10

Architecture of the New Caledonian species of Araucaria

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The genus *Araucaria* contains species that can be assigned to two of Hallé & Oldeman's (1970) architectural models. Massart's model is represented by *A. heterophylla* (native to Norfolk Island) and Rauh's model by *A. araucana* (native to Chile). Thirteen species of the genus (Table 10.1) are endemic to New Caledonia (Laubenfels, 1972), making the island the richest center for its study (Veillon, 1976).

Ecology and habit

The New Caledonian species grow on ultrabasic schistose and calcareous soils; 10 are restricted precisely to ultrabasic soils. One species, *A. montana,* grows in open vegetation on the ultrabasic and schistose soils of Grand Terre. Another species, *A. columnaris,* grows on calcareous soils in open vegetation. *A. schmidii* is a rain forest species on serito-schistose soils, restricted to Mount Panié in the northeast. This gives some indication of the range of habitat diversity.

When young, all species are typically cone-shaped (Guillaumin, 1950), but adult trees differ according to two main patterns: (1) the shape becomes round, as in *A. luxurians, A. muelleri, A. nemorosa,* and *A. rulei;* or (2) the shape becomes characteristically columnar, as in *A. bernieri, A. columnaris, A. schmidii,* and *A. subulata*. These differences can be partly explained by their architecture, which is largely determined by the short life span of self-pruning branch complexes.

Architecture

Vegetative parts

All species are alike in that they have an orthotropic trunk with indefinite, rhythmic growth and spiral phyllotaxy (Figs. 10.1–10.4). First-order branches are pseudoverticillate (Figs. 10.15,

Fig. 10.1. *Araucaria bernieri* (Massart's model). *A*. Young tree, about 14 m high, illustrating conical form. *B*. Adult tree, about 30 m high, with three successive generations of branches, producing three nesting crowns. *C*. Detail showing position of second-generation, partially reiterated model, represented by plagiotropic branch, at base of first-generation branch axis. *D*. Detail of plagiotropic branch representing third-generation plagiotropic branch, at base of first-generation branch axis. *E*. Second-order axis end-on, showing acute dihedral arrangement of third-order axes. *F*. Basal pseudowhorl of seven axes, seen from above.

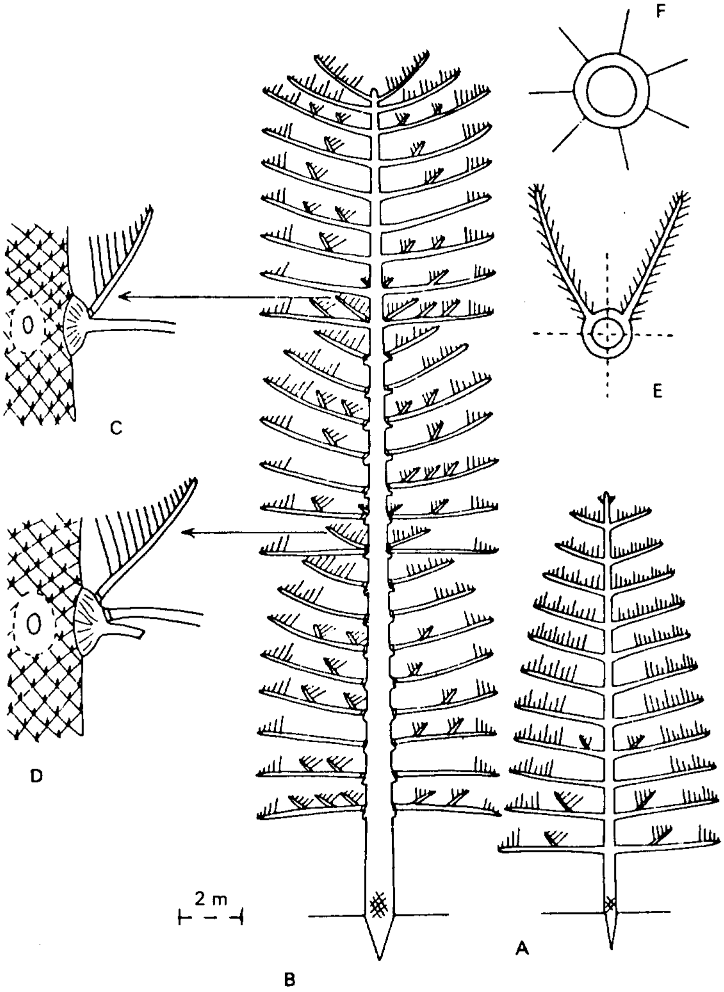
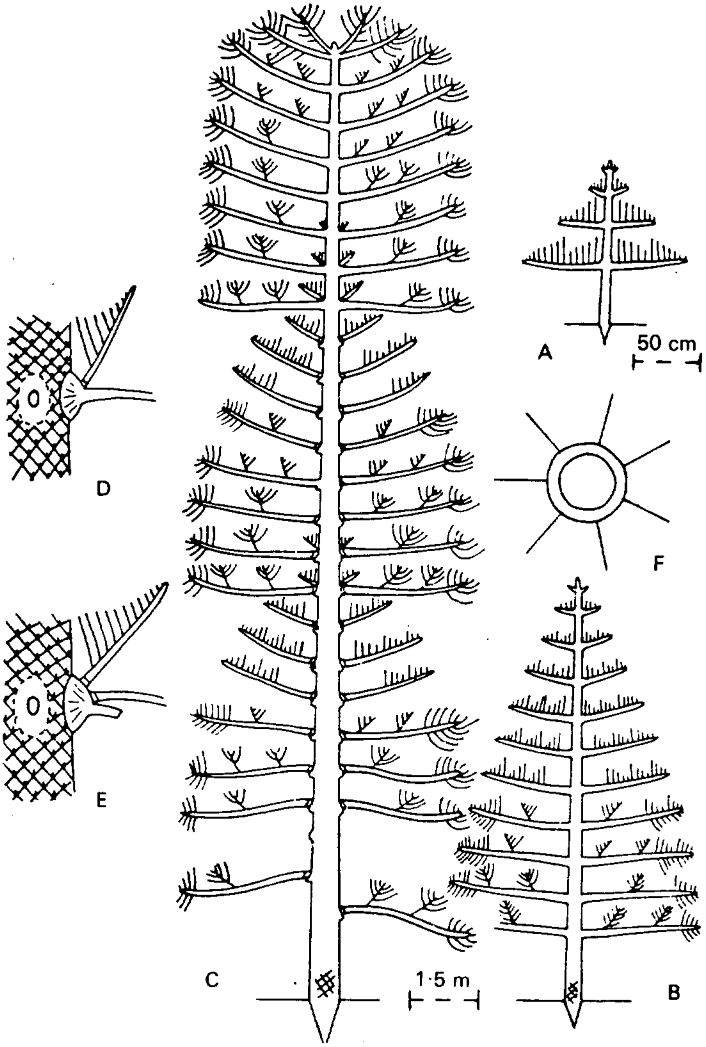
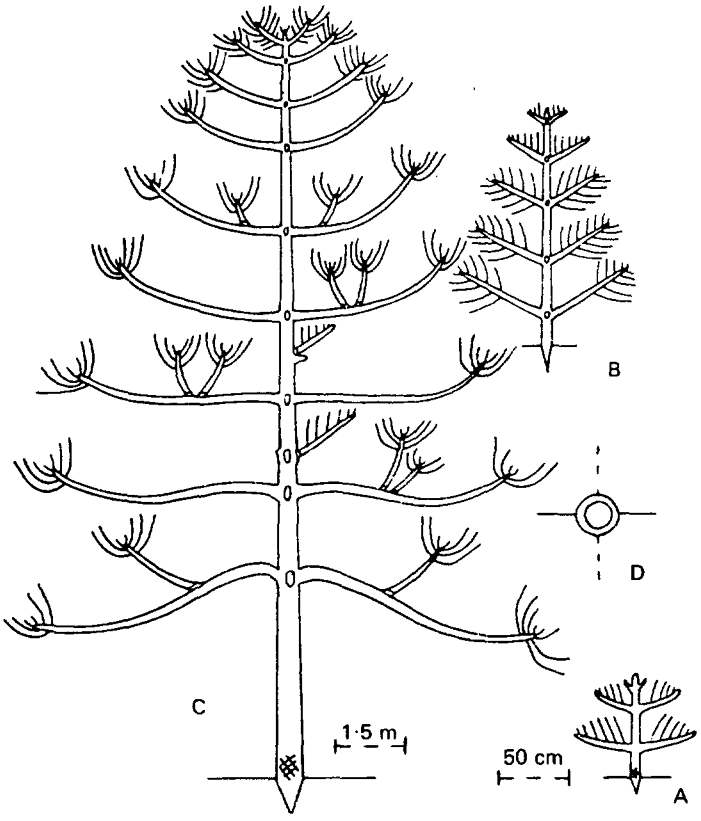


Fig. 10.2. *Araucaria columnaris* (Massart's model). *A*. Young sapling, 1 m high, establishing conical form. *B*. Young sterile tree, 15 m high, with some incomplete reiteration of older branches. *C*. Adult tree, 20 m high, with three successive nesting crowns. *D*. Detail showing position of second-generation axis (partial reiteration). *E*. Detail showing position of third-generation axis (further partial reiteration). *F*. Pseudowhorl of seven axes at base of trunk, seen from above.



10.3*D*). Depending on branch orientation, two groups can be recognized, corresponding to the architectural models mentioned above. The adult trees of the first group have plagiotropic branches, corresponding to Massart's model (Table 10.1). Examples are illustrated in Fig. 10.1*A*,*B* (*A. bernieri*) and Fig. 10.2*A*–*C* (*A. columnaris.*). Adult trees of the second group have orthotropic branches, corresponding to Rauh's model. Examples are illustrated in Fig. 10.4*B* (*A. biramulata*). The distinctive feature of these species is the distal erection of the apex of the branch, revealing the essentially orthotropic nature of the branch meristem. This feature is also shown by the non-New Caledonian species *A. araucana, A. hunsteinii,* and *A. imbricata*. The

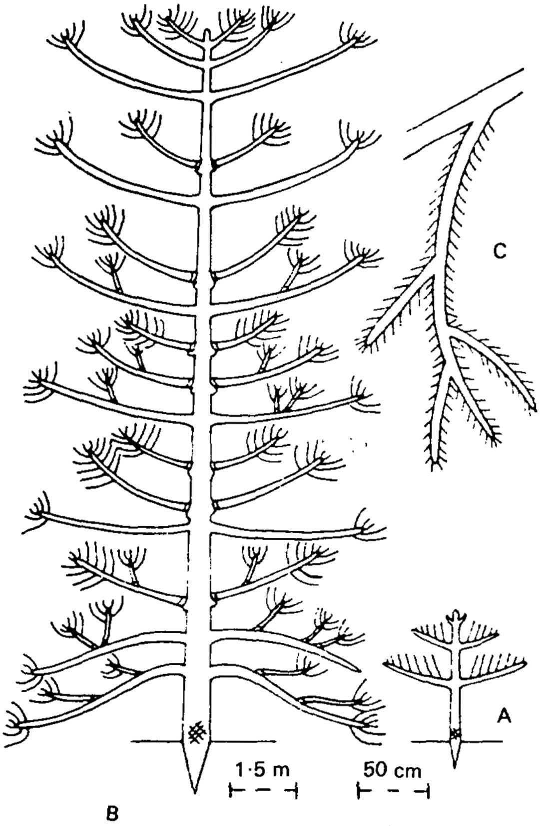
Fig. 10.3. *Araucaria rulei* (Rauh's model). *A*. Sapling, 60 cm high, with horizontal branches. *B*. Young tree, about 4 m high, with branches now more or less orthotropic. C. Adult tree, about 22 m high, with some partial reiteration along first generation of branches. *D*. Trunk axis viewed from above, showing pseudowhorl of four branches.



distal orthotropic orientation of the branch may appear only late in the development of the tree so that the sapling may closely resemble an example of Massart's model (e.g., Fig. 10.3*A*).

The ultimate (usually third-order) axes of the branch system, called "ramuli" (singular: ramulus), are characterized by determinate growth in length and diameter and are the predominant organs of photosynthesis. Some of them also bear reproductive organs. Depending on the species, ramuli on adult trees are arranged in two contrasting ways independent of the universal spiral phyllotaxis. In the first group, the ramuli have a dihedral arrangement (Fig. 10.1*E*), with the branch units in two lateral series, somewhat or markedly above the horizontal. Examples include *A. bernieri, A. humboldtensis, A. schmidii, A. scopulorum,* and *A. subulata* – all belonging to Mas-

Fig. 10.4. *Araucaria biramulata* (Rauh's model). *A*. Young plant, 1 m high. *B*. Adult tree, 22 m high, with successive nesting crowns. *C*. Detail of branched ramulus.



sart's model. The other group retains a spiral arrangement of ramuli in the adult phase, emphasizing the orthotropic condition (Figs. 10.3, 10.4), and includes all species listed in Table 10.1 as belonging to Rauh's model, both the exotic and New Caledonian species.

Sexuality

All New Caledonian species are monoecious; the cones are borne terminally on ramuli (Fig. 10.5). Female cones are at the ends of short ramuli, always in the top of the tree, corresponding to the apical zone of branches (Fig. 10.5*A*,*B*). Apparently the tree always produces female cones first; this has been confirmed on several specimens of *A. columnaris* about 18 years old. Male cones are produced by ramuli of varying ages, but always in the central and basal parts of the tree (Fig. 10.5*A*). The cones appear abruptly over a large part of the tree, with a distinct articulate attachment at which the cone is abscissed after the pollen is shed (Fig. 10.5*C*). The same ramulus continues as a photosynthetic organ by virtue of sympodial extension (Fig. 10.5*D*), but this growth is ultimately limited. The tree can be

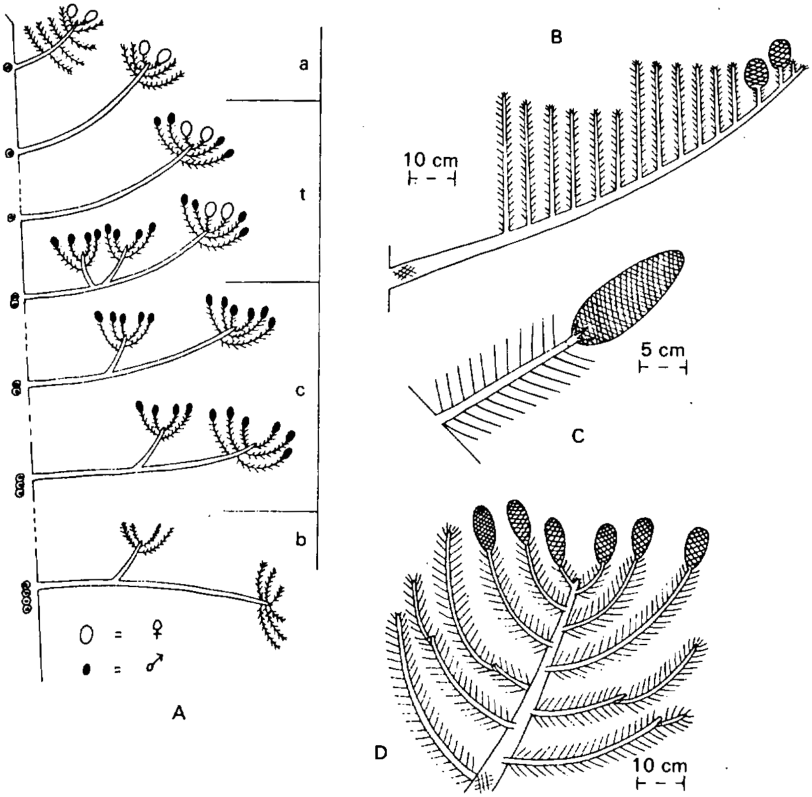
Table 10.1. *Architecture of* Araucaria *species referred to in text*[a]

Species	Model
A. araucana (Molina) Koch	Rauh
A. bernieri Buchholz	Massart
A. biramulata Buchholz	Rauh
A. columnaris (Forster) Hooker	Massart
A. heterophylla (Salisb.) Franco (=*A. excelsa* [Lamb.] R. Br.)	Massart
A. hunsteinii K. Schum.	Rauh
A. humboldtensis Buchholz	Massart
A. ~~*imbricata* Pav~~ angustifolia (Bert.) O. Ktze	Rauh
A. laubenfelsii Corbesson	Rauh
A. luxurians (Brongn. & Gris) Laubenfels	Massart
A. montana Brongn. & Gris	Rauh
A. muelleri (Carr.) Brongn. & Gris	Rauh
A. nemorosa Laubenfels	Massart
A. rulei Müll.	Rauh
A. schmidii Laubenfels	Masart
A. scopulorum Laubenfels	Massart
A. subulata Vieill.	Massart

[a] All are endemic to New Caledonia, except *A. araucana* (South America), *A. heterophylla* (Norfolk Island), *A. hunsteinii* (New Guinea), and *A.* ~~*imbricata*~~ angustifolia (South America).

divided into four distinct zones according to the distribution of male and female cones (Fig. 10.5*A*). The distal part (*a*) bears exclusively female cones; there is a transition zone (*t*) with branches bearing both kinds of cones; the central zone (*c*) bears exclusively male cones; and the basal zone (*b*) is sterile and consists of axes that either never were sexual or have lost this capability with age. There appears to be sexual specialization of branches, because male branches can never bear female cones, and vice versa.

Fig. 10.5. Sexuality in *Araucaria*. For detailed explanation, see text. *A*. Schematic representation of position of cones on tree. Areas *a*, *t*, *c*, and *b* correspond to following zones: apical (exclusively female); transitional (mixed male and female); central (exclusively male); basal (sterile). *B*. Position of female cones on lateral branch complex. *C*. Position of male cone on ramulus. *D*. Position of male cones on distal part of lateral branch complex, older branches showing sympodial growth.



Root system

Limited observations on the architecture of the root system in *Araucaria* have been made on *A. rulei* in ultrabasic soils and *A. columnaris* in calcareous soils. Young trees show a pseudowhorl of four or five major horizontal roots, arising on the collar of the taproot, about 30 cm below the soil surface. A second pseudowhorl becomes visible about 1 m below the first; this suggests rhythmic growth of the roots, although this has not been verified. The architecture of the root system remains the same in adult trees, but reiteration becomes evident in the form of additional sinkers or strongly developed vertical roots arising anywhere on the horizontal roots of the two pseudowhorled sets. They thus resemble parallel taproots.

Modification of the model

Two important modifications occur in architecture as the tree matures; both affect its shape. One is reiteration; the other is the production of successive crowns.

Reiteration

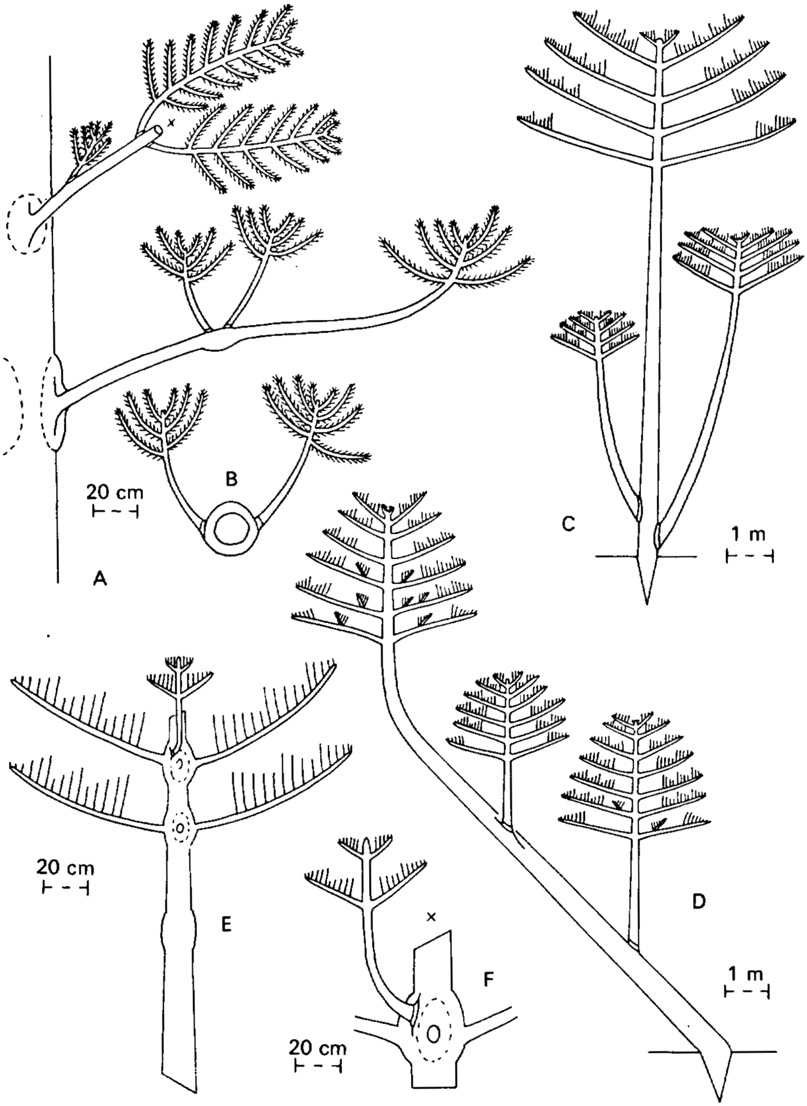
This process is essentially as defined by Oldeman (1974) and is always the result of damage to the tree (traumatization). Its features are illustrated in Fig. 10.6. Reiteration may be partial, when only part of the original model is repeated, or complete, when the whole model is repeated, except for the roots. Partial reiteration is illustrated in *A. rulei* in Fig. 10.6*A*. When the apex of a first-order branch is removed, new second-order branches are produced. These are orthotropic, as illustrated in Fig. 10.6*B*, which shows the branch end-on. This orthotropy reflects the nature of the branch system in Rauh's model. Complete reiteration may take place by the formation of new basal trunk axes, as is shown for *A. humboltensis* in Fig. 10.6*C*. An alternative method for reiteration of further models is by the epicormic stimulus for the development of previously dormant meristems on the upper surface of leaning trunks, as shown for *A. bernieri* in Fig. 10.6*D*. Distal, complete reiteration may also be induced if the leader is broken, as shown for *A. bernieri* in Fig. 10.6*EF*. The meristem involved originates from the base of one branch of the pseudowhorl closest to the break, but details are not known.

One exceptional species shows no reiteration. This is *A. muelleri*, which has very long branches (up to 4 m) that become flexuous with age. It always grows in strict conformity with the model.

Successive nesting crowns

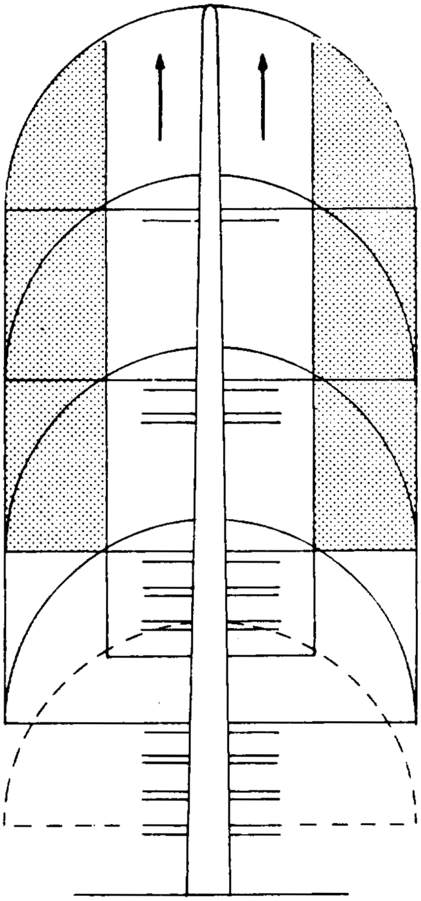
Some species of *Araucaria* are distinguished by successive crowns that encase each other, like nests of tables; they have been described as having "nesting crowns" (Fig. 10.7). After the first gen-

Fig. 10.6. Various methods of reiteration in *Araucaria*. *A*. Partial reiteration of axes on adult branch complex of *A. rulei*, cut off at X (upper branch); normal appearance (lower branch). *B*. Pseudo-whorled insertion of partially reiterated branches of *A. rulei*, seen end on. *C*. Complete basal reiteration in *A. humboldtensis*. *D*. Complete reiteration on leaning trunk in *A. bernieri*. *E*. Complete reiteration after apical damage in *A. bernieri*. *F*. Detail showing site of origin of renewal axis below broken leader in *A. bernieri*.



eration of branches is produced, they are lost by self-pruning but succeeded by several later branch generations arising from the original sites of branch insertion. As this involves production of new plagiotropic branches, partial reiteration of the model occurs. An example is provided in Fig. 10.1, for *A. bernieri.* Figure 10.1*A* shows a young tree, 14 m high, with the typical conical shape, representing the model precisely. Figure 10.1*B* shows an adult, 30 m high, with three generations of second-order axes, representing partial reiteration. The effect is that of a tree with three superposed crowns. Figure 10.1C shows a detail of the insertion of a reiterated plagiotropic axis, which originates at the base of a second-order axis of the first generation. Figure 10.1*D* shows the same process at a lower level, which

Fig. 10.7. Spatial distribution of male and female cones in *Araucaria.* For explanation, see text.



results in a third-generation axis, but again from the base of a second-order axis of the first generation and again a partial reiteration of the model.

The same features are shown for an adult *A. columnaris* (Fig. 10.2C) with an overall height of 21 m bearing three nesting crowns, representing three generations of second-order branches. All but three New Caledonian species listed in Table 10.1 develop nesting crowns; the exceptions are *A. humboldtensis*, *A. muelleri*, and *A. rulei*.

The development of nesting crowns has an influence on the distribution of cones in the developing tree, determined by the principles of sexuality established earlier. This is explained diagrammatically in Fig. 10.7. The central area delimited by the rectangle represents the spatial distribution of female cones on the tree; the shaded areas represent the region that bears male cones. Only the first-generation branches bear female cones, which are consequently restricted to the summit of the tree (the youngest crown). However, as the basal branches of successive crowns of all generations bear male cones, a much larger part of the tree is male. The oldest branches (in this diagram, the fourth generation) remain sterile. The shaded outline represents the former position of the most recently pruned crown.

Conclusion

The above brief description illustrates how tree form in *Araucaria* is determined by trunk-branch differentiation established by the architectural model the tree exhibits. It is conditioned by self-pruning. The addition of the reiterative process in the advent of further branching is readily recognized in this genus because of the very high level of model conformity and symmetry, the determinate nature of branches, and the precise process of abscission. The influence of these habit features on sexuality is precisely expressed. *Araucaria* thus supplies a model system for appreciating the preciseness of tree organization and the processes involved and lends itself to more detailed analysis and experimentation.

General discussion

Givnish: I was interested by your slides showing different species of *Araucaria* having differently shaped tree crowns: some cylindric, some rounded or cone-shaped, and others parasol or umbrella-shaped. Could you say more about the ecologic distribution or restriction of species with different crown shapes?

Veillon: As yet there is no clearly known relation between ecologic distribution and different crown shapes. Many species have a columnar shape and when they grow older become quite flat-topped. This is so regular a phenomenon that it is probably genetic rather than a reaction to ecologic conditions. The same applies to other forms of crowns. The conical or parasol-like forms are very regular. Of course, there is always an adjustment, but this would be a long-term evolutionary adjustment rather than an adjustment during the life of the tree.

Ashton: Do I understand that *Araucaria columnaris*, looking rather like the young foxtail pine trees that refuse to branch, eventually becomes flat-topped because of its genetic makeup?

Veillon: Yes, certainly, because the tabletop crown is a senescence characteristic.

Ashton: The reason I ask is because one got the impression in this species that the individual trees were spatially separate from one another, not growing in dense stands as one would expect from trees of such columnar shape. Do they maintain this isolation and columnar shape throughout the sexual stages of their life cycle and until they become senile, in contrast with most conifers? If male cones are all borne at the bottom of the column and the female cones at the top, pollination would be difficult in a dense stand. This is an unusual and interesting tree shape which may have some interest for Dr. Doyle. Could the spaces between the individuals of some such gymnosperm of the past have provided a cradle for angiosperm evolution?

Veillon: There are two species with exactly the same growth habit: *Araucaria columnaris*, which grows on isolated islands in monospecific populations, and *Araucaria bernieri*, which occurs in the rain forest.

Longman: This distribution of male and female cones, the female cones toward the top and the tips of the branches and the male in more proximal positions, is very common in temperate conifers of the Pinaceae, Cupressaceae, and other families. It is interesting to see that in the tropical Araucariaceae the monoecious habit is the same. I wonder whether this is a mechanism that tends to reduce selfing in these wind-pollinated trees.

Veillon: In large populations one may find two or three exceptions where the male sexuality covers the whole tree, but this does not seem to be correlated with the environment of New Caledonia.

Longman: It also sometimes occurs in *Pinus*.

Nozeran: The information given by Dr. Veillon can be complemented by information on the genus *Phyllanthus*. In different sections of this genus the distribution of male and female organs differs. For instance, in the group of which *Phyllanthus niruri* L. is an example, the male flowers appear first and subsequently at the end of the branches the female flowers, just as in *Araucaria*. The reverse is true for *Phyllanthus urinaria* L. and related species. In yet another species (*Phyllanthus amarus* Schum. & Thonn.) both kinds of flowers are mixed. The position of the flowers is linked to a whole complex of correlated phenomena in which the leaves probably play a particular role. The morphogenesis of *Araucaria* could be determined in the same way (i.e., by endogenous mechanisms).

Fisher: Is there a direct relation between the position of the nesting crown and the original periodicity of the leader apex? In other words, is there a correlation between the growth of the leader and the later development of nesting crowns?

Veillon: There is a variation among individuals of the same species in which the trunk growth pattern cannot be distinguished, some of them show nesting crowns and others a simple crown.

Whitmore: Are there other trees that have nesting crowns like these New Caledonian araucarias or is this something unique to New Caledonia and to *Araucaria?*

Veillon: Araucaria hunsteinii of New Guinea seems to make nesting crowns too, but not *A. cunninghamiana.*

Hartshorn: In the illustrations that accompany the key to the architectural models we see that the above-ground parts are much more complex and explicit than the below-ground parts, yet Dr. Veillon showed some slides of some interesting features of root systems in some *Araucaria* species and I would like to ask him if he knows about, or would speculate on, the relation between the above- and below-ground parts.

Veillon: The subterranean structures have been checked on two species and a total of less than 10 specimens.

Oldeman: It would be interesting to know if there is a correlation between aerial reiteration of the model and subterranean reiteration. If a new trunk is formed in the crown, does a new taproot grow below? The same model is always realized, so it would be nice if there was an underground part accompanying it.

Borchert: From Dr. Hallé's work (on rubber) and work on shoot growth in oak, it is clear that shoot growth rhythmicity is not necessarily accompanied by rhythms of root growth. In *Citrus* there are data showing that periods of root and shoot growth alternate (Marloth, 1949), so there cannot be the straightforward correlation implicit in this speculation of corresponding architectural models. Furthermore, root development is restricted by the physical nature of the soil (see Chap. 21).

Hallé: Yes, even in *Araucaria* there is a large number of tiers on the trunk, but there are just two tiers of lateral roots on the taproot. So the rhythm itself is quite different, and in some cases there is no rhythm at all in the taproot (e.g., in rubber).

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