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Relationship between architecture and successional status of trees in the temperate deciduous forest[1]

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Abstract: The architectural analysis of trees, as developed since the pioneering work of Hallé & Oldeman in the 1960s and 1970s, allows the study of the developmental pattern characteristic to each species in a global and dynamic perspective of the tree. This leads to a fundamental question: is there a relationship between architectural characteristics of a species and its successional status? The analysis of nine tree species from the deciduous temperate forest of southwestern Québec reveals that such a relationship exists, mainly at the level of the alternation of organization plans (hierarchic and polyarchic) during the growth of the trunk and the reiteration within the crown. Early successional species (*Betula populifolia* and *Populus tremuloides*) have a hierarchic architecture throughout their ontogenesis. The hierarchy of the branched system promotes a rapid growth of the trunk. The potential for total reiteration in the crown is very limited. Conversely, late successional species (*Acer saccharum*, *Fagus grandifolia* and *Tsuga canadensis*) have an architecture with several levels of organization. The alternation of hierarchic and polyarchic phases of development confers a greater shape plasticity upon the tree, to the detriment of the speed of growth of the trunk. However, reiteration within the crown is common and abundant. This process increases the lateral spread of the crown, as well as it prolongs the life span of the tree itself. Mid-successional species (*Ulmus americana*, *Fraxinus americana*, *Tilia americana* and *Carya cordiformis*) have architectural development in between these two extremes. They combine a great hierarchy in the structure of the young tree with a potential for reiteration in the crown. Two growth strategies were identified among the late successional species, one facilitating growth in the shade and the other allowing the tree to benefit from increase in light in canopy gaps.
Keywords: growth strategy, organization plan, plant succession, reiteration, tree architecture.

Résumé: L'analyse architecturale des arbres, telle que développée depuis les travaux de Hallé & Oldeman dans les années 1960 et 1970, permet d'étudier le mode de développement caractéristique des espèces selon une approche globale et dynamique de l'arbre. Une question se pose: existe-t-il un lien entre les caractéristiques architecturales d'une espèce et son statut successionnel? L'analyse de neuf espèces d'arbres de la forêt feuillue du sud-ouest du Québec révèle qu'une telle relation existe principalement à l'échelle de l'alternance des plans d'organisation (hiérarchique et polyarchique) lors de l'établissement du tronc et du potentiel de réitération dans la cime. Les espèces de début de succession (*Betula populifolia* et *Populus tremuloides*) présentent une architecture hiérarchisée tout au long de leur ontogenèse. La hiérarchie du système ramifié favorise une montée rapide du tronc. Le potentiel de réitération totale dans la cime est très limité. À l'opposé, les espèces de fin de succession (*Acer saccharum*, *Fagus grandifolia* et *Tsuga canadensis*) présentent une architecture à plusieurs niveaux d'organisation. L'alternance des phases de développement hiérarchiques et polyarchiques confère à l'arbre une plus grande plasticité de la forme, au détriment de la vitesse d'allongement du tronc. La réitération dans la cime est abondante. Elle favorise son étalement latéral et une prolongation de la durée de vie de l'arbre. Les espèces de mi-succession (*Ulmus americana*, *Fraxinus americana*, *Tilia americana* et *Carya cordiformis*) se situent entre ces deux extrêmes. Elles présentent à la fois une grande hiérarchie dans la structure du jeune arbre et un potentiel de réitération dans la cime. D'autre part, deux stratégies de croissance ont été distinguées chez les espèces de fin de succession, l'une favorisant la croissance à l'ombre et l'autre permettant de profiter de la lumière des trouées.
Mots-clés: architecture des arbres, plan d'organisation, réitération, stratégie de croissance, succession végétale.

Introduction

Tree architectural analysis allows us to account for the morphological differentiation among various categories of axes and to uncover the organization rules of structure and the development dynamics characteristic to each species (Millet, Bouchard & Édelin, 1998a; Millet, Bouchard & Édelin, 1998b). The use of four architectural criteria (growth pattern, branching pattern, morphological differentiation and position of sexual organs) has allowed Hallé & Oldeman (1970) and Hallé, Oldeman & Tomlinson (1978) to identify 23 architectural models in nature. The adaptive significance of these models was investigated. Correlations were sought between architectural criteria and architectural models, on the one hand, and the ecological characteristics of species, on the other hand. However, these studies, which were based on the concept of the architectural model, were inconclusive (Hallé, Oldeman & Tomlinson, 1978; Fournier, 1979).

New concepts have been developed in tree architecture during the last 30 years. Today, the description of the developmental pattern of a species, *i.e.*, the identification of the sequence of characteristic development phases, goes beyond the sole identification of the model. The concepts of reiteration (Oldeman, 1974), architectural unit (Barthélémy,

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Édelin & Hallé, 1989; Édelin, 1977), organization levels (Barthélémy, 1990; Hallé, 1986) and organization plan (Édelin, 1991) have been developed and permit a more detailed picture of the architecture and developmental pattern of a species. These new concepts have already given us insights, from the viewpoint of tree structure organization, on what promotes greater shape plasticity in some species (Millet, Bouchard & Édelin, 1998b; Loup, 1994; Genoyer, 1994; Nicolini & Caraglio, 1994; Prosperi, Édelin & Michaloud, 1995; Bégin, 1991; Millet & Ouellet, 1992).

Oldeman & van Dijk (1991) have used architectural characters from several organization levels (organs, axes, branching patterns, reiteration patterns), in the diagnosis of the "temperaments" of tropical forest trees. Because the diversity of tree shapes is lower in temperate forests, the classification of Oldeman & van Dijk (1991) does not allow to segregate species according to their successional status (J. Millet, pers. observ.). Additional research on the architecture of trees of temperate regions is necessary to provide evidence of the hypothesized relationships between their developmental pattern and their successional status (Millet, Bouchard & Édelin, 1998a; Millet, Bouchard & Édelin, 1998b).

The objectives of this study are (*i*) to compare the architecture of several tree species that are in close relationship with each other during forest succession in a temperate region, (*ii*) to identify traits that can discriminate tree species according to their successional status, (*iii*) to understand the influence of these various traits on the growth strategies of the species, and (*iv*) to draw conclusions about the relationships between the architecture and the developmental pattern of species and their successional status. We will test the hypothesis that these relationships are based on the alternation of hierarchic and polyarchic organization plans.

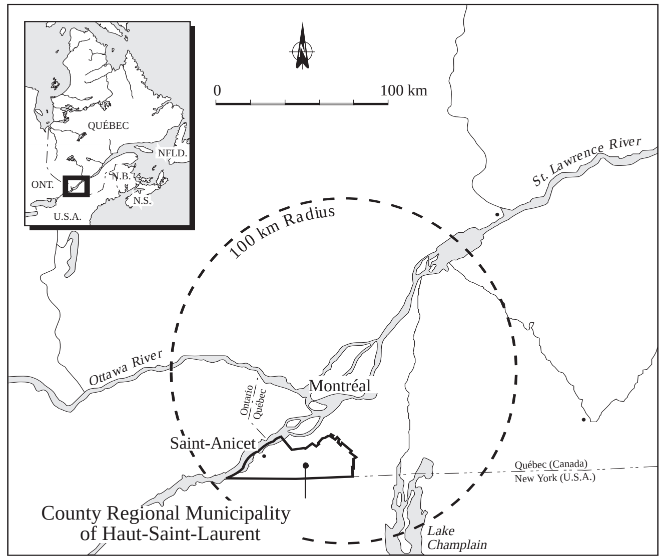


FIGURE 1. Study area, County Regional Municipality of Haut-Saint-Laurent and region of Montréal.

Material and methods

SPECIES SELECTION

The study was carried out in the sugar maple-hickory climatic zone (Grandtner, 1966) of southwestern Québec, more specifically in the County Regional Municipality of Haut-Saint-Laurent (Figure 1), an area that has been the subject of multidisciplinary studies (Bouchard & Domon, 1997; Bouchard *et al.*, 1985; Doyon, Bouchard & Gagnon, 1998) for more than ten years. This area is located within the Great Lakes-St. Lawrence forest region, Upper St. Lawrence forest section (Rowe, 1972). In total, 37 native tree species, mostly deciduous, occur in the region. This study deals exclusively with species growing on mesic soils that have developed on morainal surficial material, so that the architecture of species that are in direct relationship with one another during forest succession can be compared. Nine of the most frequently found species were selected for their representation of the various stages of forest succession and the diversity of their architecture: *Betula populifolia* Marsh. and *Populus tremuloides* Michx as early successional species; *Ulmus americana* L., *Fraxinus americana* L., *Tilia americana* L. and *Carya cordiformis* (Wang.) K. Koch as mid-successional species; *Acer saccharum* Marsh., *Fagus grandifolia* Ehrh. and *Tsuga canadensis* (L.) Carr. as late successional species (Bergeron, Bouchard & Leduc, 1988; Brisson, Bergeron & Bouchard, 1988; Domon *et al.*, 1986). The results of the architectural analysis of four species whose development is in accordance with Troll's model, in whole or in part (*Ulmus americana*, *Tilia americana*, *Fagus grandifolia* and *Tsuga canadensis)*, have been described and discussed in a previous paper (Millet, Bouchard & Édelin, 1998b). Sugar maple has been studied and described by Millet & Ouellet (1992). We present here the results of the last four species (*Betula populifolia*, *Populus tremuloides*, *Fraxinus americana* and *Carya cordiformis*), as well as a synthesis of the results for all nine species.

METHOD OF ARCHITECTURAL ANALYSIS

To describe the developmental patterns of the tree species, we used the architectural analysis method of Hallé & Oldeman (1970) that allows for the deduction of the development dynamics from the observation of traits fixed in the structure of trees. Our observations were made on approximately 150 individuals of different ages and development stages for each species studied. A survey of the architecture of individuals of a species was made from the seedling stage to the senescent tree stage. By cross-checking, the complete development sequence was deduced. An initial step was to draw sketches. Once the developmental pattern was understood, a representative individual was chosen for each development stage and drawn. Our comprehension was thus tested several times, as each stage was described in detail. The results were then verified in the field by making sure that all individuals encountered in a variety of habitats shared the proposed developmental pattern. Only the characters common to all were retained. Verifications as well as some analyses were completed within a 100-km radius of Montréal (Figure 1). The results of the analyses are presented as a descriptive text of the architecture and the development stages of each species, along with a schematic portrait of its characteristic architectural unit and a list of the characters of the different categories of axes. The field work took place from May 1993 to September 1996. Several instruments were used to facilitate observation: 10X magnifier, binoculars (Bausch and Lomb 8×40 WA) and telescope (Kowa TSN-1 with 20X to 60X zoom), tripod, razor blades for sections, and pole pruning shears. The analyses were mainly focused on the development of the young tree, the mechanisms of growth of the main stem, the differentiation of axes and the reiteration potential within the crown. To describe the various categories of axes of branched systems, we only used criteria for which we had sufficient information. A few additional elements may eventually complete the portraits (*e.g.*, position of inflorescences, cambial growth). These were not included here because there are not considered essential to our analysis.

In order to avoid any ambiguity in the meaning of words used, a few definitions are necessary. The orthotropic or plagiotropic character attributed to the axes refers to the direction of their primary growth. The term axis denotes any linear stem structure, from its origin to its extremity. In this sense, the axis can either be monopodial, constructed from a single meristem, or sympodial, constructed from a succession of modules. We assign the term module to any basic structure of a sympodium, whether it is branched or not. The term complex sympodium designates a branched system made up of a succession of monochasial sympodia and polychasial sympodia. In the monochasial sympodium only one relay is formed, whereas several are formed in the polychasial sympodium. The mixed sympodium is a sympodium that is made up of a succession of branched monopodial modules. The architectural unit is defined as a structure with a hierarchy, *i.e.*, with one or several categories of differentiated axes, the limits of which are marked by a discontinuity in the hierarchy of the plant's development. We consider that there is a polyarchy when one or several axes escape from the correlation system of a hierarchy and create a fork. The sharing of apical dominance can be transitory or persistent. Several levels of organization (Barthélémy, 1990; Hallé, 1986) can be detected in the structure of a tree. Thus, the "basic" architectural units can occur in sequence and create an architectural unit of a higher organizational level. We use the abbreviations AU1, AU2, AU3, etc. to indicate architectural units of different levels, each one being the basic structure of the one that follows. The species' architectural unit is the highest level unit recognized in a particular species and is constructed of the largest number of axis categories.

Results

ARCHITECTURE AND DEVELOPMENTAL PATTERN OF GREY BIRCH, *BETULA POPULIFOLIA*

STRUCTURE

The seedling (Figure 2a) is an orthotropic monopodium (A1) with a spiralled 2/5 index phyllotaxy and rhythmic growth. Leaves have a single bud at their base and are arranged radially around axis A1. Along the stem, the boundaries between growth units are unclear.

The sapling (Figure 2b) is made up of an orthotropic monopodial axis A1, with a spiralled 2/5 index phyllotaxy that is ramified rhythmically. Its growth units, with unclear boundaries, are acrotonic and bear lateral shoots (A2) along almost all of their length. The order 2 axes are orthotropic monopodia with spiralled 2/5 index phyllotaxy and rhythmic growth. They are arranged radially around axis A1 and have a deferred origin; they originate from buds that had remained latent during the previous winter.

The young tree (Figure 2c) has a hierarchic architecture that is branched up to the fifth order. All of the categories of axes are orthotropic linear sympodia with a spiralled 2/5 index phyllotaxy and rhythmic growth. The modules correspond to a single growth unit whose apex is aborted. The modules are derived from one another by subterminal branching; they originate from an axillary bud that had remained latent during winter, as is the case of the laterally produced axes on the acrotonic growth units (A1 to A4). Only the trunk and the oldest branch, at its base, may have in their proximal part a few monopodial growth units erected during the sapling phase. But the radial growth of these axes hides all traces of this past character, and the whole tree appears essentially as a sympodium with differentiated and linear axes. The branches (A2) are arranged in successive tiers along the trunk, whose dimensions are modest. The A2 axes are complex sympodia bearing long and thin shoots (A3). These are arranged radially around A2 axes. The A3 axes bear, in the distal part of their growth units, some A4 twigs whose diameter growth is very weak. The A4 axes are arranged radially around the A3 axes, and they bear in turn short shoots (A5) that are monochasial sympodia with very close leaves. These short shoots are on the A4 axes and at the distal extremity of the A2 branches and the main stem. The detailed characteristics of each category of axes are summarized in Figure 3.

The mature tree may reach 10 to 12 m in height and has a single trunk that is linear and orthotropic. The branches are self-thinned at the base, leaving scars on the trunk. The branches making up the crown are tiny and have a very divaricated structure, making the identification of categories of axes impossible. The trunk ends by a system of small, short forks with a structure similar to that of the divaricated branches. Figure 2d illustrates an exceptional case of a mature tree with two crowns whose structure is identical to that of the straight tree, except for the second crown.

ONTOGENESIS

The development of grey birch is divided into three major phases. The first occurs during the very first years of life of the plant. This phase is monopodial and leads to the differentiation of the A2 shoots and of the trunk.

The second development phase is sympodial. It is the A2 axes which first assume a sympodial growth, and the A1 axis. The differentiation of axes continues along in this manner and leads to the erection of a hierarchic unit with five categories of axes. It is the architectural unit of the species described at the young tree stage. Its organization is related to Rauh's model (Hallé, Oldeman & Tomlinson, 1978), although it is sympodial.

The third development phase occurs with the loss of dominance of the axes. The branches and the extremity of the main stem assume a divaricated structure with very

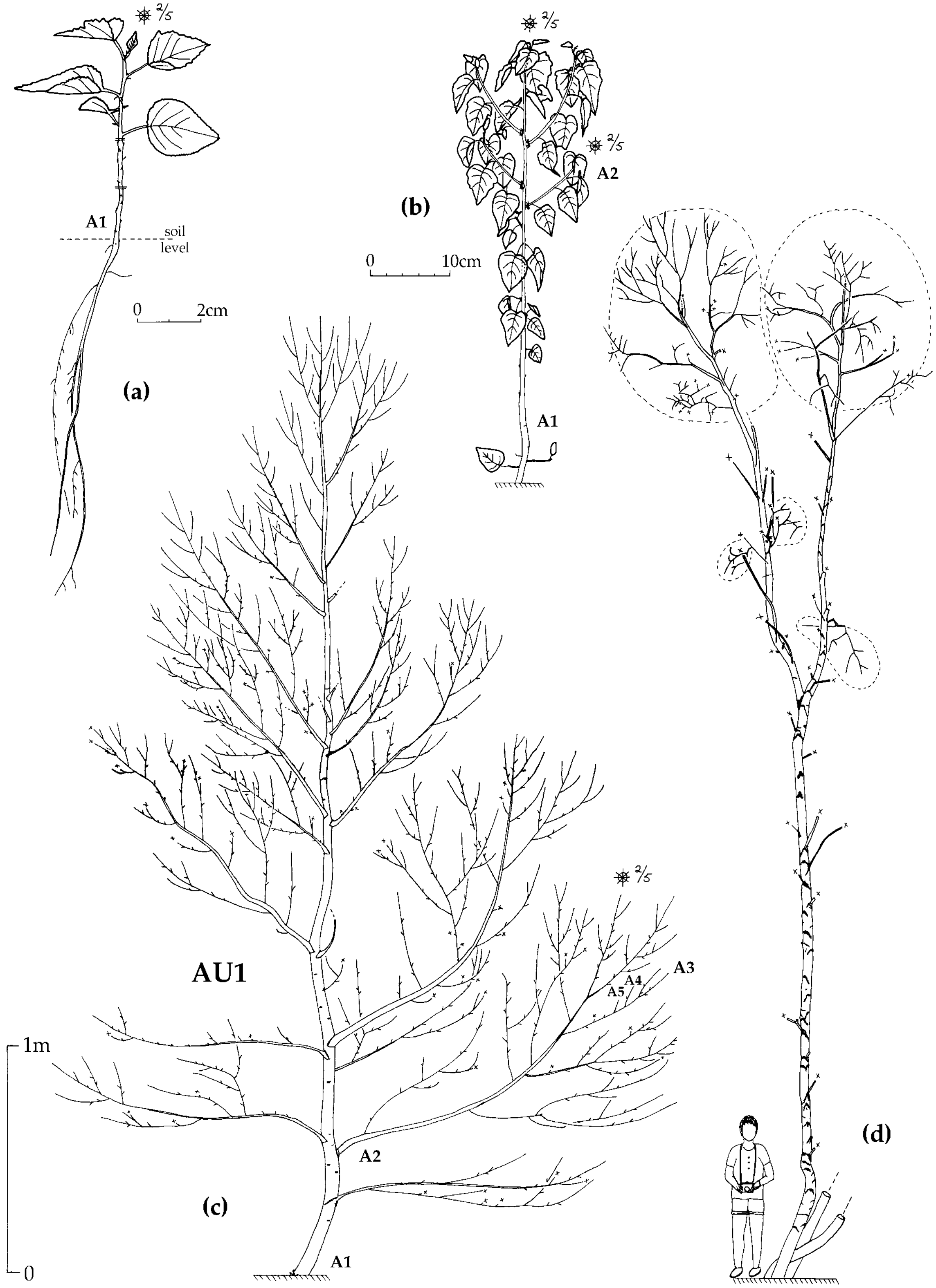
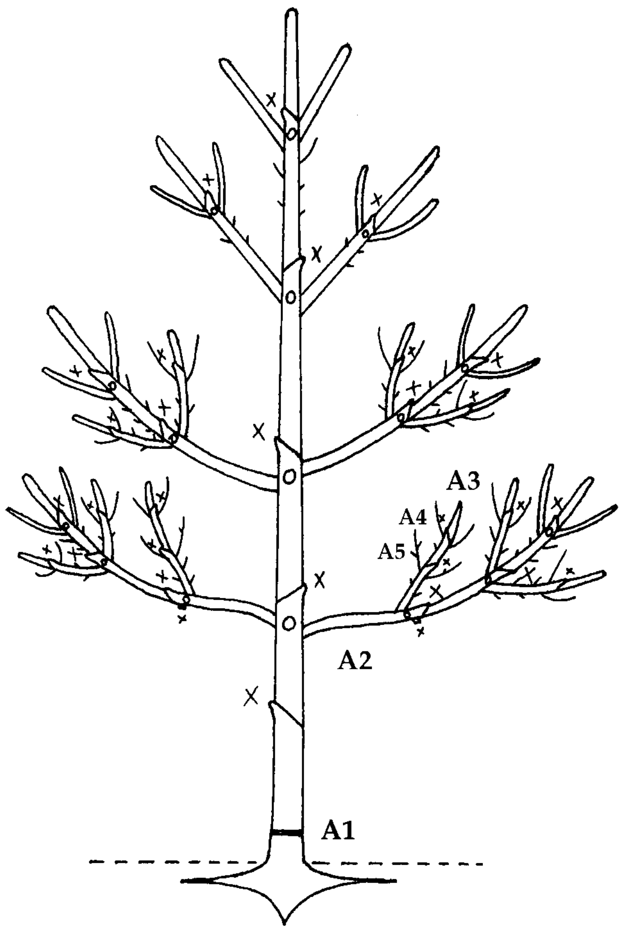


FIGURE 2. *Betula populifolia* a) 3 year-old seedling, with monopodial growth; b) 3 year-old sapling, with monopodial growth and branched with orthotropic A2 axes; c) young tree about 4 m high, whose hierarchic structure, with five categories of axes, represents the species' characteristic architectural unit (UA1); d) mature tree, about 12 m high, with two crowns; ╪ boundaries of growth units; ❋ spiraled phyllotaxy; 2/5 phyllotaxic index; × apex mortality; An: category *n* axis.



A1	A2	A3	A4	A5
Complex sympodium	Complex sympodium	Complex sympodium	Complex sympodium	Monochasial sympodium
2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy
rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	unbranched short shoot
orthotropic	orthotropic	orthotropic	orthotropic	orthotropic
radial symmetry	radial symmetry	radial symmetry	radial symmetry	radial symmetry
medium thickness growth	slight thickness growth	very slight thickness growth	very slight thickness growth	very slight or no thickness growth
indeterminate growth	long-term determinate growth	mid-term determinate growth	short-term determinate growth	short-term determinate growth

FIGURE 3. Description of *Betula populifolia* architectural unit. The schematic drawing illustrates the architecture of the young tree. For each category of axes (A1, A2, etc.), the main architectural characteristics are presented. ×: apex mortality.

short growth units, foretelling the senescence of the tree. The essence of the grey birch's ontogeny is the erection of the architectural unit. The occurrence of very small forks does not detract from the general linear shape of the trunk.

VARIATIONS

The first variation observed consists of the origin of the lateral axes. Generally deferred, it may also occur immediately. This branching pattern, although seen on occasion, has not been the object of detailed study.

The second type of variation is related to the dominance of the main stem. It sometimes occurs at a young age, generally in more shaded habitats where the leader loses its dominance. The apex aborts and a fork is created from two subterminal buds. The divaricated shapes that result are rare and most often resume their linear growth by the straightening up of one of the elements of the fork. Mature trees are occasionally seen with more than one crown (Figure 2d). In these rare cases, each crown reproduces the structure of the tree (*i.e.*, total reiteration), but the number of total reiterates is always very limited (observed maximum of two crowns per tree). The main axes of these total reiterates are long and vertical, with a narrow aperture angle between them, indicating their high degree of individuality. The phenomenon of total reiteration in the crown of the mature tree, being occasional and of very limited expression when it occurs, has not been retained as being part of the developmental pattern characteristic of grey birch.

ARCHITECTURE AND DEVELOPMENTAL PATTERN OF TREMBLING ASPEN, *POPULUS TREMULOIDES*

STRUCTURE

The seedling is an orthotropic monopodium (A1) with a spiralled phyllotaxy and rhythmic growth. The leaves are arranged radially around the A1 axis and bear a single bud at their base. Figure 4a illustrates a yearling sucker of similar structure.

The sapling (Figure 4b) is made up of an orthotropic monopodial axis A1, with a spiralled 2/5 index phyllotaxy that is rhythmically branched. The lateral shoots (A2) are inserted in the upper part of the growth units of axis A1 (acrotonic branching); the branching zone can extend to almost the entire length of the growth unit. The A2 axes (Figures 4b and 4c) are orthotropic monopodia with spiralled 2/5 index phyllotaxy, and arranged radially around axis A1. These shoots have a deferred origin; they originate from buds that had remained latent during winter.

The young tree (Figure 4d) is made up of four categories of axes whose phyllotaxy is spiralled, with a 2/5 index, and whose growth is rhythmic. The trunk (A1) is always an orthotropic monopodium and bears branches (A2) arranged in successive tiers. The branches are orthotropic monopodia with small diameters. Their growth units are acrotonic and bear long A3 shoots in their upper part. The latter are orthotropic, monopodial, and their diameter growth is very weak. The shoots located on the ventral side of the A2 axes are more developed than those born on the dorsal side, which gives a slight bilateral symmetry to the branches. The A4 axes are short shoots with radial symmetry and with leaves that are very closely set. Although the short A4 shoots do not have a clearly visible tropism, some longer shoots whose tips tend to straighten up suggest that their growth is fundamentally orthotropic. The short shoots are located all along the A3 axes, but they are also found in the lower part of the growth units of axes

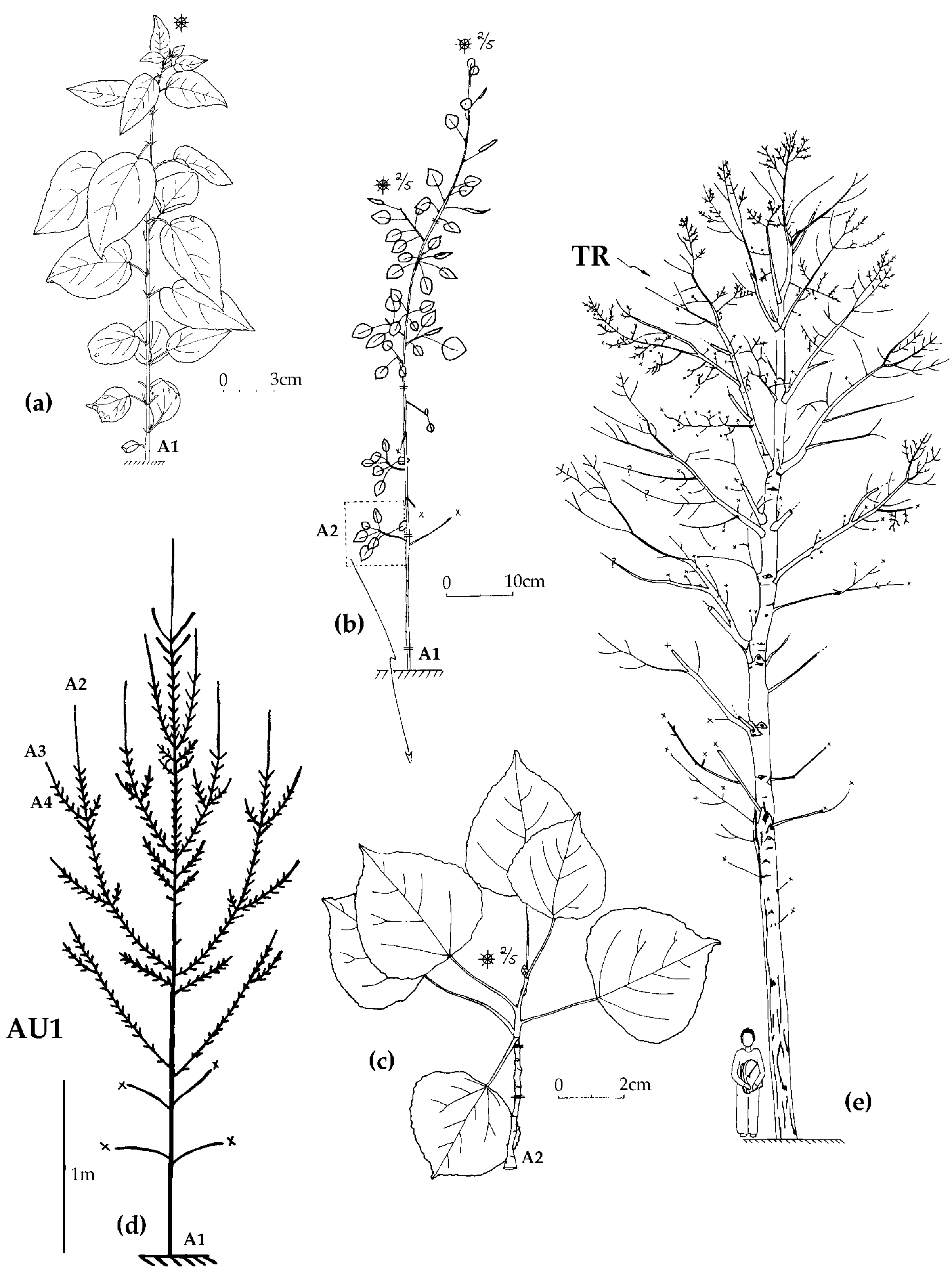
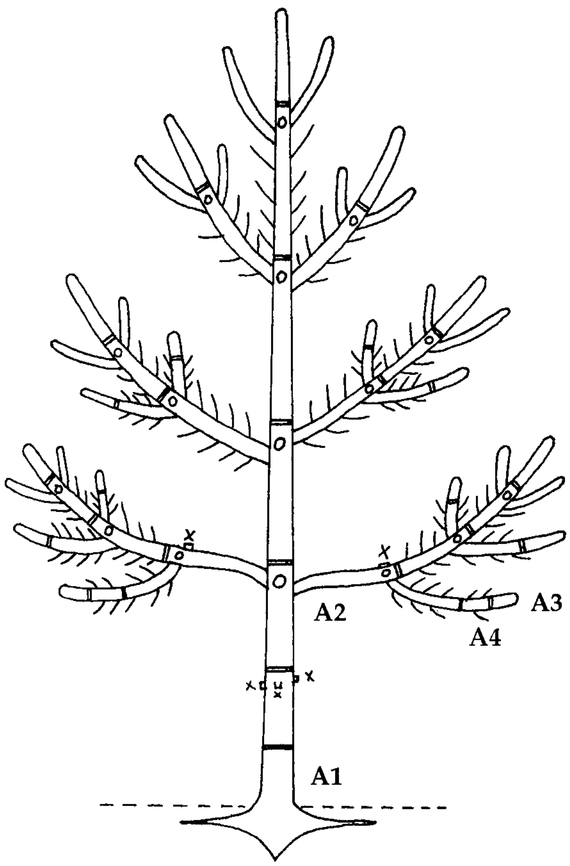


FIGURE 4. *Populus tremuloides* a) yearling sucker approximately 25 cm high; b) 5 year-old sapling about 1 m high; c) enlarged view of a 3 year-old A2 axis; d) sketch of a young tree whose hierarchic structure, with four categories of axes, represents the species' characteristic architectural unit (UA1); e) mature tree, approximately 20 m high, showing one total reiterate (TR) of the architectural unit and the preserved linearity of the trunk; ❊ spiraled phyllotaxy; 2/5 phyllotaxic index; ╪ boundaries of growth units; × apex mortality; A*n*: category *n* axis.

A2, and even on the main stem. Having a very short lifespan, they self-thin spontaneously through the means of a basal abscission zone. The detailed characteristics of each category of axes are summarized in Figure 5.

The mature tree (Figure 4e) can reach 20 m in height. Its orthotropic and monopodial trunk bears tiers of branches whose structure varies depending on their position in the crown. In the lower part of the crown, a few sparse branches have a structure that is similar to the one described for the young tree stage. Most of these branches have already abscised, as indicated by the scars left on the tree trunk. The major part of the crown is made up of larger branches characterized by the presence of forks. These branches (A2) are orthotropic monopodia that can attain 3 m in length and approximately 15 cm in basal diameter. They bear A3 shoots identical to those previously identified on the young tree, branched with A4s, but also with other longer axes, with a longer lifespan than A3 shoots. The diameter of the latter is equivalent to that of the A2 axis, and their branching extends to the fifth order. These branched structures are partial reiterates; they reproduce the structure of the axis A2 that bears them. Inserted in the subterminal part of certain growth units of axis A2, they create forks arranged in an irregular fashion along the branch. In the upper part of the crown, large diameter axes occur mixed in with the partially reiterated branches. These are uniformly branched systems up to the fifth order, and made up of four different orders of axes. The main axis is an orthotropic monopodium with a spiralled phyllotaxy and rhythmic branching. This axis is vertical and hardly shows any sagging. As opposed to neighbouring branches, it is perennial and may reach 4 m in length. The branches (third order axes) that are inserted on it in successive tiers, are in all aspects similar to those observed on the young tree (A2). The fourth order axes have the same structure as the A3 axes of the young tree, and the fifth order axes are short shoots that almost entirely cover the growth units of fourth order. In other words, these particular branches are total reiterates. Although regularly present in mature trees, these reiterates are very few and are of relatively modest size, so that the dominance and linearity of the trunk are not modified.



A1	A2	A3	A4
monopodium	monopodium	monopodium	monopodium
2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy	2/5 spiralled phyllotaxy
rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	unbranched, short shoot with basal abscission zone
orthotropic	orthotropic	orthotropic	ageotropic with orthotropic tendency
radial symmetry	slightly bilateral symmetry due to hypotony	radial symmetry	radial symmetry
great thickness growth	slight thickness growth	very slight thickness growth	very slight or no thickness growth
indeterminate growth	long-term determinate growth	mid-term determinate growth	short-term determinate growth

FIGURE 5. Description of *Populus tremuloides* architectural unit.. The schematic drawing illustrates the architecture of the young tree. For each category of axes (A1, A2, etc.), the main architectural characteristics are presented. ×: apex mortality.

Ontogenesis

The development of trembling aspen is characterized by three major phases. The first is the differentiation of the four categories of axes, and leads to the construction of the species' architectural unit (Figures 4d and 5). Its organization is in accordance with Rauh's model (Hallé, Oldeman & Tomlinson, 1978). The second phase consists of the appearance of partial reiteration by the differentiation of fifth order axes (equivalent to A4 axes on shoots that have reproduced the structure of the axis that bears them) spaced irregularly along branches. The third phase is the unpredictable appearance of a few total reiterates of relatively modest size, which are a minority within the crown. Thus, the essence of trembling aspen's ontogeny is based on the erection of the architectural unit; the occurrence of reiteration modifying only slightly the general shape of the tree.

Variations

The principal characters likely to vary from one individual to the next are: (*i*) the degree of plagiotropy or orthotropy of the branches, trees growing in shadier environments having thinner and more horizontal branches than in an open environment; (*ii*) the total reiteration, although always marginal in this species, that may be more or less abundant depending on the individual; (*iii*) the occasional loss of dominance by the main stem that, in circumstances of unknown nature, may lean horizontally and be replaced by a lower branch that takes up apical dominance.

Architecture and developmental pattern of white ash, *Fraxinus americana*

Structure

The seedling (Figure 6a) is an orthotropic monopodium (A1) with an opposite-decussate phyllotaxy and rhythmic growth. The leaves, simple and entire, bear a single bud at their base. The slightly older seedling (Figure 6b) has compound leaves with at least three leaflets.

The sapling (Figure 6c) is made up of an orthotropic monopodial axis A1 with an opposite-decussate phyllotaxy which is branched rhythmically. The lateral shoots A2 are inserted in the distal part of the growth units of axis A1. The A2 axes are monopodia, with an opposite-decussate phyllotaxy and rhythmic growth, arranged radially around axis A1. The lower A2 are plagiotropic, but with a straightened up extremity, whereas the upper ones are orthotropic. These shoots have a deferred origin; they originate from buds that had remained latent during winter. All of the leaves are composed of five to nine leaflets. Leaves inserted on the ventral side of the A2 axes generally have a longer petiole than those born on the dorsal side.

The young tree (Figure 6d) is branched up to the fourth order. All the categories of axes are orthotropic monopodia with compound leaves of five to nine leaflets, with opposite-decussate phyllotaxy and rhythmic growth. The A2 branches of small diameter are arranged in successive tiers along the trunk (A1). The lower branches are drooping and have straightened up extremities. The higher ones have a smaller aperture angle with the trunk. The growth units of the A2 axes bear long A3 shoots in their distal part. The latter have a very weak diameter growth and are often drooped. The A3 shoots located on the ventral side of the A2 axes are more developed than those born on the dorsal side, giving a slight bilateral symmetry to the branches. The A3 shoots are branched rhythmically. The A4 axes are short and arranged radially around the A3 axes; those on the ventral side are curved upwards. The short shoots are located all along the distal part of the A2 axes and of the main stem. The detailed characteristics of each category of axes are summarized in Figure 7.

The mature tree (Figures 6e and 6f) can reach 20 to 30 m in height. It has an orthotropic monopodial trunk that has forked in its upper part following the death of the apex. Lateral axes, inserted directly below the dead apex, take over the relay of the trunk. These axes are straighter and of larger diameter than the A2 axes below. Each element of the fork, taken individually, has an architecture that is similar to that of the young tree with its four categories of axes. These total reiterates end in turn by a fork and give rise to a new generation of reiterates. The tree crown has a mixed divaricated sympodium structure. White ash has the capacity to reiterate, which promotes the spread of the crown and a longer lifespan.

Ontogenesis

The development of white ash is divided into two important phases. The first consists of the erection of the hierarchic structure with four categories of axes described at the young tree stage; it is the species' characteristic architectural unit (Figures 6d and 7). Its organization is in accordance with Rauh's model (Hallé, Oldeman & Tomlinson, 1978). The second development phase consists of duplicating the architectural units after forking of the main stem. The relays of subterminal origin do not differentiate from one another, so that the growth in length of the trunk is definitively arrested. Each reiterate forks and reiterates in its turn. The miniaturization of the reiterates and the characteristics of the minimal unit have not been observed, due to the occurrence of ash dieback and the rarity of older individuals in the study area.

Variations

The first variation observed is in the orientation of branches (A2). Young trees growing in shadier environments have thinner and more horizontal branches than in open environments. Nevertheless, their tips are always straightened upwards.

The second variation is observed with main stem dominance. In generally shady environments, the loss of apical dominance of the main stem occasionally occurs and one to several forks are created. If environmental conditions allow, an element of the fork eventually straightens up and takes the relay of the trunk.

The third variation is related to the way in which forks are created. In the suppressed sapling or in the tree showing total reiteration, the top may sag slightly instead of aborting its apex. In such a case, it continues its growth while sharing dominance with an axis of subterminal origin, which is more erect and longer than the other lower branches.

The fourth variation observed is the possible expression of partial reiteration on branches before total reiteration of the architectural unit at the extremity of the trunk. The upper branches on the young tree may then have a tendency to fork, each element of the fork bearing the two characteristic branching orders (A3 and A4).

Architecture and developmental pattern of bitternut hickory, *Carya cordiformis*

Structure

The seedling is an orthotropic monopodium (A1) with a spiralled phyllotaxy and rhythmic growth. The first leaves of the seedling were not observed, but those of a seedling of a few years old (Figure 8a) are composed of five leaflets. The leaves bear two serial buds at their base.

The sapling (Figure 8b) is constructed of two categories of axes with leaves composed of five to seven leaflets, with a spiralled phyllotaxy and rhythmic growth. The A1 axis is a mixed orthotropic sympodium whose modules, made up from one to several growth units, end in a dead apex. They are derived from one another by subterminal branching from an axillary bud that had remained latent during the winter. The A2 axes are very short orthotropic monopodia with spiralled phyllotaxy. They are located in acrotonic position on the longest growth units, and have a deferred development.

The very young tree (Figure 8c) is constructed from three categories of orthotropic axes with compound leaves of seven to nine leaflets, with spiralled phyllotaxy and rhythmic growth. The A1 axis is a mixed sympodium whose last module is a long monopodium. It is rhythmically branched. The A2 and A3 axes are almost horizontal

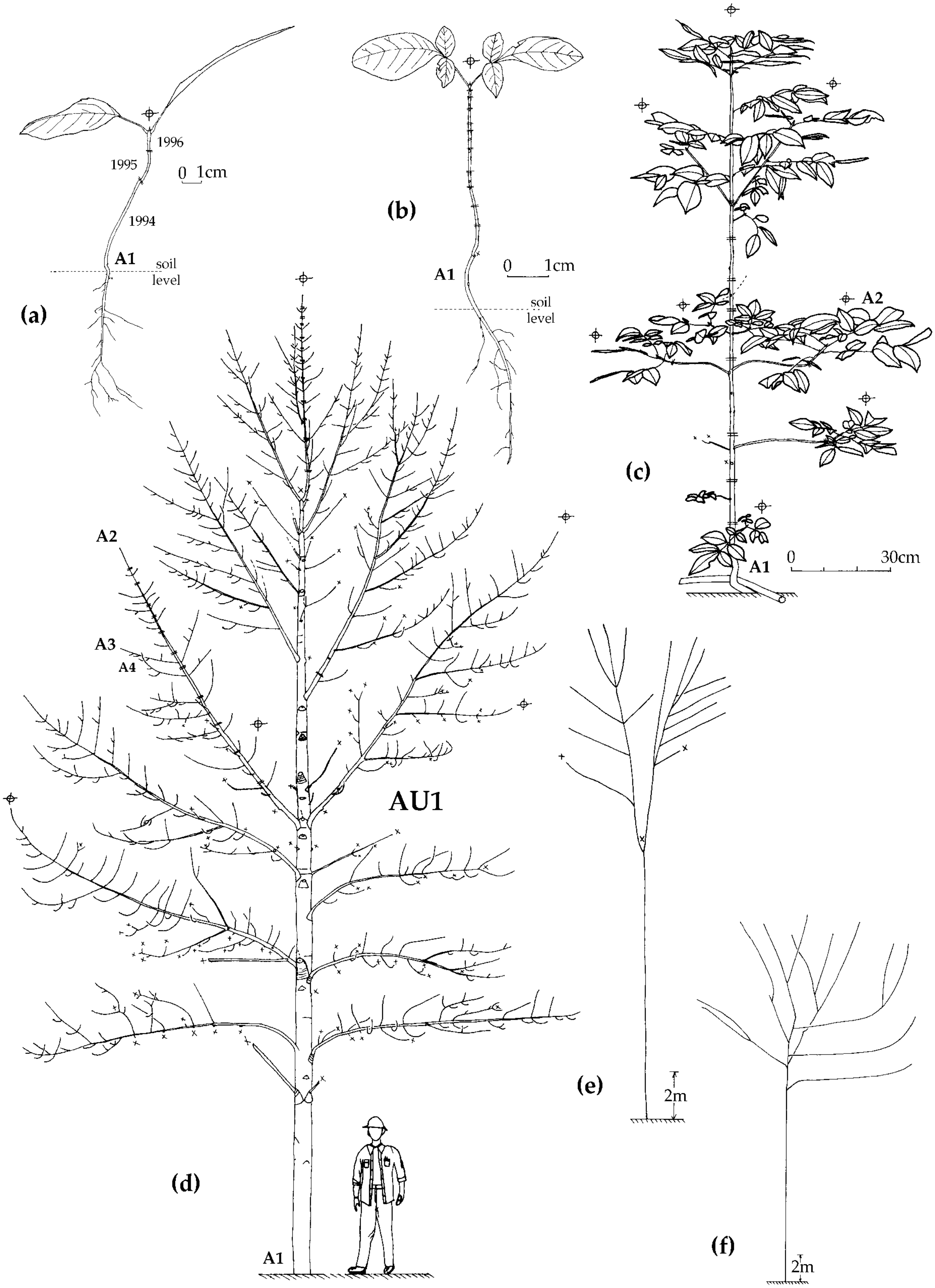
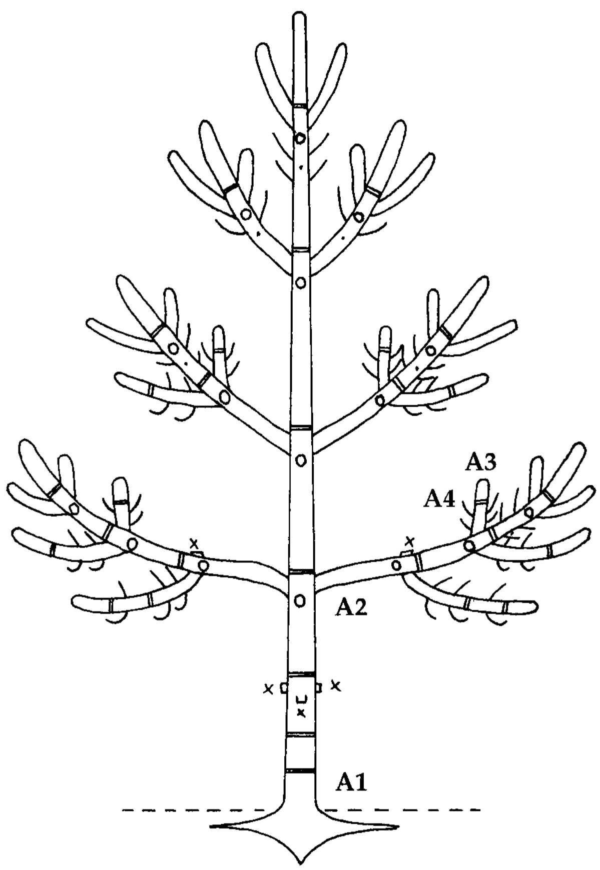


FIGURE 6. *Fraxinus americana* a) 3 year old seedling with simple leaves; b) 12 year-old seedling with compound leaves of 3 leaflets; c) sapling, about 2 m high, branched with orthotropic A2 axes; d) young tree, about 10m high, whose hierarchic structure, with four categories of axes, represents the species' characteristic architectural unit (UA1); e) sketch of a mature tree, approximately 20 m high; f) sketch of a mature tree, approximately 30 m high; ╪ boundaries of growth units; 1994: year of elongation of the growth unit; ⊕ opposite-decussate phyllotaxy; × apex mortality; A*n* category *n* axis.



A1	A2	A3	A4
monopodium	monopodium	monopodium	monopodium
opposite decussate phyllotaxy	opposite decussate phyllotaxy	opposite decussate phyllotaxy	opposite decussate phyllotaxy
rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	unbranched
orthotropic	orthotropic	orthotropic	orthotropic
radial symmetry	slightly bilateral symmetry due to hypotony	radial symmetry	radial symmetry
great thickness growth	slight thickness growth	very slight thickness growth	very slight or no thickness growth
indeterminate growth	long-term determinate growth	mid-term determinate growth	short-term determinate growth

FIGURE 7. Description of *Fraxinus americana* architectural unit.The schematic drawing illustrates the architecture of the young tree. For each category of axes (A1, A2, etc.), the main architectural characteristics are presented. ×: apex mortality.

monopodia, with an erect tip. The structure of the A2 axes varies according to their position on the trunk. On the longest growth units, the A2 shoots are long and branched. They alternate with shorter, unbranched A2 shoots, that are born on shorter growth units. The A2 shoots are arranged radially around the young trunk. The A3 shoots are short and born by the A2 axes on acrotonic growth units separated by unbranched and shorter growth units. The A3 axes inserted laterally are longer than those positioned on the ventral and dorsal sides, which gives a slight bilateral symmetry to the A2 axis.

The young tree (Figure 8d) is made up of four categories of orthotropic axes, whose leaves are composed of seven to eleven leaflets. The trunk (A1) is always a mixed sympodium. The A2 axes have a variable structure according to their position on the trunk. In the lower part are found monopodial shoots (A2) with two categories of axes described for the very young tree. They are senescent, and many are self-thinned. Higher up on the trunk, large erect branches (A2) alternate with shorter shoots; all are divaricated sympodia. The large branches have a greater diameter and have a narrower angle with the trunk. They are inserted in the subterminal part of the modules making up the trunk. They are composed of three categories of axes. The shorter A2 shoots have a smaller diameter, a wider insertion angle on the trunk, and they are inserted on the monopodial sections of the trunk. They are composed of only two categories of axes. All of the A2 axes are arranged radially around the A1 axis. The detailed characteristics of the trunk and the different categories of axes of which are composed the large branches are given in Figure 9.

The premature tree at the beginning of the crown erection stage (Figure 8e) may reach 20 m in height. It has a single trunk that is well differentiated and has three types of branches. In the lower part of the trunk, an alternation is found between large branches with three categories of axes and small branches with two categories of axes, as described in the young tree stage. In the upper part of the trunk, a few rare branches with four categories of axes alternate with the two preceding types. These are total reiterates that reproduce the structure of the young tree. They stand out from other branches by their great length, their large diameter and their pronounced erect aspect. Of limited number and modest size, they do not compete with the trunk that still maintains a perfect linear aspect.

The mature tree (Figure 8f) may reach 30 m in height. It has main branches of subterminal origin at the extremity of its trunk. Each one is a total reiterate reproducing the structure of the young tree with its four categories of axes. There is no differentiation among them, so that they create a fork and the height growth of the trunk is definitely arrested. Each total reiterate forks in turn. The crown is made up of a succession of total reiterates whose dimensions decrease from one to the next. The minimal unit stage was not observed. The capacity of the hickory to reiterate promotes crown spread and a longer lifespan.

ONTOGENESIS

The development of bitternut hickory is divided into six major phases. The first consists of erecting the first monopodial unit described for the seedling stage. It represents the first level of organization of the species, the first level architectural unit, AU1.

The second phase is the duplication of the AU1. The apex of the first unit aborts and a subterminal bud gives rise to a relay that reproduces the structure of the AU1. The

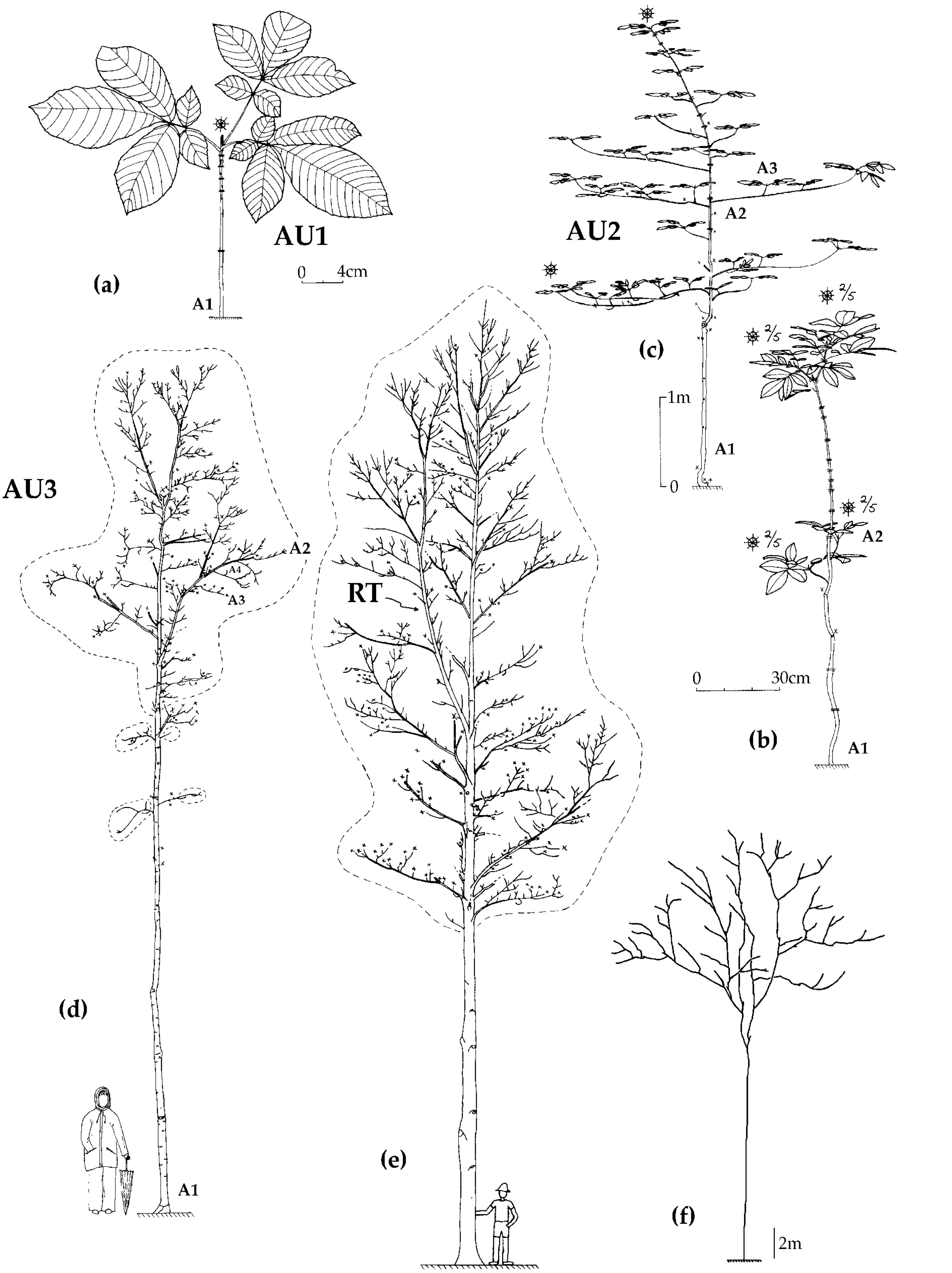
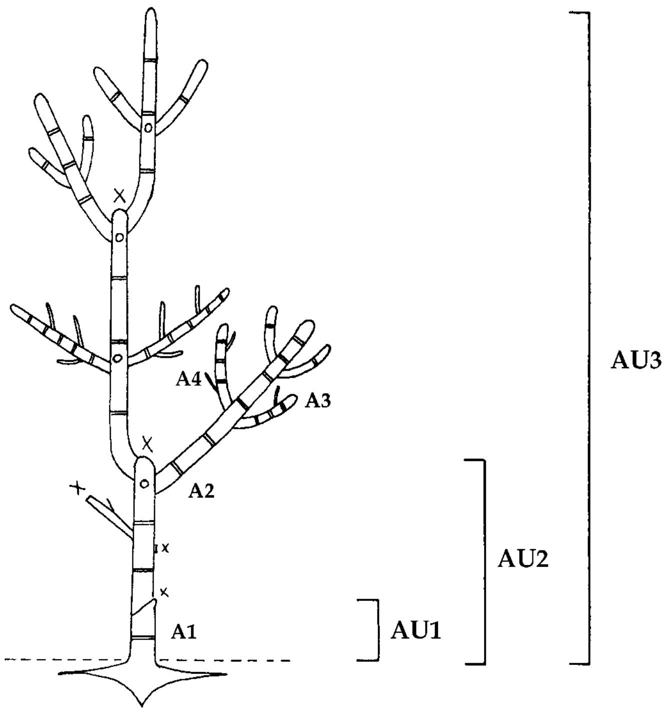


FIGURE 8. *Carya cordiformis* a) 6 year-old seedling, with monopodial growth, representing the first level architectural unit (AU1); b) 15 year-old (minimum) sapling, about 1.5 m high, whose main stem is the result of the stacking of 3 modules (or AU1); c) very young tree, about 5m high, whose hierarchic structure, with three categories of axes, represents the level 2 architectural unit (AU2); d) young tree, about 12 m high, whose hierarchic structure, with four categories of axes, represents the species' architectural unit (AU3); e) pre-mature tree, approximately 20 m high, showing one total reiterate (TR) of the architectural unit (AU3) and the preserved linearity of the trunk; f) mature tree, approximately 30 m high, showing a crown with a divaricate structure, made up of a succession of total reiterates; ╪boundaries of growth units; ×apex mortality; ❉ spiraled phyllotaxy; 2/5: phyllotaxic index; A*n* category *n* axis.



A1	A2	A3	A4
mixed linear sympodium	mixed divaricated sympodium	monopodium	monopodium
spiralled phyllotaxy	spiralled phyllotaxy	spiralled phyllotaxy	spiralled phyllotaxy
rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	rhythmic deferred acrotonic axile branching	unbranched short shoot
orthotropic	orthotropic	orthotropic	orthotropic
radial symmetry	radial symmetry	radial symmetry	radial symmetry
great thickness growth	slight thickness growth	very slight thickness growth	very slight or no thickness growth
indeterminate growth	long-term determinate growth	mid-term determinate growth	short-term determinate growth

FIGURE 9. Description of *Carya cordiformis* architectural unit (UA3). The schematic drawing illustrates the architecture of the young tree. For each category of axes (A1, A2, etc.), the main architectural characteristics are presented. ×: apex mortality.

AU1s succeed in linear fashion and form the A1 axis. During their succession, the AU1s acquire the potential to ramify laterally with axes differentiated from the main stem. The AU1s are acrotonic and produce lateral A2 axes at the level of their last growth units.

The third development phase consists of the integration of the AU1s in a structure with monopodial growth. At the end of AU1s, the apexes survive. The boundaries between AU1s can only be guessed at by the variability in the structure of the A2 axes and a rhythmicity in their arrangement, the longest branches suggesting the position of the boundaries between AU1s. In a parallel manner, A3 shoots are produced on the longest A2 axes. This completes the construction of a hierarchic structure with three categories of axes, described at the very young tree stage, and which is the level 2 architectural unit (AU2). The organization of the AU2 is in accordance with Rauh's model (Hallé, Oldeman & Tomlinson, 1978).

The fourth phase is the duplication of the AU2. The apex of the young trunk aborts and a fork is created from two subterminal buds. Each element of the fork reproduces the structure of the AU2. One becomes erect and takes over the relay of the trunk. The other droops slightly and becomes a branch with three categories of axes. The stacking of the AU2s leads to the erection of a hierarchic structure with four categories of axes, described for the young tree stage. It is the level 3 architectural unit (AU3), which is the species' characteristic architectural unit (Figures 8d and 9). Its organization is related to Koriba's model (Hallé, Oldeman & Tomlinson, 1978).

The fifth development phase consists of the duplication of the AU3. The death of the main stem's apex is followed by the creation of a fork, whose elements reproduce the structure of the young tree with its four categories of axes. One of the two elements is longer and it straightens up rapidly and takes the relay of the trunk. The other, which is smaller and more rapidly divaricated in its development, remains slightly to the side. At this stage, total reiteration is still not widespread in the crown; the total reiterates are sufficiently differentiated from one another that one gains dominance and produces a single trunk relay which continues height growth.

The sixth development phase occurs with the loss of differentiation between total reiterates and the persistence of a fork at the extremity of the trunk. The top of the tree assumes a mixed divaricated sympodium structure.

VARIATIONS

The first variation occurs in the phyllotaxy index. On all axes and at all stages of development, this index may vary from 3/8 to 2/5, sometimes changing several times along the same axis.

The second variation observed is the appearance and the persistence of forks in understory environments through the duplication of the AU1s. Occasionally at the end of a AU1, two subterminal axes are created and share dominance. A fork appears and is maintained until a differentiation between the elements occurs and allows the straightening up of one, which continues main stem growth, and sagging or death of the other.

Discussion

The nine tree species (this study; Millet, Bouchard & Édelin, 1998b; Millet & Ouellet, 1992) are somewhat similar when comparing the architecture and developmental pattern. All of the species studied have a structure composed of equivalent axes (*sensu* Oldeman, 1973); in the same species, the different axes are either all orthotropic or all plagiotropic. The development of the nine species, or at least a part of their development, is in accordance with either Rauh's or Troll's model (Hallé, Oldeman & Tomlinson, 1978):

(*i*) *Ulmus americana*, *Fagus grandifolia* and *Tsuga canadensis* : Troll's model;

(*ii*) *Tilia americana*: Troll's model, evolving toward Rauh's model;

(*iii*) *Betula populifolia*, *Populus tremuloides* and *Fraxinus americana*: Rauh's model;

(*iv*) *Carya cordiformis* and *Acer saccharum*: model related to Koriba's model with sub-units corresponding to Rauh's model.

These results are in agreement with the observations of Oldeman (1973), who recognized that trees of temperate regions had a high frequency of unspecialized models, with equivalent axes, particularly Rauh's and Troll's models. The low degree of differentiation among the axes is considered an element of "flexibility" of the structure, allowing a greater adaptability of the architecture of plants of temperate regions as opposed to plants of tropical regions (Oldeman, 1973).

In the nine species studied, the equivalence of axes is found in the phyllotaxy, the orientation of primary growth, the symmetry (although slightly different for some A2s) and branching pattern (axile in orthotropic species and bilateral in plagiotropic species). The nine species have deferred, rhythmic and acrotonic branching. Despite these similarities, some differences still occur. Table I summarizes the few differing elements brought out by the architectural analyses.

One difference is obviously that some species are orthotropic and others are plagiotropic (orientation of the A1 axis of the sapling, Table I). We have discussed separately the results of the analyses of the plagiotropic species (Millet, Bouchard & Édelin, 1998b), because of the particular influence of the axes' autodifferentiation potential on the growth strategy of species. Nevertheless, the plagiotropic or orthotropic character of the axes does not help in discriminating species according to their successional status. Orthotropic species and plagiotropic species are found equally at mid- and late succession. However, it is noteworthy that there are no early-successional plagiotropic species. Orthotropy has most often been associated with high light environments, and plagiotropy with shaded environments (Givnish, 1984; Fournier, 1979).

Another difference is the monopodial or sympodial growth pattern (Table I). Again, this characteristic does not discriminate between species according to their successional status. Monopodial and sympodial species occur equally during early and mid-succession. Édelin (1991) has suggested that the organization plan (hierarchic or polyarchic) may be more important than the growth pattern, monopodial or sympodial, in accounting for the architectural reality of a plant and its relationship with its environment. The hierarchy within a branched system is reflected in the differentiation between the trunk and the branches, and ensures the predominance of trunk growth over the spread of branches. All of the species studied have a sufficiently hierarchic development that they grow in height as typical trees. All of

TABLE I. Characteristics of the development pattern of nine tree species growing on mesic soils in southwestern Québec

Species	Successional status	Annual growth pattern	Phyllotaxy	Type of leaf	Orientation of the A1 of the sapling	Species' architectural unit	Growth pattern of the main stem	Total reiteration in the crown	Replacement of axes	Source
Tsuga canadensis (L.) Carr.	Late succession					A5				Millet, Bouchard & Édelin, 1998b
Fagus grandifolia Ehrh.	Late succession					A5			optional	Millet, Bouchard & Édelin, 1998b
Acer saccharum Marsh.	Late succession					A4				Millet & Ouellet, 1992
Carya cordiformis (Wang.) K. Koch	Mid-succession					A4				this study
Tilia americana L.	Mid-succession					A5				Millet, Bouchard & Édelin, 1998b
Fraxinus americana L.	Mid-succession					A4				this study
Ulmus americana L.	Mid-succession					A5				Millet, Bouchard & Édelin, 1998b
Populus tremuloides Michx	Early succession					A4				this study
Betula populifolia Marsh.	Early succession					A5				this study

monopodial growth, sympodial growth, spiralled phyllotaxy, alternate-distichous phyllotaxy, opposite-decussate phyllotaxy, needle, simple leaf, compound leaf, plagiotropic, orthotropic, A_4 or A_5 ultimate category axis, considering trunk as A1, and orthotropic trunk and branches, and plagiotropic distal extremity of the trunk and branches, and alternation of hierarchic and polyarchic development phases, and hierarchic development, few or no total reiteration in the crown, divaricate sympodium of total reiterates , deferred development of plagiotropic A2 branches.

the species are also capable of interrupting their hierarchic growth to erect a fork (polyarchic development) when growth conditions are too difficult. However, only a few species have as a characteristic of their developmental pattern the ability to alternate between hierarchic and polyarchic phases during trunk growth. The breaks in hierarchy along the trunk delineate the architectural units. The variable degree of hierarchy and integration among the units has allowed the detection of different organization levels (each level being represented by an architectural unit). A variable number of organization levels was identified in the studied species. The alternation of the organization plans during trunk growth, and the more or less pronounced reiteration potential in the crown are the two elements brought out in the analyses that are associated with the successional status of the species (Table I and Figure 10).

In early successional species (*Populus tremuloides* and *Betula populifolia*), a hierarchic organization plan is maintained throughout ontogenesis: only one, very hierarchic level of organization is present. The aspen is a monopodium and the birch is a sympodium with a hierarchic development similar to that of a monopodium. The uninterrupted hierarchy of development is similar to that of a monopodium. The uninterrupted hierarchy of development promotes the rapid growth of the trunk. The life cycle of the tree is completed with the erection of a single architectural unit (Figure 10). Total reiteration is virtually non-existent. Both species have a growth strategy based on efficiency and height growth.

The mid-successional species (*Ulmus americana, Fraxinus americana, Tilia americana* and *Carya cordiformis)* are characterized by a hierarchic development of the young tree and a reiteration potential in the crown. For the majority of these species (Table I and Figure 10), there is only one organization level, which is very hierarchic, and made up of a single architectural unit (*Fraxinus americana*) or with a progressive integration of the AU1s within an AU2 which becomes hierarchic (*Ulmus americana* and *Tilia americana*). The ash is a monopodium. Elm and basswood are sympodia whose development becomes hierarchic and similar to that of a monopodium (Millet, Bouchard & Édelin, 1998b). The hickory is different. It has several levels of organization that segregate it from the other species (Figure 9). Nevertheless, its growth is more hierarchic than that of late successional species and its successional status remains unchallenged (see discussion later on about the difference between *Acer saccharum* and *Carya cordiformis*). The great development hierarchy displayed by mid-successional species promotes rapid trunk growth. However, in contrast to the early successional species, they have characters that may lend a greater shade tolerance during the first

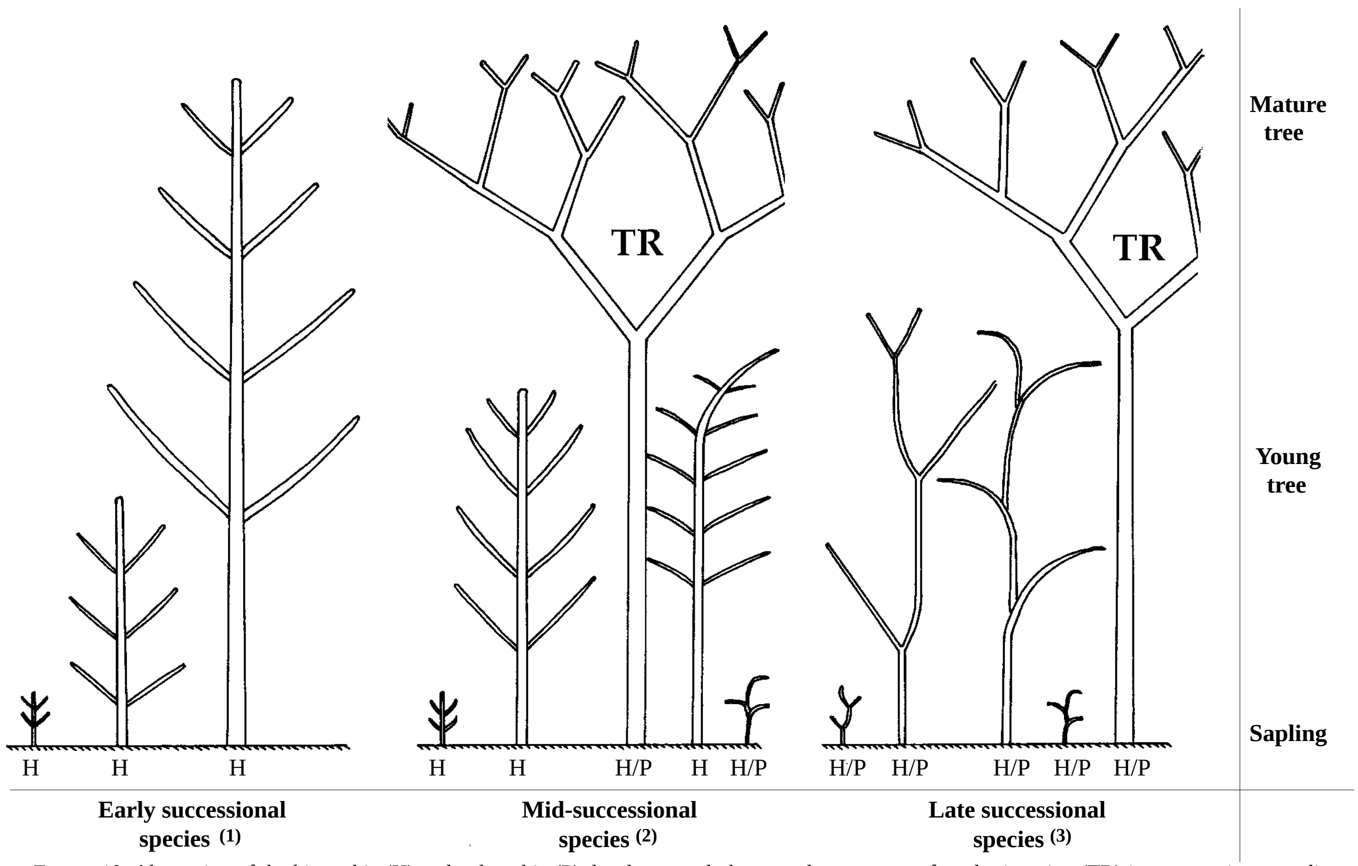


FIGURE 10. Alternation of the hierarchic (H) and polyarchic (P) developmental phases and occurrence of total reiteration (TR) in tree species according to their successional status. H/P: alternation of the two phases, (1) *Betula populifolia* and *Populus tremuloides;* (2) *Ulmus americana, Fraxinus americana* and *Tilia americana* (Millet, Bouchard & Édelin, 1998b)*. Carya cordiformis* is an exception because it has an alternation of phases H and P throughout its development, but see discussion on the hierarchy of its development; (3) *Acer saccharum, Fagus grandifolia* and *Tsuga canadensis* (Millet & Ouellet, 1992; Millet, Bouchard & Édelin, 1998b). Hemlock does not have TR at the extremity of the trunk, but it has a mechanism for replacing its axes (partial reiteration) and a possibility of total reiteration in its branches.

stages of growth: plagiotropic axes in basswood and elm, and large compound leaves in ash and hickory. Plagiotropy of axes, including the main axis, allows a lateral spread of the foliage without compromising the hierarchy of the system. The secondary straightening up of the main stem ensures the efficiency of height growth (Millet, Bouchard & Édelin, 1998b). The large compound leaves also allow for widespread foliage, while using less energy than would be required for branches (Givnish, 1978). The energy can then be expended on height growth of the main axis (Givnish, 1978). Finally, the total reiteration of the architectural unit is associated with the long lifespan of the tree and prolongs the flowering period. Total reiteration promotes the lateral spread of the crown and increases the competitive ability of the species. The four mid-successional species thus benefit from a growth strategy based on rapid trunk growth, with a certain shade tolerance, and a spreading crown.

In late-successional species like *Acer saccharum, Fagus grandifolia* and *Tsuga canadensis,* two to three organization levels are observed in the structure of the young tree, as well as reiteration in the crown (Figure 10). The alternation of hierarchic and polyarchic development phases during trunk growth is an endogenous characteristic of the development of these species. It promotes greater shape plasticity, and regularly allows greater lateral spread of the foliage to the detriment of rapid height growth. Height growth is less favoured, but the adaptation to variable growth conditions and to low light conditions is greater. The erection of the species' characteristic architectural unit is followed by reiteration that allows for longer lifespan of the individuals. The three late-successional species have a growth strategy based on shape plasticity, shade tolerance and a long lifespan. For maple and beech, total reiteration in the crown promotes lateral spread and increases the species' competitive abilities. For hemlock, partial reiteration ensures the renewal of a structure able to maintain itself under conditions of deep shade.

A closer look at the developmental pattern of late-successional species and bitternut hickory reveals two distinct growth strategies that are based on the orthotropic or plagiotropic character of the axes, and whose influence on the ecology of the species seems significant. For species with a hierarchic development (*Betula populifolia, Populus tremuloides, Ulmus americana, Fraxinus americana,* and *Tilia americana*), the orthotropic or plagiotropic character of the axes does not change the fact that apical dominance is always made to promote trunk growth (Millet, Bouchard & Édelin, 1998b). Trees whose plagiotropic axes straighten up secondarily are comparable to tree whose axes are orthotropic. However, for species with several levels of organization (*Carya cordiformis, Acer saccharum, Fagus grandifolia* and *Tsuga canadensis*), depending on the orthotropy or plagiotropy of the axes, apical dominance is regularly either shared between the two elements of a fork ,or transferred from one module to the next. The major difference between these two situations pertains to their influence on trunk growth dynamics.

In orthotropic species like *Acer saccharum* and *Carya cordiformis*, the polyarchic developmental phase that occurs between two AU1s or two AU2s is characterized by the creation of a fork. The future trunk relay initially shares apical dominance with one or several other axes before dominating. Although the fork may represent a shape adaptation to particular growth conditions, it is generally only a temporary solution because with its occurrence, the differentiation of a single trunk is compromised. The fork must be resorbed by the straightening up of one of its elements for successful resumption of trunk growth to occur. If the fork persists for too long, in extreme shade conditions for example, the resumption of trunk growth may be compromised. Both hickory and maple then take advantage of increased light from canopy gaps to reinstate hierarchic orthotropic growth, and thus produce efficient trunk growth. In short, apical dominance always benefits totally or in part to the development of the trunk relays, which confers an advantage for height growth. However, the adjustment of the shape to extreme conditions of shade most often implies the creation of forks that prevent main stem differentiation, at least temporarily.

For plagiotropic species like *Fagus grandifolia* and *Tsuga canadensis*, the polyarchic development phase occurring between two modules results in the transfer of apical dominance between these two modules. This transfer does not necessarily imply the creation of a fork and the loss of the differentiation between the main stem and the branches. The latent form, under extreme shade conditions, has a very slow height growth but its main stem may remain linear and well differentiated. Its plagiotropic extremity can persist in this position for long periods of time, while still benefiting from apical dominance in its development. However, the top is not required to straighten up in order for main stem growth to resume. The de-differentiation potential of the axes (Millet, Bouchard & Édelin, 1998b) gives the tree structure great flexibility that facilitates the alternation of two functions: lateral development and height development. Apical dominance can alternately contribute to both functions without compromising the global hierarchy of the system. Apical dominance may thus contribute to the development of a terminal axis that may later on assume the role of a branch, before it is transferred to the next module (Millet, Bouchard & Édelin, 1998b). The adjustment of the shape to conditions of extreme shade, by means of an increase in the persistence of plagiotropy of the top and the successive stacking of modules, provides a permanent structure that does not hinder trunk differentiation. However, height growth is less efficient in these species than in orthotropic species, but shade tolerance is increased.

This interpretation supports the conclusions of Canham (1988) that beech (*Fagus grandifolia*) is best adapted to stable conditions of shade and that sugar maple (*Acer saccharum*) is best adapted to more variable conditions, and has a development that is stimulated by light in canopy gaps. Canham (1988) reached these conclusions by studying quantitative development characters such as growth rate of axes and leaf area index, and by comparing the differences for each species in relation to environmental conditions. Our analysis allows us to relate these two strategies to the architectural and developmental characteristics of the two species, and to suggest that eastern hemlock is similar to beech, as bitternut hickory is similar to sugar maple. The four species can be ranked according to their shade tolerance and efficiency of their height growth in canopy gaps from the most shade intolerant to the most shade tolerant: *Carya cordiformis, Acer saccharum, Fagus grandifolia, Tsuga canadensis.*

The ranking of the species according to their successional status (Bergeron, Bouchard & Leduc, 1988; Brisson, Bergeron & Bouchard, 1988; Domon *et al.*, 1986; Doyon, Bouchard & Gagnon, 1998) usually separates bitternut hickory from the three other species. The study of the alternation of organization plans and of reiteration does not allow a clear separation between bitternut hickory and sugar maple. Nevertheless, field observations reveal a greater hierarchy in the architecture of bitternut hickory. Compared to sugar maple, its branches are generally shorter, more rapidly divaricated and are rapidly self-thinned. It is difficult to observe several consecutive A3 axes along an A2 axis, and even more difficult to observe several consecutive A4 axes along an A3 axis. The development of the trunk is clearly favoured over the development and maintenance of branches. Perhaps the use of quantitative methods of describing the architecture of the two species would identify the difference between them. For now however, it is most interesting to note that sugar maple's growth strategy is more similar to that of bitternut hickory than it is to that of beech or hemlock.

Conclusion

Our study shows the existence of a functional link between the architecture of nine tree species and their successional status in the temperate deciduous forests of southwestern Québec. Species that have an higher frequency of alternations of the organization plans of their structure (hierarchic and polyarchic) are those that are the most shade tolerant and the most dominant in the late stages of forest succession. Conversely, the species with the most hierarchic development dominate the sites receiving most light in the early stages of succession.

This rule is valid for the species we studied on mesic soils in a temperate deciduous forest. Other studies are necessary to determine whether it could be applied in other situations. Previous works by Oldeman (1990) and Vester (1997) under other ecological conditions support this interpretation. However, to adequately understand successional dynamics, the important thing is not to assign certain characteristics to the successional status of species, but rather to compare the architecture of the species occurring in a chosen environment. This study showed that the degree to which architectural units are integrated within the structure of a tree is one of the important elements of successional dynamics.

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