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Original article

Three gradients in the architecture of trees

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Abstract – An earlier paper by the same author set out a symbolic notation for tree architecture designed to codify the Hallé-Oldeman tree models. This was used to construct a number of rules of tree architecture with the aim of discovering the limits of tree architectures. The present paper continues this search with six more rules. Applying the rules reveals eight new models or extensions of existing models which probably do not exist. Ten of the rules are combined to suggest three gradients, directions in which differences between trunk and branch axes can occur. There are gradients in in determinacy and tropy of trunk and branch axes and in the modes by which trunk axes relay, branch axes are attached and branch axes relay.

tree / architecture / model / rule / gradient

Résumé – Trois tendances dans l'architecture des arbres. Un article antérieur par le même auteur a proposé une notation symbolique pour l'architecture des arbres, conçue pour codifier les modèles Hallé-Oldeman des arbres. Cette notation a été utilisée pour découvrir les limites des architectures des arbres. Ici nous continuons cette recherche avec six règles de plus. En appliquant les règles nous découvrons huit modèles nouveaux ou extensions des modèles existants qui probablement n'existent pas. Nous combinons dix des règles de façon à obtenir trois tendances, directions dans lesquelles peuvent se présenter les différences dans la détermination et le tropisme entre les modules du tronc et des branches, et aussi les différences entre les modes de relais des modules de tronc, d'attachement des branches et de relais des modules des branches.

arbre / architecture / modèle / règle / gradient

1. INTRODUCTION

The architecture of trees can be approached from many viewpoints, according to the features of trees which are of greatest importance to the investigator. One approach is that set out in Hallé and Oldeman [4] but refined and made more widely known in Hallé, Oldeman and Tomlinson [5]. The basis of this classification is the combination of meristematic units (axes) which make up the trunk and main branches. The axes themselves are classified in terms of determinacy (determinate, indeterminate) and tropy (orthotropic, plagiotropic, orthoplagiotropic). Axes may spring from other axes terminally, continuously or diffusely, dichotomously, rhythmically, zonally or, in the case of trunk axes, basally or underground. The authors found that there were 23 standard combinations of these features among existing trees, which they set out as models and assigned to each the name of an eminent botanist who had some connection with the recognition of the model or the description of trees exhibiting that model of growth. Actual trees did not always conform precisely to these models, growth always being liable to be modified by environmental or accidental factors.

This system of architecture received wide acceptance, the system as a whole being attacked only by Guédès

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[3], who proposed an alternative scheme. There were a few suggestions of further models to accommodate fossil trees (Beck's Model, Trivett [8]) and Gay [2] for the fern *Lomogramma guianensis*. Philipson and Molloy [6] described two members of the family Araliaceae which did not seem to conform to any of the models, but proposed no new models. Cremers and Edelin [1] were unconvinced by the argument which separated off Tomlinson's Model since it is the only case where basal production of trunks is used to distinguish models. They proposed its deletion and the assignment of its members to Holttum's or Corner's Model.

In [7] I attempted a symbolic classification of tree architectures which would be as close as I could devise to the Hallé-Oldeman system, and would enable us to ask what other structural possibilities there were and why they did not happen. The method was to represent each model by a string of symbols which represented the determinacy and tropy of trunk axes and branch axes and their methods of attachment. It proved impossible to make an exact matching between the strings and the 23 models; some models were represented by alternative strings and others were distinguished from one another by features which I had not built into my description.

The framework gave rise to about 2000 possible architectural strings. These were scanned to find patterns that did not correspond to any of the 23 models and thus to identify a number of rules of combination. Nine general rules, four trunk rules, two branch rules and ten attachment rules, specific to the attachment of branches to the trunk, were found. Some of these rules were logically necessary, some codified what appeared to be the case, but had no obvious basis in necessity. Others lay between these extremes. Even after excluding the structures which violated one or more of these rules, there were many structures expressible that could not be described as equivalents of the Hallé-Oldeman models. This failure to exclude everything but the Hallé-Oldeman models left the research in a somewhat unsatisfactory state. The notation was also put forward as valuable in its own right as a framework within which trees could be recorded without preconceptions as to the existence of models.

The present investigation began as an attempt to eliminate all strings which do not correspond to Hallé-Oldeman models in order to complete the deduction of a set of suggested constraints on tree growth, in the expectation that this might shed some light on the nature or organisation of trees, and possibly of plant growth in general. Six more rules were obtained, as given below. However, the collection has become unwieldy and we turn to alternative ways of expressing the constraints. One of these ways is through three gradients, consistent directions in which changes, in determinacy, tropy and attachment and relaying, take place as we move from tree trunk to branches.

2. MATERIALS AND METHODS

The materials for this investigation are the tree models as presented by [5] and the analysis of [7].

2.1 Growth axes

Higher plants grow by means of meristems. The shoot directly produced by a single meristem is an *axis*. Axes are of two types: *determinate* and *indeterminate*. In determinate growth the axis terminates either in an aborted bud or in an inflorescence which forms no part of the growth architecture. In indeterminate growth the axis continues growing indefinitely. (There are other meanings given to the word "determinate": in particular growth in some trees, especially conifers, is said to be determinate because the whole year's growth is present in bud before growth starts ([5] p. 34).)

There are two basic tropies: *orthotropic* in which the axes generally grow more or less vertically upwards and the phyllotaxis is spiral, and *plagiotropic* in which the branches grow more or less horizontally and the phyllotaxis, either primarily or secondarily, such as by petiole bending, puts the leaves in a roughly horizontal plane, making a line down each side of the stem. These tropies are combined in some shoots, called *orthoplagiotropic* which are at first orthotropic in direction and phyllotaxis and at some point change more or less rapidly to plagiotropic. Branch axes may also be *plagiotropic by apposition* or *substitution*. The axes are basically orthotropic but are constrained by their position on the tree into a horizontal direction until, after bearing one or more branches, the terminal part of the axis turns in an upward direction. The phyllotaxis is primarily spiral throughout but secondarily distichous; as the shoot turns upwards, the spiral phyllotaxis is reasserted. If the shoot terminates either in an inflorescence or an aborted bud immediately after the branching the tropy is termed plagiotropic by substitution. If the shoot continues vegetatively for a distance, though it may be ultimately determinate, it is called plagiotropic by apposition.

2.2 Attachment

There are five patterns of attachment of axes to the axis from which they spring as lateral meristems. In *continuous* or *diffuse* branching the parent axis bears other axes in an unpatterned way, possibly from every lateral bud, but more usually only from a few of them. In *dichotomous* branching the apical meristem of a shoot divides evenly in two. In the analysis in [7] this division is treated as creating two new meristems and so two new axes. In [5], both are treated as continuations of the same axis. The growth pattern is very rare and is not accepted by all researchers. In *rhythmic* branching growth occurs in bursts (flushes), usually, especially in regions with a dormant season, one flush per year. There are can be more; in *Camellia sinensis* (tea) there are up to four flushes per year. A rhythmic architecture results on indeterminate axes in new axes being produced in groups close to or at the same level on the parent axis. On determinate axes the corresponding mode of attachment is *terminal.* New axes, which may be relaying trunk axes or branch axes, arise only near the end of the parent axis. This form of attachment also occurs in plagiotropy by substitution.

Zonal branching occurs on determinate and indeterminate axes and consists of branching springing from a single zone on the parent shoot, generally accompanied by a change in the direction of the parent axis from more or less vertical to sloping or horizontal This is typical of orthoplagiotropic axes, but is not confined to them, occurring also where axes are orthotropic (Champagnat's Model) or plagiotropic (Troll's Model). The change in direction is opposite to this, from secondarily plagiotropic to orthotropic, in plagiotropy by apposition.

To these forms of branching must be added *basal* branching, whereby new trunks can spring from the base of earlier trunks, and *underground,* whereby new trunks arise at some distance from the original trunk, as in such clonal trees as the aspen (*Populus tremula*). These forms are used in [5] to distinguish Tomlinson's Model from Holttum's and Corner's, but also occur in other models, where they are not necessarily reported.

2.3 Architecture rules

The following architecture rules were developed in [7]. Rule A7 has been omitted because it is in clear conflict with several of the models and must be erroneous. G7 and A10 have been corrected and B2 and A4 have been slightly restated. Rule A9 has an exception in that one version of Prévost's Model has orthoplagiotropic trunk axes and branches plagiotropic by substitution. The asterisks indicate those rules which are summarised by the three gradients stated later, and the brackets indicate those rules which are more or less direct consequences of the definition of the terms.

General rules

(G1) Indeterminate axes do not produce other axes terminally;

(G2) Basal or underground branching can only be used to produce trunk axes;

G3 Dichotomous branching never occurs with other kinds of branching, except basal or underground, always produces axes of the same tropy as those branching, and involves only determinate axes;

G4 Determinate axes never bear other axes rhythmically;

G5* Axes produced continuously do not themselves produce axes rhythmically or zonally;

G6* Axes produced rhythmically do not themselves produce axes continuously;

G7* Axes produced zonally only bear axes zonally or terminally;

G8 Orthoplagiotropic axes never produce other axes dichotomously, terminally or rhythmically;

G9 Determinate orthotropic axes do not bear other axes zonally.

Trunk rules

(T1) Trunk axes are never produced continuously, dichotomously or rhythmically;

T2 Trunks do not consist of determinate plagiotropic axes;

T3 Plagiotropic trunk axes are not produced basally or underground;

T4 Trunks do not consist of axes plagiotropic by substitution or apposition.

Branch rules

(B1) Branches with plagiotropy by substitution or apposition always involve terminal or zonal branching;

B2 Mature branch axes give rise to further branch axes except in some cases when they are plagiotropic.

Attachment rules

A1* Orthoplagiotropic branches are only found with orthoplagiotropic trunks;

A2* Orthoplagiotropic trunks do not bear orthotropic branches;

A3* Plagiotropic trunks bear only plagiotropic branches;

A4* Branch axes attached terminally only give rise to further axes terminally;

A5 Non-orthotropic trunks do not bear branches rhythmically;

A6 Where the trunk is a sympodium of determinate axes, the branches must be attached in the same manner as the trunk axes;

A8 Only sympodial trunks relaying zonally bear branches zonally;

A9 Branches attached zonally consist of axes of the same determinacy and tropy as the trunk axes that bear them;

A10* Branches plagiotropic by substitution or apposition only spring from orthotropic or orthoplagiotropic trunk axes.

3. RESULTS

3.1 Further rules

Further examination of the tree architectures by the methods of [7] but taking the features in a different order resulted in six more rules:

A11 A tree whose trunk is a sympodium relaying by zonal attachment must have branches (besides the distal parts of the trunk axes);

A12 Monopodia do not bear branches zonally;

A13* Determinate monopodia do not bear indeterminate branches;

A14 Indeterminate trunk axes only bear branches continuously if the trunks are orthotropic;

A15* Indeterminate branch axes are never borne terminally;

T5 Trunks without branches are always orthotropic.

These are certainly not all the rules which could be extracted from the list of Hallé-Oldeman models. Any different way of looking at the patterns of occurrence is likely to produce new observations. Nor does this list contain sufficient rules to prevent all the non-observed tree structures, although it does reduce them to manageable numbers. A check showed that there were the following survivors, some of which might be assigned to named models:

(a) Determinate orthoplagiotropic monopodia with determinate orthoplagiotropic branches continuously attached: these might be assigned to McClure's Model;

(b) Determinate orthoplagiotropic monopodia with continuously attached determinate branches plagiotropic by substitution;

(c) Determinate orthotropic monopodia with determinate plagiotropic branches continuously attached, closest to Stone's Model;

(d) Determinate orthotropic monopodia with continuously attached determinate branches plagiotropic by substitution;

(e) Determinate orthotropic monopodia with determinate plagiotropic branches terminally attached and relaying;

(f) Determinate orthotropic sympodia with indeterminate orthotropic branches terminally attached;

(g) Indeterminate orthotropic monopodia with determinate plagiotropic branches attached rhythmically and not relaying: this is closest to Cook's Model;

(h) Indeterminate orthotropic monopodia with determinate plagiotropic branches attached rhythmically and relaying terminally or zonally.

We have a list of 30 rules which seem to be obeyed by all trees. Some of these rules will have individual value in encouraging us to consider why they hold, and so possibly discovering some deeper regularity or constraint in the structure of trees or indeed all higher plants.

If we seek meaning in the list as a whole there remains the task of "seeing the wood for the trees", selecting and arranging them into a smaller number of principles which are more easily grasped by the mind.

3.2 Gradients

Examination of these rules and the symbolic list of models in [7] suggests gradients in determinacy, tropy and attachment. That is, as we move from trunk to branches or from trunk relaying to branch attachment to branch relaying the determinacy, tropy or attachment either stays the same or changes in a consistent direction, not necessarily to the next state.

3.3 Gradient in determinacy

Table I shows the combinations of determinacy in trunk and branches. If trunk and branches are not of the same determinacy, it is usually the trunk that is indeterminate and the branch axes determinate. Only one version of Nozeran's Model goes in the opposite direction. Thus we have a gradient from trunk to branches:

indeterminate – determinate.

Table I. Determinacy combinations.

Trunk	Branch	Models
I	–	Corner's, Tomlinson's
I	I	Aubréville's, Massart's, Roux's, Cook's, Rauh's, Attims's, Mangenot's, Champagnat's, Troll's
I	D	Fagerlind's, Petit's, Roux's, Cook's, Scarrone's, Stone's
D	D	Schoute's, McClure's, Leeuwenberg's, Koriba's, Prévost's, Nozeran's, Stone's, Mangenot's
D	–	Holttum's, Tomlinson's, Chamberlain's
D	I	Nozeran's

(D = determinate, I = indeterminate, – = absent).

3.4 Gradient in tropy

Trunk and branch axes exhibit the combinations of tropies shown in *table II*.

Table II. Tropy combinations.

Trunk	Branches	Models
O	–	Holttum's, Corner's, Tomlinson's Chamberlain's,
O	O	Schoute's, Leeuwenberg's, Koriba's, Scarrone's, Stone's, Rauh's, Attims's, Champagnat's
O	P	Nozeran's, Massart's, Roux's, Cook's
O	PS	Prévost's, Petit's, Fagerlind's
O	PA	Fagerlind's, Aubréville's
OP	OP	Mangenot's
OP	P	McClure's
OP	PS	Prévost's
P	P	Troll's

(O = orthotropic, OP = orthoplagiotropic, P = plagiotropic, PA = plagiotropic by apposition, PS = plagiotropic by substitution, – = absent.)

These variations can be summed up in the second gradient:

orthotropic – orthoplagiotropic – plagiotropic – plagiotropic by apposition or substitution.

3.5 Gradient in relaying and attachment

Basal and underground attachment apply only to trunk axes and dichotomous branching never occurs with any other branch attachment type, so these can be set on one side. We can then draw up the list in *table III*.

Table III. Relaying and attachment combinations.

Trunk relay	Branch attachment	Branch relay	Models
–	–	–	Holttum's, Corner's, Tomlinson's
–	C	–	Cook's
–	C	C	McClure's, Roux's, Attims's
–	C	T	Petit's, Roux's, Stone's
–	R	–	Massart's
–	R	R	Massart's, Rauh's
–	R	Z	Fagerlind's, Aubréville's
–	R	T	Fagerlind's, Scarrone's
Z	Z	Z	Mangenot's, Champagnat's, Troll's
Z	Z	T	Prévost's
T	–	–	Chamberlain's
T	T	–	Nozeran's
T	T	T	Koriba's, Prévost's, Nozeran's
–	T	T	Leeuwenberg's

(– = absent (for trunks this signifies a monopodium), C = continuous or diffuse, R = rhythmical, T = terminal, Z = zonal.)

We can combine all these into a third gradient:

continuous or diffuse – rhythmic – zonal – terminal.

4. DISCUSSION

4.1 Missing models

The establishment of the architecture rules has thrown up the combinations (a) to (h). Examples of them could be looked for and model descriptions widened or new models erected to contain them. On the other hand, each could be examined for indications of non-viability.

4.2 Gradients

But the intended purpose of the rules was to aid the discovery of basic principles of tree architecture. In this the rules have individual roles, but also roles in combination. Ten of them have given rise to the three gradients. Other rules can be grouped to set out the conditions under which, for example, zonal branching can occur, or to explore the consequences of a trunk being a determinate monopodium, the tree therefore being to some extent limited in height.

The gradient in determinacy indeed amounts to very little. It is merely a statement that we do not find determinate trunks with indeterminate branches, and we even need to qualify this with an admission that in one version of Nozeran's model they are so found. Certainly a determinate monopodium with indeterminate branches would seem more limited in height than width, a feature unexpected in a tree, but a sympodial trunk of determinate axes with indeterminate branches would not suffer that disadvantage. The extreme rarity of the condition perhaps says something about the way in which the growth instructions are coded in the tree.

The gradient in tropy fits well with our general mental picture of a tree as a plant which has more scope for growing upwards than outwards. An orthotropic trunk facilitates upward growth, while plagiotropic branches facilitate outward spread. Certainly, many trees exist with other combinations, but achieve the end by making secondary modifications to the primary natures of their axes.

The third gradient seems to deal with the limitation of the production of branches. If a shoot developed from the axil of every leaf, the tree would soon be hopelessly congested, since the number of branches that could be grown increases exponentially with the radius from the trunk, but the volume (per unit height) only increases as the square. Some trees deal with this by developing only some buds, apparently under local control, that is, where there is space and light. This will give rise to diffuse branching.

Under an alternative strategy, found especially in trees with strong seasonal growth, shoots have two sections, a rapid extension section where leaves are well-spaced and axillary buds do not normally develop, and a section with shorter internodes where the axillary buds will develop into next season's shoots. In determinate shoots there will usually be only one section of each type and the attachment and relaying will be terminal. If on the other hand the axis is indeterminate there will often be several sections of each type and the attachment of subsequent axes will be rhythmical. Alternatively axes of either determinacy may have a single zone in which new shoots are attached, with more rapid extension and no laterals on either side of the attachment zone.

Congestion is not a problem at the trunk, and becomes more severe as we move outwards, rewarding mechanisms to restrict branch initiation in accordance with the third gradient.

A point of interest is that the continuous or diffuse category comes first in the gradient, while trunks cannot by their nature be continuously or diffusely relayed. Thus this style of branch attachment occurs only with monopodia. Trees with Cook's model have branches which are short lived and do not relay, thus avoiding congestion. Trees wth McClure's or Attims's models or one version of Roux's model are continuous or diffuse throughout. The other models relay their branches terminally only.

4.3 Reflection on method

This set of gradients is a stage in a process of successive discarding of information and focussing on what is relevant. The process began with the observations on individual trees, which were combined into descriptions for the species. From these, Hallé and Oldeman distilled their architecture models by recognising similarities. These models were translated into a symbolic representation by concentrating on determinacy, tropy and relaying and attachment, dicarding various other features, such as timing and exact positioning of branch placement. The symbolic representation made it possible to extract general rules of symbol combination which represent general rules of feature combination. Finally, faced with a collection of rules more numerous than the models they were intended to define, we are drawn to concentrate on one aspect at a time, and so discover the three gradients. At each stage we have the option of concentrating on different aspects and so discovering different regularities in the total pattern of the architecture of trees.

4.4 Implications

The greatest importance of this research is as a part of the attempt to understand the organisation of organisms. The existence of these gradients may say something about the way architectural features are coded within a tree and how each axis determines the nature of the axes to which it gives rise. An investigation of this kind cannot find a mechanism, but the more we know about the effects, the better chance we have of finding a mechanism which results in the observed pattern.

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