Plant Growth Rule Systems

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Introduction.

The concept behind growth rule systems appeared first in the work of Aristid Lindenmayer (Frijters 1978), where the notation is quite different from that used here. While they have been used by computer scientists in designing the computer simulation of the growth of plants (e.g., Prusinkiewicz & Lindenmayer 1990), and in their own right as branching systems, they do not seem to have been adopted by botanists. Growth rule systems were described in Robinson (1986), in symbols approximately of the kind used in this paper, in an attempt to set out the idea in a way easier for the botanist to use in identification and taxonomy. The present paper is a further development of the approach, as described in my talk to the Canterbury Botanical Society in February 1992.

Each kind of plant has a characteristic mode of growth, which is genetically determined, but may be modified, at least in the size to which the plant grows, by its immediate environment. Traditionally the emphasis in plant description has been on the morphology of the reproductive structures and to a lesser extent on the stems and leaves; taxonomists have developed a detailed vocabulary to express these aspects. Much less attention has been given to how these organs are arranged on the plant; there are descriptions of the inflorescence in terms which are often used imprecisely, and little else. The hope is that the present approach, which is capable of precision and versatility, and also expresses structure in a way which can provide taxonomic characters, will prove of interest and use.

The basic concepts can be applied to all the higher plants, and certainly to the Gymnosperms, but the details have so far been worked out for the context of Angiosperms. The essential feature is that the plant should have a node structure, and the rules take the form of expressing what happens at the next nodes apically and axillarily from a given node. Presence or absence of features are recorded, distances, sizes and angles are ignored, except in so far as the inevitable occurrence of vestigial presence makes some sort of judgment necessary.

In these terms a plant bears only a few different sorts of node, and there is one rule for each sort, the collection of all the rules for the plant being its growth rule system. Within minor variations, all specimens of the same species have the same growth rule system, which may also be shared with related species. In some cases, such as Brassicaceae (Cruciferae), virtually the whole family has the same system. In other cases, although there are differences, they are clearly variations on the same theme, and it may be possible to conjecture an ancestral form from which the present species can be derived by suppression of different features or other changes. This applies certainly to the vetch and clover part of the Fabaceae (Leguminosae).

The node types in the rules are the record of different states of the apex as the plant grew and formed the nodes successively. What caused the state of the apex to change lies outside the purpose of this paper. When describing the growth process we may refer to the apex types, and when describing the resulting plant, to the node types.

Individual Rules

We begin by considering a selection of individual rules, which indicates the range of possibilities. At the same time, comparison of the rule and description with the schematics will indicate the conventions used in the schematics. In these, there is a single symbol for each of flower, leaf and bract irrespective of the shapes in particular examples. Suppressed internodes are shown by broken lines. Reference is also made as appropriate to the expression of the various node types in the various examples (case-studies) which follow.

There are ten node types, F, C, O, P, Q, R, S, T, U, V, of which the first three are terminal types, and the rest each give rise to a particular type of rule.

F, C, O

These are the states at the end of a shoot. F stands for flower and C for capitulum, and is used not only for the composite heads of the Asteraceae (Compositae), but for all situations where flowers are collected into 'heads' so compactly that discussion of the internal structure of the head in terms of growth rules would be impossible. O is used for an aborted apex, or for the axils in situations where there is no axillary bud, or it never develops. The examples below will demonstrate their use.

R

Type R is named as the raceme-builder, though its use is wider than can be put under that term. Consider the common weed *Linaria purpurea,* which has small, pink or purple spurred snapdragon flowers. The flowers are on pedicels springing from the axils of bracts (Fig. 1a). We write this as a rule R -> B(- F) - R.

The rule is read as follows (most types follow the same pattern). The R at the left indicates that this is an R rule, and the arrow indicates that what lies to the right of it is what happens at the node and the states of the next node up this shoot and the first node on the axillary shoot. The B without a number shows that there is one bract at the node. This is followed by (- F), the brackets containing the axillary growth. The hyphen, read 'stem' in this context, indicates that the internode (in fact a pedicel) is expressed, and the F indicates that the first node is a flower. As F is a terminal state, this is in fact the only node on this shoot. The 'stem' after the bracket indicates the state of the internode before the next node up the present shoot as expressed, not

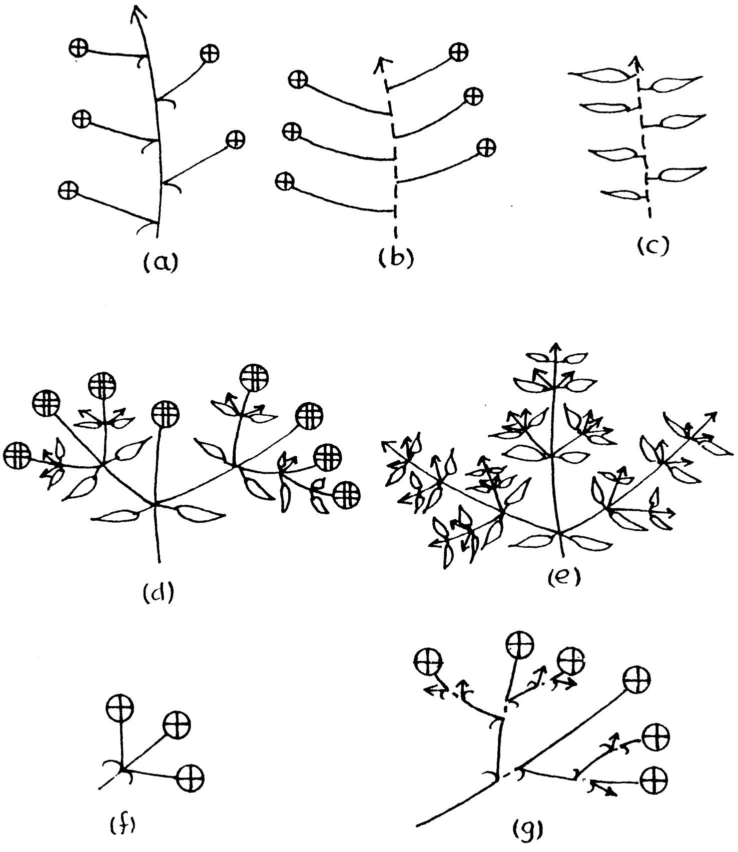

Figure 1. Schematics generated by individual rules.
(a) R -> B(- F) - R; (b) R -> E(- F) . R; (c) R -> L(. O) . R; (d) Q -> 2L(- Q) - C; (e) P -> 2L(- P) - P; (f) T -> 2B(- F) - F; (g) S -> B(- S) . B(- S) - F

suppressed. The final R shows that the next node is also in state R. Indeed, we use R precisely in those situations in which the next node up the shoot is in the same state as the node to which the rule refers, but the first axillary node is in a different state. The arrow head in the schematic indicates that the raceme continues.

The bract at the node may be replaced by a leaf (L instead of B) or there may be neither, as occurs in the Brassicaceae, when we use E, from 'ebracteate'. Thus for most Brassicaceae the raceme grows by the rule R -> E(- F) - R. Candytuft (*Iberis umbellata*) is an exception as the internodes are very short. This is shown by a dot (.) in place of the stem (-) in the main shoot internode position: R -> E(- F) . R (Fig. 1b). There are judgments to be made here; using ' . ' instead of ' - ' when the internode length is consistently shorter than its width seems to give the most useful results. Other patterns of suppression give the heads of clovers (*Trifolium repens* and *Trifolium pratense* in the case studies).

A vegetative role for R is as a rosette builder. If the axillary shoots never produce any growth the first axillary node is type O, and the non-existent axillary internode is given state ' . ' to maintain the rule format. We then have R -> L(. O) . R (Fig. 1c).

Q

The cymose type of rule is given the symbol Q. Here it is the first axillary node which has the same state as the present node, while the next node on the main shoot is different. Opposite leaves are more common in cymose than racemose structures. A common rule, to be found in many members of the Caryophyllaceae, such as chickweed (*Stellaria media*) (see the case-study below) is Q -> 2L(- Q) - F , where the next node is a flower. The 2 indicates that there are two leaves at the node. (In this notation we use L for leaflike structures whatever their position and B only for simplified and usually small structures, which may or may not be green.)

A variant occurs in *Dahlia* and *Cosmos* in the Asteraceae, where the simple flower F is replaced by a capitulum C: Q -> 2L(- Q) - C (Fig. 1d). So far the notation cannot show the gradual reduction of leaves to bracts which occurs in many Asteraceae and elsewhere.

P

State P is named as the panicle-builder. In this role it must be teamed with another rule, for the distinguishing mark of the P type is that present node, next node and first axillary node are all of the same type. In order to create an inflorescence we need a pair of rules, such as P -> L(- P) - P; P -> C. Such a pair is common in the Asteraceae, for example in most members of the genus *Senecio*. A panicle with simple flowers is shown for *Griselinia lucida* below

This situation introduces the simple transformation of node type, as it were in the middle of the internode. In principle any non-terminal type can be transformed into any other type, or another rule belonging to the same family, as we shall see in the case studies.

P-rules are however much more common in the vegetative parts of plants, where most will have a rule P -> L(- P) - P or P -> 2L(- P) - P (Fig. 1e) for the basal part. In many plants many of the axillary buds do not develop.

T

The great majority of plants so far analysed use only rules of types P, Q and R, but logically there are two more types which use the same format but have different patterns of equality between present, next and first axillary node types. Both types occur, though they are less common than P, Q and R, usually as the result of some reduction in the plant structure. In rule T, the types of the next and first axillary nodes are the same, but different from the present node. The principle occurrence of this is where flowers occur in threes, where we write a rule such as T -> 2B(- F) - F (Fig. 1f).

V

The last case of a structure which has the format of the rules described so far is V, where present node, next node and first axillary node are all different. This occurs, for example in the pair of bracts (valves) which encloses the umbel in *Agapanthus orientalis* (Healy & Edgar 1980, p. 47). We have a rule V -> 2B(. O) . U (Fig. 2). Another V-rule is used in *Schizostylis coccinea* below.

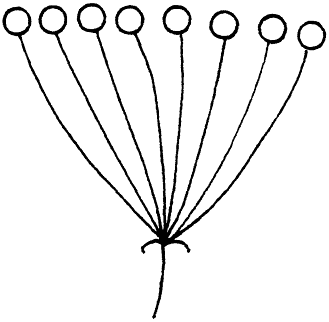

Figure 2. Schematic for the inflorescence in *Agapanthus orientalis*.

U

U is the umbel-builder, and the usage is that it can be employed wherever there are more than two shoots mounted terminally on a shoot, whose last node may be suppressed, and where there is no clear continuation of the main shoot among them. A U-rule has a simpler form than the rules that have gone before. It begins with the number of branches, if that is fairly constant (*Malva neglecta*) or with 'n' if the number is more variable (*Apium prostratum*). The *Agapanthus* rule for U is U -> nE(- F), (Fig. 2) indicating that there are no bracts and that the internodes end in flowers. If there are bracts, there does not have to be the same number of bracts as internodes springing from the node.

S

The last type is S, for skew-cyme. Shoots bearing two bracts, often with a shortened internode between them, and terminating in a flower are common enough and sufficiently characteristic of certain families to warrant a special type. The typical situation is an inflorescence constructed with skew cymes springing from an R-type shoot, the S rule being S -> B(- S) . B(- S) - F (Fig. 1g), which is from a plant of *Geum coccineum* (Rosaceae). In the case studies it appears under *Aquilegia vulgaris* and *Apium prostratum,* being terminated with an umbel instead of a flower in the latter case.

There are a few situations in which the axillary products from a S-shoot are not of the same type, or one may never develop.

Other Rules

As remarked when considering P rules, the growing apex may change its type between nodes. This happens most often from the R and P states. For example, a raceme cannot continue for ever. Often it simply peters out from the failure of buds to grow. We do not write a rule to represent this. But sometimes as in the sweet pea (*Lathyrus odoratus*), and indeed many of the Fabaceae, there is a definite end, a short growth beyond the last flower. This is recorded as a rule R -> O. On other occasions the raceme ends in a terminal flower, as in some Rosaceae, and *Aquilegia vulgaris* below. This is recorded by a rule R -> F.

While the rule of one shoot from each axil holds for many plants, others have more than one. Typically the true axillary shoot grows first, and later 'accessory' shoots are also produced. Sometimes these play an essential part in the structure of the plant. See for example *Malva neglecta* in the case studies, where the accessory shoots permit the continued branching of the plant.

Case Studies

The structure of a plant can therefore be described by its collection of growth rules; its growth rule system. The following plants were chosen to give some idea of the range of systems, to illustrate single rules mentioned above and to make certain other points about growth rule systems. Each is illustrated by a schematic from an actual plant.

***Capsella bursa-pastoris* (Brassicaceae (Cruciferae)) shepherd's purse (Webb et al. 1988, p. 410) (Fig. 3)**

This is a well-known weed; the flowers are small and white, but the triangular seed-pods (the purses) are instantly recognisable.

The architecture is typical of the family. There is a basal rosette with an R-rule, not shown in this sample, the axillary growths from which branch with a P-rule. Eventually this changes to another R-rule which builds the inflorescence. We thus distinguish the R-rules as R1 and R2. The inflorescence is a raceme without a definite end. The flowers have definite pedicels which spring from bractless nodes.

SYSTEM R1 -> L(- P) . R1
P -> L(- P) - P
P -> R2
R2 -> E(- F) - R
R1 -> P

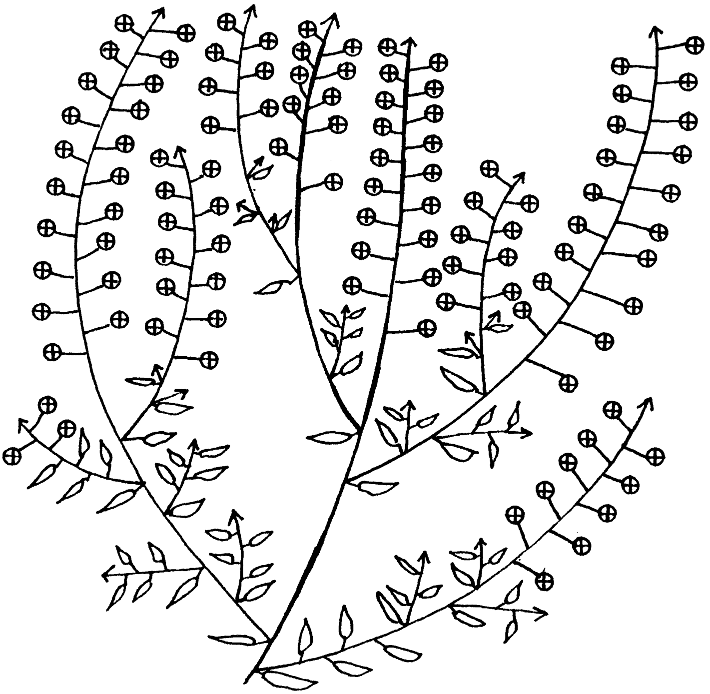

Figure 3 Schematic for *Capsella bursa-pastoris.*

***Trifolium repens* (Fabaceae (Leguminosae)); white clover (Webb et al. 1988, p. 690) (Fig. 4)**

White clover has a creeping habit and a tendency to root from nodes that find themselves suitably placed. We do not build these 'adventitious' roots into our growth rules.

The plant will begin with the customary P-rule, but as flowering begins the P changes to an R, which produces the flower heads on long peduncles as its axillary growths. But we notice that in this specimen the only heads spring from well-separated nodes, and that from the other nodes come leaf-bearing growths, presumably producing shoots like the main one shown. There will thus be a rule converting R back into P, whence it will subsequently become R once more. Other specimens showed the same general pattern, but it did sometimes happen that several successive nodes bore peduncles.

A simple microscope or even a hand lens will show us the structure of the heads. The flowers are seen to have well-formed pedicels which spring from the axils of bracts. With so many flowers springing from a short central stem, the internodes are very short. But the stem ends in a short spike. The head is then a modification of the raceme structure common in pea flowers. We thus have a second R-rule.

We note that the notation automatically allows the head to be raised on a long peduncle, while within the head the internodes are short.

```
SYSTEM    P -> L( - P) - P,
          P -> R1
          R1 -> L( - R2) - R1
          R1 -> P
          R2 -> B( - F) . R2
          R2 -> O
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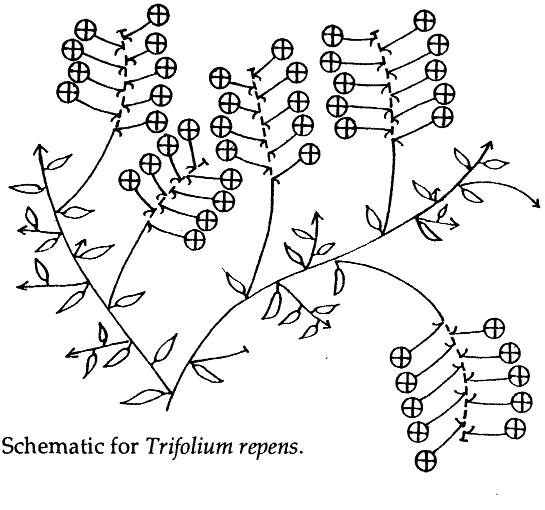

Figure 4. Schematic for *Trifolium repens.*

***Trifolium pratense* (Fabaceae (Leguminosae)); red clover (Webb et al. 1988, p. 690) (Fig. 5)**

Red clover is a more upright plant than white clover. The structure of the plant is also slightly different in several details.

The heads are held in a cup formed by the stipules at the bases of a pair of leaves, and appear to be terminal on the shoot. The head is held on a short peduncle or may appear sessile. Terminal heads would raise particular difficulties in relating the structure here to that of the white clover, where the heads are definitely axillary. The situations where there are two heads together, and sometimes extra leaves, gives an important clue. They could not both be terminal, but they could both be axillary, and in particular the first head would then be in the axil of the lower leaf. This situation emphasises that it is impossible to draw a schematic until such questions of structure have been decided.

The large pink heads themselves consist of small pea-flowers arranged very close together. They are sessile, and only the flowers at the bottom of the head have bracts. As in the white clover, the spike comes to a definite end.

SYSTEM P -> L(- P) - P,
P -> R1
R1 -> L(- R2) . R1
R1 ->O
R2 -> E(- F) . R2
R2 -> O.

Other clovers have comparable variations on the same theme.

Figure 5. Schematic for *Trifolium pratense.*

***Stellaria media* (Caryophyllaceae); chickweed (Webb et al. 1988, p. 508) (Fig. 6)**

Throughout, the leaves are opposite. The basal part of the plant has P-type branching, though the axillary buds often do not develop. Once flowering starts the branching is Q-type, with terminal flowers on long stalks.

SYSTEM P -> 2L(- P) - P
P -> Q
Q -> 2L(- Q) - F

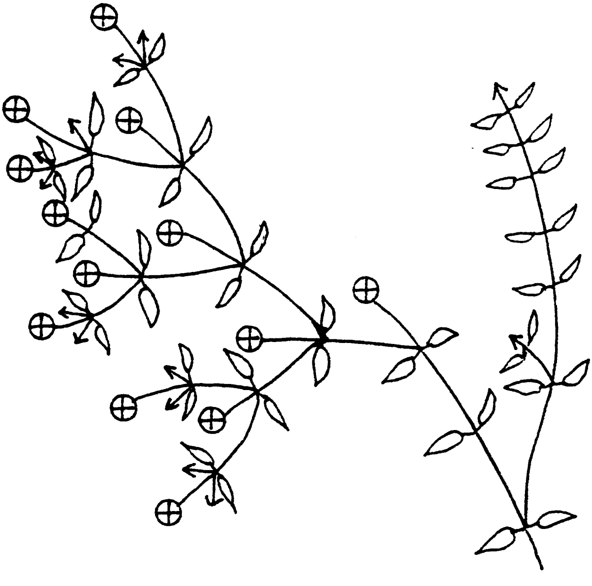

Figure 6. Schematic for *Stellaria media*

Griselinia lucida (Cornaceae); broadleaf (Allan 1961, p. 442) (Fig. 7)
The schematic shows a short piece of stem from this shrub, bearing two panicles. This was a male plant; the species is dioecious. We do not record this nature of the flowers here, but would distinguish between male and female flowers in a monoecious plant, since their different positioning is significant. Above the panicles there is a reversion to a P-type vegetative branching.

The panicles certainly show some structure, but it is not of such a kind that it can be captured by the present approach. The initial internode of the panicle is suppressed.

SYSTEM (of this part of the plant)

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R  -> L( . P2) - R
P2 -> B( - P2) - P2
P2 -> F
R  -> P1
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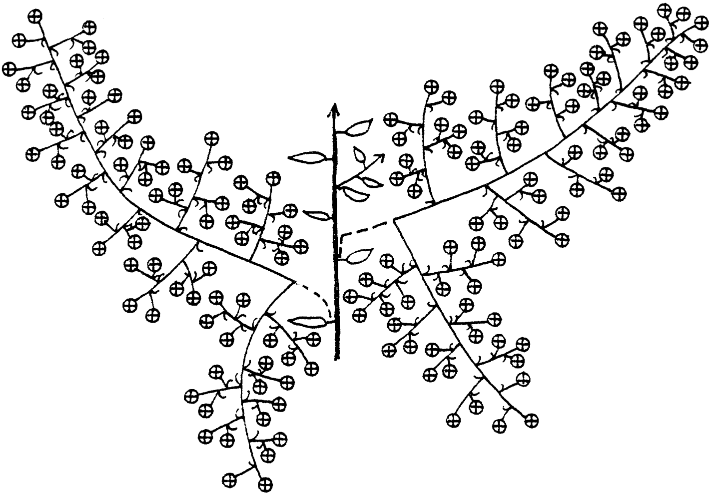

Figure 7. Schematic for *Griselinia lucida*.

***Galeobdolon luteum* (*Lamiaceae (Labiatae)*); *aluminium plant* (*Webb et al. 1988, p. 769*) (*Fig. 8*)**

Many labiates flower with an R-generated spike, from the axils of which spring cymes (Q -rules) reduced in various ways. In this species, grown as a ground cover, the cymes have been reduced to an almost constant five sessile flowers whose interrelationship can reasonably be described as in the schematic. When we translate this into the symbols of the system we find the Q replaced by a V and a T. In its vegetative growth the plant is little branched, leading to a first R-rule. In the inflorescence part there is a second R-rule. This may terminate at the top of the inflorescence or may revert, as here, to the first R-rule.

SYSTEM

R1 -> 2L(. O) - R1
R1 -> R2
R2 -> 2L(. V) - R2
V -> 2E(. T) . F
T -> E(. F) . F
R2 -> R1

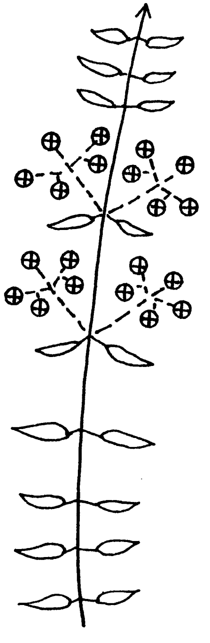

Figure 8. Schematic for *Galeobdolon luteum*.

Schizostylis coccinea (Iridaceae); kaffir lily (Healy & Edgar 1980, p. 133) (Fig. 9)
This introduced flower from South Africa grows wild in quantity along the West Coast Road from Christchurch to Kirwee, bearing spikes of bright crimson flowers from March to May. The whole plant is reminiscent of a *Gladiolus,* but the petals are equal in size and shape. The plant grows from a rhizome rather than a corm, as with *Gladiolus,* but the structure of the plant, with an unbranched stem carrying a raceme of flowers each enclosed between two bracts is the same as with *Gladiolus.*

The whole plant is arranged along a single axis, so the vegetative part has an R-rule with no axillary growths. At first sight the inflorescence is a simple raceme, or rather, since the pedicels are absent, a spike. There certainly is an R-rule, but the unit is not simply a flower. In the Iridaceae the flower is enclosed by two 'spathe-valves' (bracts), the outer of which is the bract on the main stem. The axillary growth of this bract on the main stem comprises a completely suppressed internode, bearing the second bract with no axillary bud, another suppressed internode (the pedicel) and then the flower. Since the initial state of this shoot, the empty bract axil and the terminal flower are all different, we have here a V-rule, and the first axillary node for rule R2 is in a state V.

At the top of the spike there is a vestigial small flower enclosed in membranous valves, produced as the main apex is in the process of aborting. Thus we have a final rule R2 -> O.

SYSTEM
R1 -> L(. O) - R1
R1 -> R2
R 2 -> B(. V) - R2
V -> B(. O) . F
R2 -> O

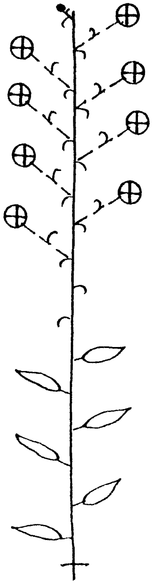

Figure 9. Schematic for *Schizostylis coccinea.*

Aquilegia vulgaris (Ranunculaceae): columbine (Webb et al. 1988, p. 1004) (Fig. 10)

This is the garden *Aquilegia*. The inflorescence begins with an R-type shoot of variable length, in this case of 5 internodes. From its axils come S-type shoots bearing bracts and with variable length middle internodes not short enough to be marked as suppressed. The R-shoot terminates in a flower.

SYSTEM R -> L(- S) - R
S -> B(-S) - B(- S) - F
R -> F

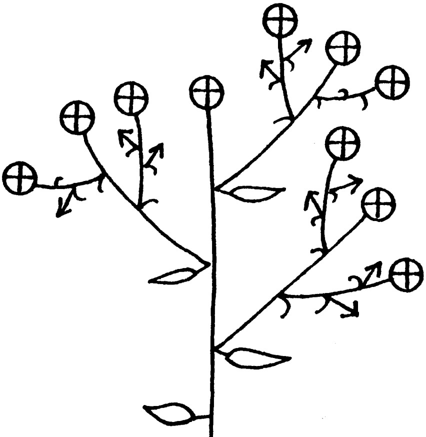

Figure 10. Schematic for *Aquilegia vulgaris*.

***Apium prostratum* (Apiaceae (Umbelliferae)): native celery (Webb et al. 1989, p. 120) (Fig. 11)**

This is a coastal native umbellifer, agreeing with most members of the family in having a double umbel, but in this case the internode directly below the umbel is suppressed.

The growth below the umbels in this plant consists of S-shoots, not uncommon in the family. There may have been longer shoots in the part of the plant not collected. There are no bracts at the base of either level of the umbel.

SYSTEM (this part of the plant)

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S  -> L( - S) - L( - S) . U1
U1 -> n( - U2)
U2 -> n( - F)
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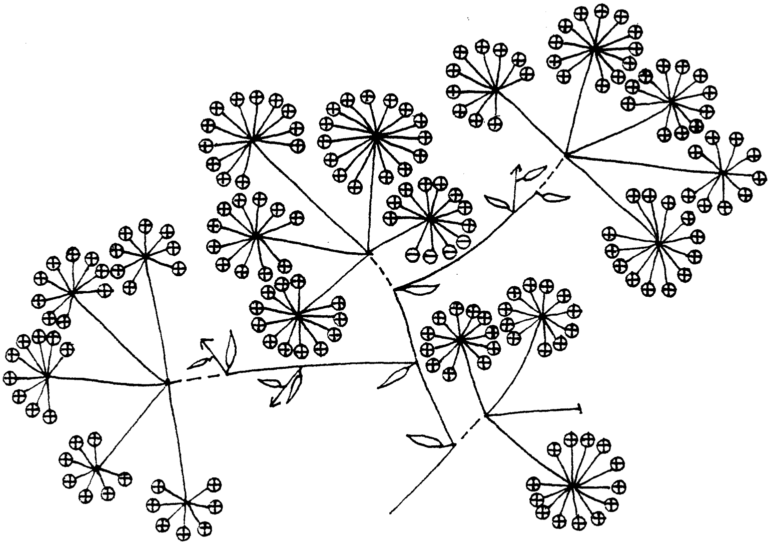

Figure 11. Schematic for *Apium prostratum*.

Malva neglecta (Malvaceae): dwarf mallow (Webb et al. 1988, p. 833) (Fig. 12)

This is one of the smaller-flowered mallows, the flowers on this specimen being about 16 mm across, almost white, with three pink lines on each petal.

The plant structure is the common one for mallows. The plant sends out trailing shoots which produce axillary clusters of two or three flowers. These flower one after the other, but begin their development at about the same time, so we will count them as an umbel, though this description must be admitted to be tentative.

When the flowers have finished, a new shoot, which we may consider an accessory shoot, appears from some of these nodes. It is clearly of the same kind as the R-shoot from which it springs, though it does not develop to the same extent. We show an accessory shoot in the notation by a further bracket after the axillary bracket. In other instances the accessory shoots (of which there may be several) may be of the same type as the axillary shoot. Thus if we take the plant as beginning with the usual P-type apex, and standardise the number of flowers in each axil at 3, we will obtain this system:

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SYSTEM     P -> L( - P) - P
           P -> R
           R -> L( . U)( - R) - R
           U -> 3E( - F)
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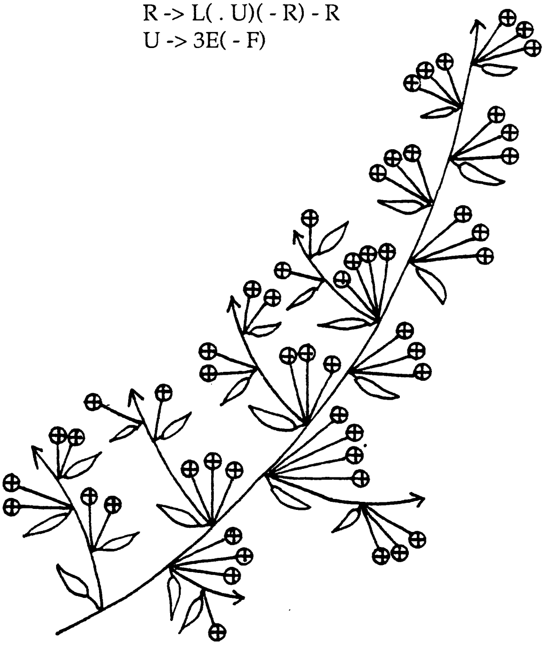

Figure 12. Schematic for *Malva neglecta*.

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