symposium on Models for Plant Growth, Environmental Control and Farm Management in Protected Cultivation*. Wageningen: ISHS. Acta Horticulturae **456**: 105–116.

Remphrey WR, Davidson CG. 1994. Shoot preformation in clones of *Fraxinus pennsylvanica* in relation to site and year of bud formation. *Trees* **8**: 126–131.

Remphrey WR, Powell GR. 1984. Crown architecture of *Larix laricina* saplings: shoot preformation and neoformation and their relationships to shoot vigour. *Canadian Journal of Botany* **62**: 2181–2192.

Remy P. 1951. L'étude de la période juvénile chez les arbres fruitiers. *Revue Horticole* **123**: 543–547.

Ritterbusch A. 1990. The measure of biological age in plant modular systems. *Acta Biotheoretica* **38**: 113–124.

Rivals P. 1965. Essai sur la croissance des arbres et sur leurs systèmes de floraison (Application aux espèces fruitières). *Journal d'Agronomie Tropicale et de Botanique Appliquée* **12**: 655–686.

Rivals P. 1966. Essai sur la croissance des arbres et sur leurs systèmes de floraison (Application aux espèces fruitières). *Journal d'Agronomie Tropicale et de Botanique Appliquée* **13**: 91–122.

Robbins WJ. 1957. Physiological aspects of aging in plants. *American Journal of Botany* **44**: 289–294.

Robbins WJ. 1961. Juvenility and the induction of flowering. *Recent Advances in Botany* **2**: 1647–1652.

Roloff A. 1985. *Morphologie der Kronenentwicklung von Fagus sylvatica L. (Rotbuche) unter besonderer Berücksichtigung möglicherweise neuartiger Veränderungen*. PhD thesis, Georg-August University, Gottingen.

Roloff A. 1988. Morphologie der Kronenentwicklung von *Fagus silvatica* L. (Rotbuche) unter besonderer Berücksichtigung neuartiger Veränderungen. II. Strategie der Luftraumeroberung und Veränderung durch Umwelteinflüsse. *Flora* **180**: 297–338.

Roloff A. 1989. *Kronenentwicklung und Vitalitätsbeurteilung Ausgewählter Baumarten der Gemäigten Breiten*. Frankfurt am Main: J.D. Sauerländer's Verlag.

Room PM, Maillette L, Hanan JS. 1994. Module and metamer dynamics and virtual plants. *Advances in Ecological Research* **25**: 105–157.

Roux J. 1968. Sur le comportement des axes aériens chez quelques plantes à rameaux végétatifs polymorphes. Le concept de rameau plagiotrope. *Annales des Sciences Naturelles, Botanique* **12**: 109–256.

Rowe NP, Speck T. 2005. Plant growth forms: an ecological and evolutionary perspective. *New Phytologist* **166**: 61–72.

Rua GH, Gróttola MC. 1997. Growth form models within the genus *Paspalum* L. (Poaceae, Paniceae). *Flora* **192**: 65–80.

Sabatier S. 1999. *Variabilité morphologique et architecturale de deux espèces de Noyers: Juglans regia L., Juglans nigra L. et de deux Noyers hybrides interspécifiques.* PhD thesis, University Montpellier 2.

Sabatier S, Barthélémy D. 1995. Architecture du Cèdre de l'Atlas, *Cedrus atlantica* (Endl.) Manetti ex Carrière (Pinaceae). In: Bouchon J eds. *Architecture des Arbres Fruitiers et Forestiers, Montpellier (FRA), 23–25 Novembre 1993*. Les Colloques no. 74, Paris: INRA Editions, 157–173.

Sabatier S, Barthélémy D. 1999. Growth dynamics and morphology of annual shoots according to their architectural position in young *Cedrus atlantica* (Endl.) Manetti ex Carrière (Pinaceae). *Annals of Botany* **84**: 387–392.

Sabatier S, Barthélémy D. 2001*a*. Bud content in relation to shoot morphology and position on vegetative shoots of *Juglans regia* L. (Juglandaceae). *Annals of Botany* **87**: 117–123.

Sabatier S, Barthélémy D. 2001*b*. Annual shoot morphology and architecture in Persian Walnut, *Juglans regia* L. (Juglandaceae). *Acta Horticulturae* **544**: 255–264.

Sabatier S, Barthélémy D, Ducousso I, Germain E. 1995. Nature de la pousse annuelle chez le Noyer commun, *Juglans regia* L. var. *Lara* (Juglandaceae): préformation hivernale et printanière. In: Bouchon J ed. *Architecture des Arbres Fruitiers et Forestiers*. Les colloques no. 74. Paris: INRA Editions, 109–124.

Sabatier S, Barthélémy D, Ducousso I, Germain E. 1998. Modalités d'allongement et morphologie des pousses annuelles chez le noyer commun, *Juglans regia* L. *cv.* 'Lara' (Juglandaceae). *Canadian Journal of Botany* **76**: 1253–1264.

Sabatier S, Barthélémy D, Ducousso I, Germain E. 1999. Allongement et morphologie de pousses annuelles issues de greffe chez le Noyer commun, *Juglans regia* L. *cv*. Lara (Juglandaceae). *Canadian Journal of Botany* **77**: 1595–1603.

Sabatier S, Barthélémy D, Becquey J, Perrier S. 2000. Taille et architecture chez de jeunes noyers hybrides. *Forêt Entreprise* **132**: 54–58.

Sabatier S, Baradat P, Barthélémy D. 2003*a*. Intra- and interspecific variations of polycyclism in young trees of *Cedrus atlantica* (Endl.) Manetti and *Cedrus libani* A. Rich (Pinaceae). *Annals of Forest Science* **60**: 19–29.

Sabatier S, Barthélémy D, Ducousso I. 2003b. Periods of organogenesis in mono- and bicyclic annual shoots of *Juglans regia* L. (Juglandaceae). *Annals of Botany* **9**: 1–8.

Sachs J. 1874. *Traité de Botanique, conforme à l'état présent de la science*. Traduit par Van Tieghem. Paris: Librairie F. SAVY.

Sachs T. 2004. Self–organization of tree form: a model for complex social systems. *Journal of Theoretical Biology* **230**: 197–202.

Sandt W. 1925. Zur Kenntnis der Beiknospen. Zugleich ein Beitrag zum Korrelationsproblem. *Botanische Abhandlungen* **7**: 1–160.

Sanoja E. 1992. *Essai d'application de l'architecture végétale à la systématique. L'exemple de la famille des Vochysiaceae.* PhD thesis, University Montpellier 2.

Sattler R. 1978. What is theoretical plant morphology? *Acta Biotheoretica* **27**: 5–20.

Sattler R, Rutishauser R. 1997. The fundamental relevance of morphology and morphogenesis to plant research. *Annals of Botany* **80**: 571–582.

Schaffalitzky de Muckadell M. 1954. Juvenile stages in woody plants. *Physiologia Plantarum* **7**: 782–796.

Schaffalitzky de Muckadell M. 1959. Investigations on ageing of apical meristems in woody plants and its importance in sylviculture. *Forstl Forsogsvags* **25**: 310–455.

Schoute JC. 1909. Uber die Verästelung bei monokotylen Bäumen. II. Die Verästelung von *Hyphaene*. *Recents Travaux Botaniques Néerlandais* **15**: 211–232.

Schwabé WW. 1976. Applied aspects of juvenility and some theoretical considerations. *Acta Horticulturae* **56**: 45–56.

Scotland RW, Olmstead RG, Bennett J. 2003. Phylogeny reconstruction: the role of morphology. *Systematic Biology* **52**: 539–548.

Sellier D, Fourcaud T, Lac P. 2006. A finite element model for investigating effects of aerial architecture on tree oscillations. *Tree Physiology* **26**: 799–806.

Soler C, Sillion FX, Blaise F, de Reffye Ph. 2003. An efficient instantiation algorithm for simulating radiant energy transfer in plant models. *ACM Transactions on Graphics* **22**: 204–233.

Soria A, Meyer-Berthaud B. 2004. Tree fern growth strategy in the Late Devonian cladoxylopsid species *Pietzschia levis* from the study of its stem and root system. *American Journal of Botany* **91**: 10–23.

Souza MS, Puntieri J, Barthélémy D, Brion C. 2000. Bud leaf primordia content and its relation to shoot size and structure in *Nothofagus pumilio* (Poepp. et Endl.) Krasser (Fagaceae). *Annals of Botany* **85**: 547–555.

Späth HL. 1912. *Der Johannistrieb*. Inaugural-Dissertation zur Erlangung der Doktorwürde, Friedrich-Wilhelms-Universität, Berlin.

Stecconi M. 2006. *Variabilidad arquitectural de especies nativas de Nothofagus de la Patagonia (N. antarctica, N. pumilio, N. dombeyi)*. PhD thesis in Biology, Centro. Regional Universitario Bariloche – Universidad Nacional del Comahue, Argentina.

Stecconi M, Puntieri J, Barthélémy D. 2000. Annual–shoot growth in *Nothofagus antarctica* (G. Forster) Oersted (Fagaceae) from northern Patagonia. *Trees, Structure and Function* **14**: 289–296.

Steeves TA, Sussex IM. 1989. *Patterns in plant development*, 2nd edn. Cambridge: Cambridge University Press.

Stokes P, Verkerk K. 1951. Flower formation in Brussels sprouts. *Medelingen van de Landbouwhogeschoological te Wageningen* **50**: 143–160.

Stoutmeyer VT. 1964. Juvenility and flowering potential in woody plants. *American Horticultural Magazine* **43**: 161–167.

Temple A. 1977. *Ericaceae*: polymorphisme architectural d'une famille des régions tempérées et tropicales d'altitude. *Comptes Rendus de l'Académie des Sciences*, *Paris, Sér. D* **284**: 163–166.

Tomlinson PB. 1971. The shoot apex and its dichotomous branching in the *Nypa* palm. *Annals of Botany* **35**: 865–879.

Tomlinson PB., 1986. Plagiotropy. *Comptes Rendus du Colloque International sur l'Arbre, Montpellier, 9–14 Septembre 1985, Naturalia Monspeliensia, No. Hors Série*: 451–463.

Tomlinson PB. 1987. Architecture of tropical plants. *Annual Review of Ecology and Systematics* **18**: 1–21.

Tomlinson PB, Esler AE. 1973. Establishment growth in woody monocotyledons native to New Zealand. *Principes* **19**(C): 83–99.

Tomlinson PB, Gill AM. 1973. Growth habit of tropical trees: some guiding principles. In: Meggers JB, Ayensu ES, Duckworth WD,

eds. *Tropical forest ecosystems in Africa and South America: a comparative review*. Washington, Smithsonian Institute Press, 129–143.

Tomlinson PB, Posluszny U. 1977. Features of dichotomizing apices in *Flagellaria*. *American Journal of Botany* **64**: 1057–1065.

Tomlinson PB, Zimmermann MH. 1966. Anatomy of the palm *Rhapis excelsa* III. Juvenile phase. *Journal of the Arnold Arboretum* **47**: 301–312.

Trippi VS. 1963. Studies on ontogeny and senility in plants. III. Changes in proliferative capacity *in vitro* during ontogeny in *Robinia pseudoacacia* and *Castanea vulgaris* and in adult and juvenile clones of *R. pseudoacacia*. *Phyton* **20**: 153–159.

Troll W. 1937. *Vergleichende Morphologie der höheren Pflanzen*. Berlin: Borntraeger.

Troll W. 1957. *Praktische Einführung in die Pflanzenmorphologie 2 Teil: die blühende Pflanze*. Jena: Fischer Verlag.

Troll W, Rauh W. 1950. Das Erstarkungswachstum krautiger Dikotylen, mit besonderer Berücksichtigung der primären Verdickungsvorgänge. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften*. Mathematisch- naturwissentschaftliche Klasse. Jahrgang 1950. 1. Abhandlung: 1–86.

Turnbull C. 2005. *Plant architecture and its manipulation. Annual plant reviews*, Vol. 17. Oxford: Blackwell Publishing.

Uranov AA. 1975. Age spectrum of the phytocoenopopulation as a function of time and energetic wave processes. *Biologicheskie Nauki* **2**: 7–34.

Van den Berg D, Lanner RM. 1971. Bud development in lodgepole pine. *Forest Science* **17**: 479–486.

Varossieau WW. 1940. On the development of the stem and the formation of leaves in *Coffea* species. *Annales du Jardin Botanique de Buitenzorg* **50**: 115–198.

Veillon JM. 1978. Architecture of the New Caledonian species of *Araucaria*. In: Tomlinson PB, Zimmermann MH eds. *Tropical trees as living systems.* Cambridge: Cambridge University Press, 233–245.

Veillon JM. 1980. Architecture des espèces néo-calédoniennes du genre *Araucaria. Candollea* **35**: 609–640.

Venkatanarayana G. 1957. On certain aspects of the development of the leaf of *Cocos nucifera* L. *Phytomorphology* **7**: 297–305.

Vester H. 1997. *The trees and the forest. The role of tree architecture in canopy development; a case study in secondary forests (Araracuara, Colombia).* PhD thesis, University Amsterdam.

Vester HFM. 2001. Tree Temperaments. In: Labrecque M, Director . *L'arbre 2000, the Tree*. Canada: IQ Collectif, Institut de Recherche en Biologie Végétale, 25–30.

Vester HFM. 1999. Architectural diversification within the genus *Vismia* (Clusiaceae) in the Amazonian rain forest (Araracuara, Colombia). In: Kurmann MH, Hemsley AR eds. *The evolution of plant architecture*. Kew: Royal Botanical Gardens, 147–158.

Visser T. 1964. Juvenile phase and growth of apple and pear seedlings. *Euphytica* **13**: 119–129.

Visser T, De Vries DP. 1970. Precocity and productivity of propagated apple and pear seedlings as dependent on the juvenile period. *Euphytica* **19**: 141–144.

Wang Y, Li J. 2005. Genes controlling plant architecture. *Current Opinion in Biotechnology* **17**: 1–7.

Wardle P. 1963. Evolution and distribution of the New Zealand flora as affected by Quaternary climates. *New Zealand Journal of Botany* **1**: 3–17.

Wareing PF. 1959. Problems of juvenility and flowering in trees. *Journal of the Linnean Society of London, Botany* **56**: 282–289.

Wareing PF. 1961. Juvenility and induction of flowering. *Recent Advances in Botany* **2**: 1652–1654.

Webber HJ, Batchelor LD. 1948. *The citrus industry, Vol. I. History, botany and breeding.* Berkeley: University of California Press.

Weberling S. 1989. *Morphology of flowers and inflorescences*. Cambridge: Cambridge University Press.

White J. 1979. The plant as a metapopulation. *Annual Review of Ecology and Systematics* **10**: 109–145.

Wiens JJ. 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology* **53**: 653–661.

Wolfe LM, Mazer SJ. 2005. Responses to environmental heterogeneity: fitness consequences of phenotypic stability *vs.* sensitivity in wild radish (*Raphanus sativus*: Brassicaceae). *International Journal of Plant Sciences* **166**: 631–640.

Wright IJ, Westoby M, Reich PB. 2002. Convergence towards higher leaf mass per area in dry- and nutrient-poor habitats has different consequences for leaf life span. *Journal of Ecology* **90**: 534–543.

Wu R, Hinckley TM. 2001. Phenotypic plasticity of sylleptic branching: genetic design of tree architecture. *Critical Reviews in Plant Science* **20**: 467–485.

Wu R, Stettler RF. 1998. Quantitative genetics of growth and development in *Populus*. III. Phenotypic plasticity of crown structure and function. *Heredity* **81**: 299–310.

Yan HP, de Reffye P, Pan CH, Hu BG. 2003. Fast construction of plant architectural models based on substructure decomposition. *Journal of Computer Science and Technology* **18**: 780–787.

Yan H-P, Kang MZ, de Reffye P, Dingkuhn M. 2004. A dynamic, architectural plant model simulating resource-dependent growth. *Annals of Botany* **93**: 591–602.

Zeevaart JAD. 1962. The juvenile phase in *Bryophyllum daigremontianum. Planta* **58**: 543–547.

Zhao M-Z, de Reffye P, Barthélémy D, Hu B-G. 2003. Interactive simulation of plant architecture based on a dual-scale automaton model. In: Hu B, Jaeger M eds. *Plant growth modelling and applications (PMA03). Proceedings of the 2003 International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications*, Beijing, China, 13–16 October 2003. Beijing: Tsinghua University Press, Springer: 144–153.

Zimmerman RH. 1972. Juvenility and flowering in woody plants: a review. *Hortscience* **7**: 447–455.

Zimmerman MH, Brown CL. 1971. *Trees: structure and function*. Berlin: Springer-Verlag.