# THE DENDROID SPURGES OF MACARONESIA SOME FUNCTIONAL AND BIOGEOGRAPHICAL ASPECTS

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*ABSTRACT.* The dracoid growth form of most of the Macaronesian woody *Euphorbia* species is a functional adaptation. It must be organized and maintained by a control system during the growth of the individual plants. Similar control systems seem to have developed in other plants of dracoid habitus (*Dracaena draco*, *Kleinia neriifolia*, etc.), too.

Some aspects of inflorescence formation, biogeographic distribution, and human connexions are discussed.

## INTRODUCTION

On the East Atlantic Islands (Azores, Madeira, Selvages, Canaries, and Capeverdeans) as well on the juxtacanarian parts of North West Africa and in the Mediterranean basin, there are woody species of the genus *Euphorbia* which share a lot of properties. They all have the similar appearance of shrubs or small trees, with nearly the same growth form, leaf shape and morphology of the inflorescences. With two exceptions, they also all inhabit areas with similar ecological condicions (LÖSCH *& al.* 1990; BRAMWELL *&* BRAMWELL 1990). This means the following species: *Euphorbia dendroides* (Mediterranean Basin), *E.obtusifolia/E.regis-jubae* (Canaries, NW Africa), *E.bourgaeana* (Tenerife), *E.atropurpurea* (Tenerife), *E.bravoana* (Gomera), *E.broussonetii* (Canaries), *E.berthelotii* (Gomera), *E.lambii* (Gomera), *E.piscatoria* (Madeira), *E. tuckeyana* (Cape Verde Islands), *E.balsamifera* (Canaries, NW Africa, Arabia), *E.mellifera* (Madeira, Tenerife, La Palma, La Gomera), *E.stygiana* (Azores), *E. anachoreta* (Selvagens). This paper points to some aspects of solved and unsolved problems connected with these particular plants.

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## MORPHOLOGY OF THE VEGETATIVE BODY

In these dendroid *Euphorbia* species, there are three different different types of growth (SCHENCK 1907): 1. the so-called "Federbusch" type ("dracoid" type) (SCHENCK 1907) with a more or less short stem and an umbrella-like canopy which occurs, in most of the regarded species, 2. a globular shrub type with an extremely short stem represented by *Euphorbia balsamifera*, and 3. a habit of a small tree or shrub, also with a stem like before but with a more or less irregular shaped canopy. This third growth type occurs with *E. mellifera* and *E. stygiana*; a similar shrub is *E.meuleniana* from the Hadramaut.

The very regular growth habit of plants belonging to type 1 is striking because it deserves a tight control, both by internal and external parameters. The nature of these interesting control mechanisms is unknown at moment. It does not only occur in these *Euphorbia* species but also in a variety of other plants which grow on the East Atlantic Islands such as *Dracaena draco, Kleinia neriifolia*, and members of the genera *Aeonium*, *Echium*, *Argyranthemum*, *Globularia*, and *Asteriscus*.

The canopies of the true "Federbusch" plants show a sympodial growth with quasi-dichasial or quasi-pleiochasial ramification. The young trunk, and later on the branches stop their growth at a certain signal in order to develop a terminal inflorescence. After fructification, two or more of the uppermost buds start to grow and to form a new branch, each. This process repeats several times resulting in a very regular branching. Regularity of ramification is also achieved because all (or nearly all) branch ends form inflorescences (and later on young branches), at the same time. This means that the signal for flowering and subsequent branching reaches all branch ends at the same time.

As in *Dracaena draco*, leafs are formed only in the youngest, *i.e.* terminal portions of the branches so that the interior canopy is void of leaves.

There is also regularity in the lengths of the branches and subbranches: The younger the subbranches are (*i.e.*, the higher the order of ramification is) the shorter they are. In few, individual cases, one or another branch retains growth without flowering and branching so that this regularity of canopy formation is not a totally strict one. Irregularities may also occur after traumatic events such as rupture or atrophication of certain branches after storms, fire, animal grazing, insect and fungal infestations.

From a mathematical standpoint, these "Federbusch" plants (at least in their ideal structure) are examples of self-similarity (MANDELBROT 1991) insofar as every subbranch with its system of ramification is similar to the branch and its ramification system to which it belongs, for every order of ramification.

The globular growth type can be derived from the "Federbusch" type if one assumes that the young stem ramifies immediately above the ground. The canopy of such a plant seems to lie directly on the surface of the substrate where the plant grows ("Kugelbusch").

The third growth type can be derived from the "Federbusch" type, too, if one assumes

that ramification does not obey such strict rules as in the "Federbusch" plant but is under looser control. Interestingly, *E.obtusifolia* exemplars grown in greenhouses under temperate climatic condicions, may loose their regular "Federbusch" shape and also attain the more irregular growth form of the *E.mellifera* type (ZIMMER, personal communication).

## FUNCTIONALITY OF THE VEGETATIVE BODY

In these dendroid spurges, there are conflicting demands on anatomy, according to physiological requirements, in several instances as is shown below.

In the habitats where most of these plants grow, water is not easily available during all time of the year, and so the plants are forced to take up atmospheric water from dew or fog, at least during the drought period. This is well known from *E.tuckeyana* of the Cape Verde islands which prefers mountanous habitats exposed to mist, cloud, and dew. The *Euphorbia* species inhabiting the Canarian *tabaibal* depend on nocturnal dew and diurnal fog, in their water supply. Also in the juxtacanarian biotopes of *E.obtusifolia* extended nocturnal dew and diurnal fog is formed as is shown by meteorological data for the the Tarfaya district (SW Morocco) (DELANNOY 1975). Seemingly also *E.dendroides* provides itself, at least partly, with atmospheric water. Only *E.mellifera* and *E.stygiana* live in places which are moist and foggy, at least during most of the year, and are thus not so much forced to economize water. This seems also to be the case with the above-mentioned greenhouse exemplars which will be watered by the gardeners regularly.

The small fog droplets must cast on the leave surfaces and be fixed there, then several small droplets must coalesce to form bigger drops which afterwards either fall down from the leaves or flow down over the branches and the trunk, to reach the soil surface (it is not known whether dendroid spurges take up water by their leaf stomata directly). The canopy furnishes a windless space where these droplets have the opportunity to sediment on the plant surface. Also dew will form by condensation of gaseous water, on the surface of the plant, especially of the leaves. Thus, on one hand, the total leaf surface must be maximal for photosynthesis and for water retention from mist and fog but it must be minimal for protection of the plant from evaporative loss of water by heat and wind.

During the dry season when the dendroid spurges will shed their leaves, water is retained in the woody parts of the plants. Because of this, the dendroid spurges are often erroneously considered by botanists to be succulents what they positively are not: Also deciduous trees of temperate and hot climate areas will shed their leaves during the unfavorable season and store water within their wood without being regarded by any botanist to be succulent plants; only *Kleinia, Plumeria*, and tree-like cactiform *Euphorbia* species can rightly be considered to be true succulents. Therefore the expressions "succulent bush" or "succulent shrub" for the Macaronesian biocenoses is not quite exact. The three Canarian

species *E.canariensis*, *E.handiensis* and *E. aphylla* are true succulents, however (BEYHL 1993).

Thickness of trunk and branches in the dendroid spurges must be maximal for maximal supporting capacity, for protection from rupture by wind and for water and nutrient storage but it must be minimal for protection of the plant from rupture by overweight and for saving material and built-up energy costs.

Such kinds of conflicting demands are typical for so-called *frustrated systems* (EBELING & *al.* 1988) where solutions only will arise by structural optimization. Here, optimization results in an umbrella-like canopy, in regular ramification, and in the formation of a leaf mosaic along the canopy surface. But the results of optimization processes depend very much on the internal and external condicions under which they were brought about and are very easily prone to disturbances. This may explain why plants inhabiting moister biotopes will lose part of the strict growth control and attain a more irregular shape.

These internal and external signals which regulate and control ramification and leaf mosaic formation must be both strict and simple, in the case of the "Federbusch" trees. This assumption is suggested by the fact that it is possible to simulate, by computer modelling, both the "Federbusch" shape (NEUREITHER 1992) and leaf mosaics (FISHER & HONDA 1979).

## FLOWERS AND INFLORESCENCES

As in all *Euphorbia* species, flowers are arranged in so-called cyathia which are some kind of a "functional equivalent" of true flowers. In the dendroid spurges, both bisexual, unisexual, and sterile cyathia occur. This secondary monoecy and sterility of cyathia can also be found in other, nonrelated *Euphorbia* species (BEYHL, to be published). Cyathia may form inflorescences as if they were flowers. The arrangement into inflorescences, of these cyathia, varies much in the different species and shows interesting traits (BEYHL, 1994). In the dendroid spurges, there are three types of cyathia arrangement (also see SCHENCK 1907): 1. single terminal cyathia which are surrounded by a rosette of bracts (*E.balsamifera*), 2. cyathia organized into a terminal panicle (*E.mellifera* and *E.stygiana*), and 3. cyathia arranged into dichasial inflorescences which altogether form a terminal umbel. This umbel is surrounded by a rosette of bracts (the remaining species).

The third type of inflorescence formation also occurs with other, unrelated *Euphorbia* species and also obeys to strict ramification rules (BEYHL, 1994). The formation of only one terminal cyathium, at least accidentally, is found also in other, unrelated species and can be derived from the umbellular inflorescence (BEYHL, to be published). At the moment, it is not clear, however, whether the panicle-like inflorescence type is derived from the umbellular or *vice versa*. In any case, these three different types of inflorescence formation correspond well to the three growth types.

## BIOGEOGRAPHY AND TAXONOMY

The "Federbusch" type spurges inhabit places with similar environmental properties. As they all have similar shapes there is no adaptive radiation between these species but they are true vicariants of each other. The opposite is the case with *Aeonium* species which both show quite different shapes and inhabit places of different ecological properties which means that this genus underwent adaptive radiation (LÖSCH *& al.* 1990). The genus *Echium* is intermediate between *Euphorbia* and *Aeonium*, in this respect: There are both vicariant species of the same shape (in similar biotopes) and radiating species of different shapes (in different biotopes), in Macaronesia.

*E. balsamifera* is a different ecological type which is also found in Africa and Arabia. Also *E. mellifera* and *E. stygiana* represent a different ecotype.

Taxonomy of all these species (and also of *E. dendroides* and *E. meuleniana*) should be worked out again using both anatomical, phytochemical, and ecological-geographical parameters. A phylogenetic tree should then be established which shows the descendence of these species and their relation to other groups within the genus *Euphorbia*. This phylogenetic tree should also show how these members of the genus came to colonize their present habitats.

## SPURGE AND MAN

It is supposed that the actual extent of the Macaronesian *tabaibal* as well of the corresponding formations in North West Africa and in the Mediterranean is anthropogenic, at least in part. So it is interesting to learn what the original extent and species composition of these plant formations was.

The Canarian name *tabaiba* seems to be of Arabic origin (from *tabîb* "physician") and means "little doctor", "lady doctor", or "medicine". This raises the question which plant species it meant originally (*E. balsamifera, E. resinifera*, or else?) and how it came to the Canaries. Where there Arabic expeditions to these islands, were there Arabic trading posts or settlements, was there some early exploitation of such medicinal plants? What was the true indigenous Canarian name of the plant which is now called *tabaiba*?

Since the Canarian and Madeiran habitats of all these *Euphorbia* species are threatened by expanding urbanization (BEYHL 1993) and the Capeverdean ones by expanding agriculture and afforestation some typical areas of these formations should be protected!

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