

## Interpretation of metameric architecture in dominant shrubs of the Chilean matorral

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**Summary.** The seasonal progression of phenophases in 21 shrub species of the Chilean matorral was analyzed. Five "modules" or basic units that are responsible for the aboveground architecture of the plants were characterized. These modules appear to be organized in seven different spatial arrangements. In drought-deciduous species a module type with an "absolute short shoot" with limited apical growth, leafy or spiny, predominated. In evergreen species "long shoot" and "temporal leafy short shoot" module types were more frequent. The spatial arrangement of morphologically different modules and the temporal sequence of their formation allow a dynamic interpretation of the modular architecture of the plants.

**Key words:** Modular organisms – Metameric growth – Architecture – Long shoot – Short shoot

In mediterranean environments growth and plant biomass are limited to a great extent by water availability (Kozłowski 1972; Mooney et al. 1977; Miller 1981; Montenegro et al. 1989), temperatures (Mooney et al. 1977; Aljaro and Montenegro 1981; Miller 1981; Di Castri 1981) and soil nutrients (Beadle 1966; Specht 1979; Mooney 1981; Lamont and Kelly 1988). These environmental factors display seasonal variations limiting biological activity in plants to certain periods of the year (Mooney et al. 1974) generating growth patterns with a clear seasonal cycle (Montenegro 1987; Montenegro et al. 1989), as has been observed for a variety of growth forms already described for dominant species in mediterranean plant communities of southern France (Floret et al. 1989), Israel (Orshan 1989a), southern Africa (Le Roux et al. 1989) and central Chile (Montenegro et al. 1989). These growth cycles result from an interaction between the timing and type of development of renewal buds and organs that fall periodically due to

senescence, in relation to the type of organs that remain on the plant throughout the year (Brown 1971; Orshan 1989b). The dynamic sequence of these events allows the interpretation of plant architecture and leads to the determination of the different module types responsible for the specific type of architecture (Harper and Bell 1979; Bell 1986).

Growth in woody plants has two components: increment of biomass – resulting from physiological processes leading to net carbon, water and nutrient uptake – and the orderly arrangement of this biomass in space (Küppers 1989). This second component, resulting from branching patterns, is generated by the addition of new components to an existing framework (Bell 1986; Franco 1986). Branching patterns follow an intrinsic order of growth even in the most complicated architectural system. A thorough understanding of this sequence requires a knowledge of the nature of the building blocks for a given plant; in other words, the module types.

In this work a "module" is the result of the development of an axillary or terminal bud: a branch or shoot unit (Halle and Oldeman 1970; White 1984; Watkinson and White 1986).

The purpose of this work was to identify the different module types responsible for the branching patterns of the dominant species in the matorral of central Chile, throughout their annual life cycles, and to determine the timing and frequency of these different modules during the growing season.

### Material and methods

The study area was located along an east-west altitudinal gradient extending from sea level to the Andean foothills (1500 m.a.s.l.) at 33° S latitude, within the central zone of Chile, with a semi-arid mediterranean climate (Di Castri 1981; Quintanilla 1985). The plant community structure corresponds in general to the "matorral" type. Summer-deciduous shrubs, evergreen sclerophyll or malacophyll shrubs, and herbaceous species are found among the dominants (Mooney et al. 1970, 1977; Montenegro et al. 1979, 1981).

The species analyzed are listed in Table 1 along with their growth form and leaf phenology.

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Table 1. Classification and growth form of species studied

SPECIES	FAMILY	GROWTH FORM
<b>EVERGREEN</b>		
<i>Baccharis linearis</i>	Compositae	Malacophyll Shrub
<i>Cestrum parqui</i>	Solanaceae	Malacophyll Shrub
<i>Colliquaja odorifera</i>	Euphorbiaceae	Sclerophyll Shrub
<i>Cryptocarya alba</i>	Lauraceae	Sclerophyll Tree or Shrub
<i>Escallonia pulverulenta</i>	Saxifragaceae	Malacophyll Shrub
<i>Gutierrezia resinosa</i>	Compositae	Sclerophyll Shrub
<i>Kageneckia angustifolia</i>	Rosaceae	Sclerophyll Tree or Shrub
<i>K. oblonga</i>	Rosaceae	Sclerophyll Tree or Shrub
<i>Lithrea caustica</i>	Anacardiaceae	Sclerophyll Shrub
<i>Luma chequen</i>	Myrtaceae	Sclerophyll Shrub
<i>Maytenus boaria</i>	Celastraceae	Malacophyll Tree or Shrub
<i>Peumus boldus</i>	Monimiaceae	Sclerophyll Shrub
<i>Quillaja saponaria</i>	Rosaceae	Sclerophyll Shrub
<i>Sophora macrocarpa</i>	Leguminosae	Malacophyll Shrub
<i>Tetraglochin alatum</i>	Rosaceae	Malacophyll Shrub
<b>SUMMER DECIDUOUS</b>		
<i>Bridgesia incisifolia</i>	Sapindaceae	Malacophyll Shrub
<i>Flourensia thurifera</i>	Compositae	Malacophyll Shrub
<i>Fuchsia lycioides</i>	Onagraceae	Malacophyll Shrub
<i>Satureja gilliesii</i>	Labiataea	Malacophyll Shrub
<i>Talguenea quinquinervia</i>	Rhamnaceae	Spiny Malacophyll Shrub
<i>Trevoa trinervis</i>	Rhamnaceae	Spiny Malacophyll Shrub

The seasonal progression of phenomorphological events was determined by random selection of 10 individuals of each species. Ten shoots per shrub were marked at the level of the last leaf formed during the previous growth period (Montenegro et al. 1979). The position of renewal buds, the flushing period, and the type of shoot arising from each bud were noted. Observations were carried out once a week during the growth period and each month during the rest of the year. The annual cycles analyzed here are partly based on information that has already been published elsewhere (Hoffmann 1972, 1981; Hoffmann and Hoffmann 1976; Montenegro et al. 1980, 1988, 1989).

The module types formed by each species were obtained through the analysis of the species growth cycles. A  $\chi^2$  test of homogeneity ( $P < 0.05$ ) was used to compare frequency of different modules between evergreen and summer-deciduous species.

## Results

The modules found in the species analyzed allow us to identify five basic structural units, originating from the development of either a terminal or an axillary bud (Fig. 1; nomenclature as in Orshan 1989b). Terminal buds were found to differentiate into either an inflorescence, or a vegetative long shoot (Fig. 1A and B) which has the potential to continue growing vegetatively in the next season from its apical meristem. Axillary buds showed a greater ontogenetic plasticity: they were able to differentiate into any of the five different module types found. Besides the modules already described, a temporal short shoot may be developed, which may or may not flower from its axillary buds (Fig. 1E). These temporal short shoots will elongate producing a long shoot in the next growing season.

Axillary buds may also give rise to an absolute short shoot with limited growth, in which case their terminal bud produces an inflorescence (Fig. 1F), and an absolute

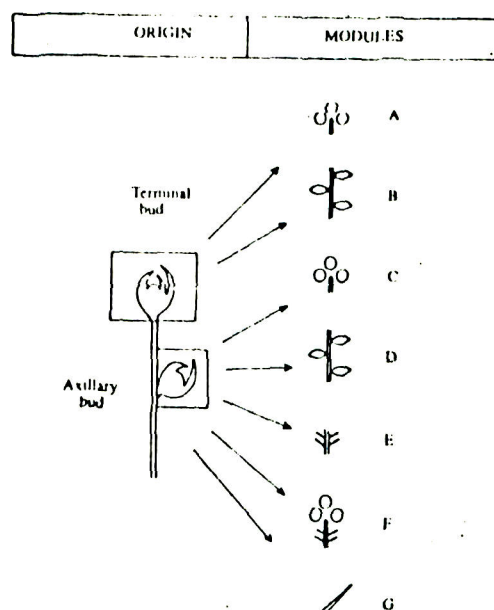


Fig. 1. Module types originating from the development of either a terminal or axillary bud. Modules A and C, inflorescences; Modules B and D, long shoots; Module E, temporal short shoot; module F, absolute short shoot; Module G, thorn. Nomenclature follows Orshan (1989b)

short shoot that lignifies and differentiates into a thorn (Fig. 1G).

The frequency of occurrence of the different modules is shown in Fig. 2. Modules A and D appear more frequently and seem to be responsible for the basic metameric architecture of the plant. The less frequent modules generate the principal differences observed in the architecture of the matorral shrubs.

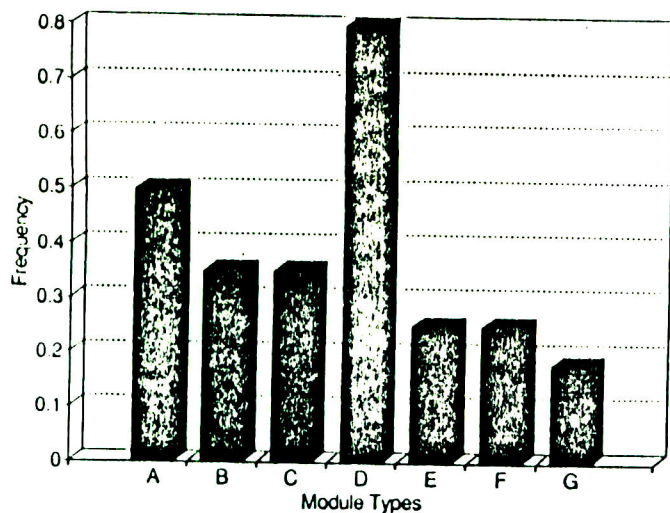


Fig. 2. Frequency of occurrence of module types for all species analyzed ( $n = 58$ )

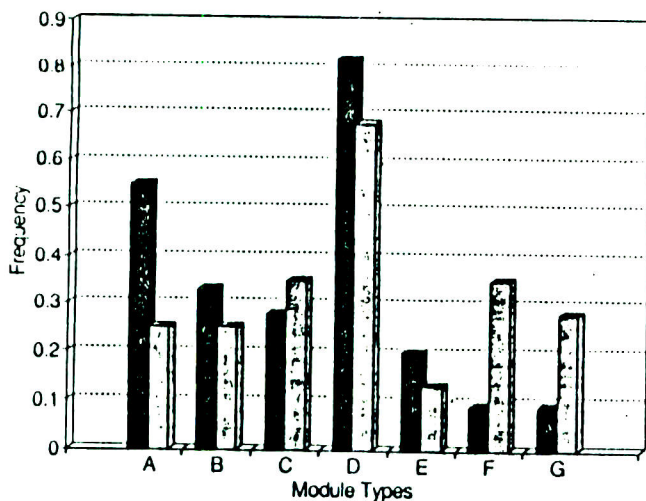


Fig. 3. Frequency of occurrence of module types for evergreen shrubs ( $n=40$ ) (darker shading), and summer-deciduous shrubs ( $n=18$ ) (lighter shading)

When evergreen and summer-deciduous shrubs are compared in terms of the different modules found the following patterns emerge (Fig. 3). In evergreen species inflorescences or long shoots in apical position (modules A and B respectively), and temporal short shoots in axillary position (module E), predominate. In summer-deciduous species axillary inflorescences (module C) and absolute short shoots, both leafy (module F) and spiny (module G), predominate.

The spatial arrangement of these basic modules appear to form seven different combinations. Four different modules were the maximum found in any one particular arrangement (Fig. 4).

The first modular combination or arrangement (Fig. 4A) is shown by species whose terminal buds differentiate into a reproductive structure, limiting vegetative development of the plant to axillary buds, which grow directly into long shoots. Another type of arrangement occurs when flowers develop only from axillary buds,

MODULAR ARRANGEMENT	SPECIES	MODULAR ARRANGEMENT	SPECIES
[A]	C. patqui C. odorata E. pulverulenta E. thurifera K. angustifolia K. oblonga P. boldus Q. sapotaria	[D]	G. resinosa S. gilliesii
[B]	B. macroloba C. alba E. caustica E. chequeni M. boaria S. macrocarpa	[E]	B. linearis
[C]		[F]	E. quinquenervia E. trinervis
		[G]	E. alatum

Fig. 4A-G. Spatial arrangement of module types and the species that show each type of arrangement. Basal branch is heavily shaded. Figures show percentage of species analyzed with that type architecture. For full species names see Table 1

and vegetative growth of the plant occurs from both axillary and terminal buds, developing long shoots (Fig. 4B). These two types of arrangement appear to be the most frequent; they are found in the architecture of 67% of the species analyzed. A variation of the second arrangement is observed in *Fuchsia lycioides* (Fig. 4C), which, in addition to generating vegetative growth throughout the development of both axillary and apical long shoots, can also differentiate absolute short shoots in an axillary position.

Another modular arrangement is seen in *Satureia gilliesii* and *Gutierrezia resinosa* (Fig. 4D), in which the formation of a long shoot occurs only by the elongation of a temporal short shoot; these long shoots have limited growth due to apical flowering.

The arrangement shown in Fig. 4E is formed by the combination of temporal and absolute short shoots in an axillary position, along with the formation of long shoots by elongation of the temporal short shoots.

The last two modular combinations include plants that develop absolute short shoots, transformed into thorns by lignification. *Talguenea quinquenervia* and *Trovoa trinervis* (Fig. 4F) both develop long shoots directly from axillary buds which, in turn, will form two types of short shoots: absolute leafy shoots flowering at the apex and spines. The most complex architecture found was that of *Tetraglochin alatum* (Fig. 4G), in which long shoots may originate from the growth of temporal short



**Table 2.** Frequency of formation of the different modules for (a) all species analyzed, and (b) for each growth form; right half, evergreen shrubs; left half, summer-deciduous shrubs

a							
	A	B	C	D	E	F	G
Autumn	—	—	—	—	—	—	—
Winter	0.19	0.37	0.28	0.48	0.25	0.75	—
Spring	0.28	0.63	0.44	0.52	0.50	—	1.00
Summer	0.55	—	0.28	—	0.25	0.25	—

b							
	A	B	C	D	E	F	G
Winter	0.22 (—)	0.17 (1.00)	0.20 (0.50)	0.33 (0.83)	0.33 (—)	— (1.00)	— (—)
Spring	0.22 (0.50)	0.83 (—)	0.40 (0.50)	0.67 (0.17)	0.33 (1.00)	— (—)	1.00 (1.00)
Summer	0.56 (0.50)	— (—)	0.40 (—)	— (—)	0.33 (—)	1.00 (—)	— (—)

shoots, or from the apical meristem of the basal long shoot. Some axillary buds produce spines; the plant flowers from axillary buds located on temporal short shoots.

The overall frequency of formation of the different modules in all species analyzed showed a marked seasonality (Table 2a). Most of the modules are formed in spring – apical and axillary long shoots, axillary inflorescences, temporal short shoots and thorns – while absolute short shoots and apical inflorescences are formed in winter and summer, respectively. Growth does not take place during autumn.

Differences were also found between evergreen and summer-deciduous shrubs. In evergreen species (Table 2b) the peak formation of absolute short shoots occurs in summer, at the end of the growing season, while in deciduous shrubs growth begins with the formation of absolute short and long shoots. Temporal short shoots in deciduous species appear in spring, while in evergreens they are formed regularly throughout the growing season.

## Discussion

The development of terminal and axillary buds may generate different growth modules which could also represent a specific adaptation to the environment. The module units that produce vertical vegetative growth are the long shoots and the temporal short shoots, in either terminal or axillary position (Fig. 1). Temporal short shoots do not allow plants to grow as tall as long shoots, because little or no internodal elongation occurs during development (Brown 1971). Species that produce only shoots with short internodes have slower vertical growth than those species that also develop shoots with long internodes.

Given that the most important environmental resource for plants is probably light (Horn 1971), the occu-

pation of a higher stratum above ground may give a competitive advantage over shorter plants (Lovell and Lovell 1985), because the capture of space is a means of gaining access to more resources (Franco 1986).

Terminal and axillary inflorescences represent a differentiation of basic modules into structures with a specific function, i.e. sexual reproduction. Temporal and absolute short shoots permit rapid replacement of leaf area to increase photosynthetic capacity with low amounts of resources and effort expended in the formation of internodes. The development of thorns has been interpreted as fundamentally an adaptation against mammalian herbivores (Cooper and Owen-Smith 1986) or as a mechanism to reduce transpiration in arid zones (Orshan 1954).

This partitioning of functions into specialized basic architectural units gives more plasticity to the plant, and the proportion of modules assigned to different roles is strongly dependent on interactions with their environment (Lovell and Lovell 1985; Barthelemy 1986; Gottlieb 1986; Hardwick 1986). Species able to increase photosynthetic capacity within the constraints imposed by the mediterranean climate will be able to allocate more energy for reproduction as well as defense against herbivores – two important aspects in the species competition (Solbrig and Orians 1977).

The differences found in distribution of various modules among different growth forms (Fig. 3) can be related to the type of environment where each of them predominate. Correlations between growth habit and environment have long been known, suggesting that particular architectures and their fundamental branching patterns are advantageous in particular habitats (Menges 1987; Küppers 1989).

In general summer-deciduous species, which dominate at the xeric edge of the environmental gradient (Armesto et al. 1979; Montenegro et al. 1985), show a predominance of absolute short shoots that originate from basal long shoots at the beginning of the growing season. These absolute short shoots produce most of the foliage during the short period in which vegetative growth can occur (Brown 1971; Montenegro et al. 1988, 1989) – when optimum soil moisture and temperature conditions prevail. The majority of reproductive structures in summer-deciduous species develop from both the terminal and axillary buds of the absolute short shoots, making abundant flowering possible. Because resource investment in the formation of internodes is low, more resources can be assigned to the formation of reproductive organs. At the end of the vegetative and reproductive periods, the plants shed their absolute short shoots and their long shoot leaves, lowering maintenance costs of these structures (Orians and Solbrig 1977; Lovell and Lovell 1985).

Temporal short shoots were associated predominantly with the evergreen habit (Fig. 3), which dominates the mesic edge of the environmental gradient (Armesto et al. 1979; Montenegro et al. 1985). This module maintains the leaves in evergreens towards the end of the growing season, when environmental conditions become limiting. In the next growing season, when precipitation



and temperature conditions are adequate, the internodes of these short shoots elongate, increasing the vertical stratification of the system.

The growth habit of long shoots, with a rapid elongation of internodes followed by dormant periods, predominated in evergreen species (Fig. 3), apparently representing an adaptation to the stress period but also producing a wide range of vertical stratification, allowing the association of different species within the community (Brown 1971; Küppers 1989).

Besides the differences found in the distribution of module types between evergreen and summer-deciduous species (Fig. 3), the dissimilar peaks of modular formation (Table 2b) are a sign of the way in which each growth form exploits the environmental resources.

Architecture and growth dynamics in matorral shrub species are determined by the spatial and temporal organization of the different modules described. The different spatial arrangement of the modules permits the construction of a great variety of plant architectures (Fig. 4), and the variability in architectural construction is greater if the sequence and temporal formation of each of these modules is also considered (Montenegro and Ginocchio 1991).

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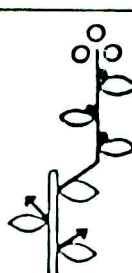



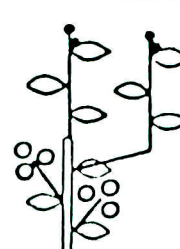




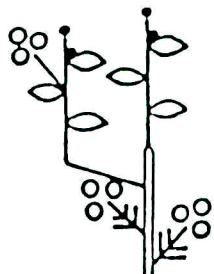



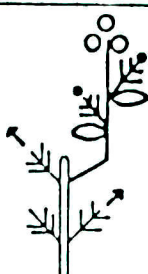




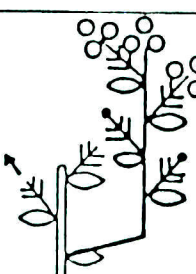



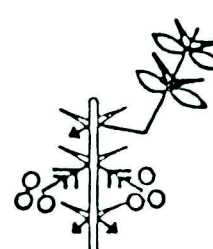




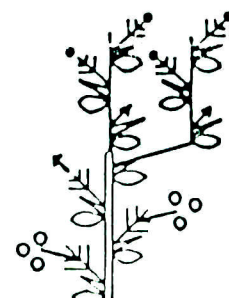
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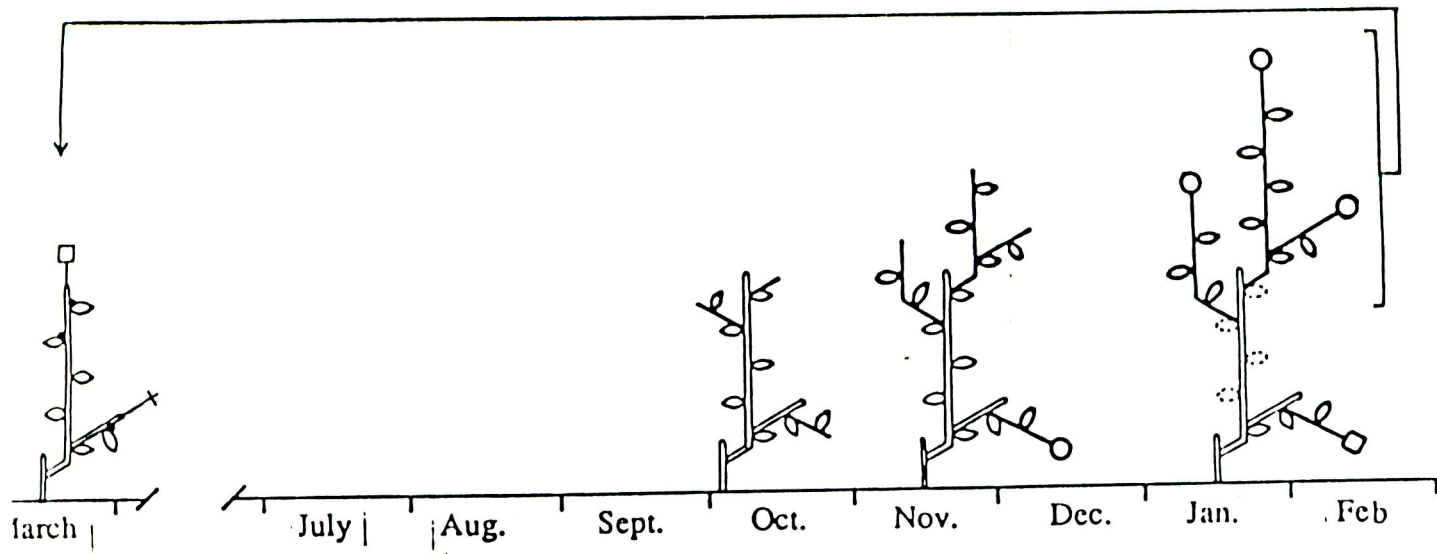
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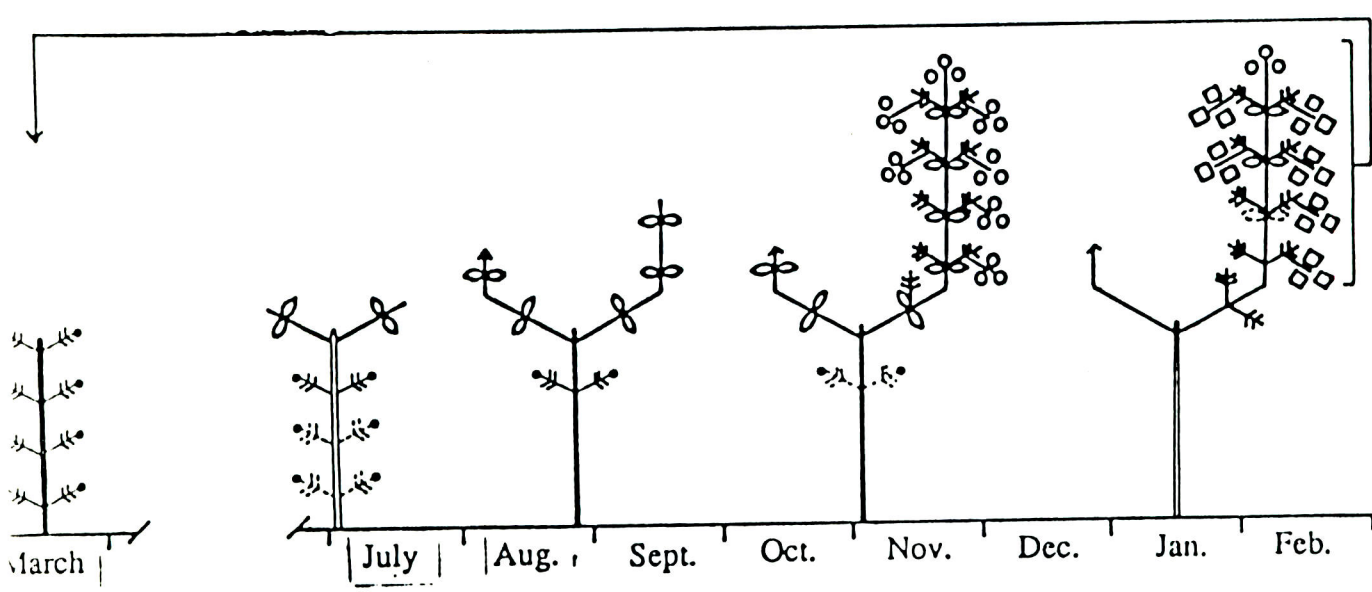
MODULAR COMBINATION	SPATIAL ARRANGEMENT	SPECIES
<div>1</div> <div>   </div> <div>(A)   (D)</div>	<div>  </div> <div>38%</div>	<i>C. parqui</i> <i>C. odorifera</i> <i>E. pulverulenta</i> <i>F. thurifera</i> <i>K. angustifolia</i> <i>K. oblonga</i> <i>P. boldus</i> <i>Q. saponaria</i>
<div>2</div> <div>    </div> <div>(B)   (C)   (D)</div>	<div>  </div> <div>29%</div>	<i>B. incisifolia</i> <i>C. alba</i> <i>L. caustica</i> <i>L. chequen</i> <i>M. boarya</i> <i>S. macrocarpa</i>
<div>3</div> <div>     </div> <div>(B)   (C)   (D)   (F)</div>	<div>  </div> <div>5%</div>	<i>F. lycioides</i>
<div>4</div> <div>    </div> <div>(A)   (D)   (E)</div>	<div>  </div> <div>10%</div>	<i>G. resinosa</i> <i>S. gilliesii</i>
<div>5</div> <div>     </div> <div>(A)   (D)   (E)   (F)</div>	<div>  </div> <div>5%</div>	<i>B. linearis</i>
<div>6</div> <div>    </div> <div>(D)   (F)   (G)</div>	<div>  </div> <div>10%</div>	<i>T. quinquinervia</i> <i>T. trinervis</i>
<div>7</div> <div>     </div> <div>(B)   (D)   (C)   (G)</div>	<div>  </div> <div>5%</div>	<i>T. alatum</i>



*Quillaja saponaria*



*Satureja gilliesii*



*Talguenea quinquinervia*

