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Age structure and growth of *Dracaena cinnabari* populations on Socotra

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Abstract Unique *Dracaena cinnabari* woodlands on Socotra Island—relics of the Mio-Pliocene xerophile-sclerophyllous southern Tethys Flora—were examined in detail, especially with regard to their age structure. Detailed statistical analyses of sets of 50 trees at four localities were performed in order to define a model reflecting relationships between specific growth habit and actual age. The problematic nature of determining the age of an individual tree or specific populations of *D. cinnabari* is illustrated by three models relating to orders of branching, frequency of fruiting, etc. which allow the actual tree age to be calculated. Based on statistical analyses as well as direct field observations, *D. cinnabari* populations on Socotra do not regenerate to a great extent and their age structure generally indicates overmaturity. The unique Firmihin *D. cinnabari* woodland will reach the stage of intensive disintegration within 30–77 years with 95% probability. According to our analysis of dead trees, it is evident that, on average, *D. cinnabari* in populations at Firmihin dies after reaching 17 orders of peripheral branches.

Keywords Age determination · Arborescent *Dracaena* · *Dracaena cinnabari* woodland · Socotra Island · Yemen

Introduction

Dragon's blood, a highly prized product of the ancient world (Milburn 1984), still makes the tree *Dracaena* relatively famous. This deep red liquid exuding from injured bark is known in Arabia as 'damalachawin' or 'cinnabar'. Local people from Socotra still use it to cure gastric sores, dye wool, glue and decorate pottery and houses (Miller and Morris 1988). Although comprehensive information on chemical features of the dragon's

blood resin is available (Himmelreich et al. 1995; Vachalkova et al. 1995), too few studies on growth dynamic, phenology and ageing of arborescent *Dracaena* sp. have been implemented.

The age of fabulous dragon trees is thus still generally clouded in overestimation by Humboldt (1814) who hypothesized that a huge *Dracaena draco* with 15 m stem girth from Orotava, Tenerife was several thousand years old. A more probable average figure of up to 700 years old was suggested by Byström (1960). However, later observations by Symon (1974) and Magdefrau (1975) brought both a precise record of the age of cultivated trees and also the first clues on determination of ageing. Nevertheless, no authentic study on ageing of natural populations of *Dracaena* tree species has been published.

The dragon tree group provides an example of two major biogeographical disjunctions between East and West Africa, being of Tethyan origin according to fossil and paleoclimatic data. Hooker (1878) first proposed that the dragon tree, together with other species of the Macaronesian laurel forest, is probably a relic of an old vegetation which once existed in northwestern Africa. Axelrod (1975) proposed that subtropical elements, such as *Dracaena* and *Sideroxylon*, found refuge in eastern and western Africa, as a consequence of the desertification of the Sahara in the late Oligocene (Quézel 1978). However, it is also clear that *Dracaena* sp. stretched throughout the Mediterranean region into southern Russia (Gwyne 1966). According to pollen analyses from the Neogene, two extinct *Dracaena* species have been identified. Pollen of the first species, *D. saportae* Van Campo and Sivak, comes from Bohemia whilst the second, *D. guinetii* Van Campo and Sivak, was found in Tunes (Van Campo and Sivak 1976). Current species of the dragon tree group are, therefore, only a depleted and relic representation of the Mio-Pliocene Laurasian subtropical flora. These species supposedly thrived at the edge of closed forests. It is likely that they occurred in sunny and exposed areas of rocky slopes, cliffs and escarpments (Axelrod 1975).

The genus *Dracaena* comprises between 60 (Mabberley 1990) and 100 species (Bos in Kubitzki 1998). Recent

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taxonomic ambiguity has caused its classification within three families i.e. Agavaceae, Liliaceae and Dracaenaceae, the latter as a family arching over the former confusion. Most of the *Dracaena* species grow as shrubs or geophytes often having ornamental potential. There are only six species having the growth habit of a tree. These arborescent taxa of *Dracaena* can be found: (1) on Socotra—*D. cinnabari* Balf., (2) in south-western Arabia—*D. serrulata* Baker, (3) in eastern Africa—*D. ombet* Kotschy & Peyr, *D. schizantha* Baker, (4) on Macaronesian islands and in Morocco—*D. draco* L., in the latter location distinguished as subsp. *ajgal* Benabid et Cuzin, and (5) in Gran Canaria (Canary Islands) with the recently described *D. tamaranae* A. Marrero, R.S. Almeida and M. González-Martín.

All of these dragon tree species live in thermosclerophyllous plant communities of tropical-subtropical regions which are rather xerophyllous, sharing similar ecological requirements with a rainfall range of 200–500 mm and average temperatures of 18–20°C (Marrero et al. 1998). They are found between 10°N (Somalia) and 33°N (Madeira), and there is also some correlation between latitude and altitude. Populations in Madeira may be found at sea-level whilst those of Somalia never occur below 1,400–1,800 m altitude (Byström 1960).

Socotra Island, once linked to peninsular Yemen, probably comprises the woodiest part of what was once called “Happy Arabia”. The island, with an area of 3,609 km² (Aitken 2000) is situated on the African continental shelf 225 km east of Cape Guardafui, Somalia. At times it has been described with mythical attributes such as Island of the Phoenix or The Abode of Bliss, the latter probably owing to its biodiversity wealth related to an exceptional 8% forest coverage that is uncommon on mainland Arabia (Pavliš 2000). The prehistoric origin of local plants and their degree of endemism reaching some 35% (Miller and Cope 1996) place the island among the most environmentally significant places on Earth. Vegetation of the island, represented by several distinctive formations, derives from the Tethyan flora (Bramwell and Richardson 1973) and its unique character is the result of a long period of isolation; separation from Africa supposedly occurred in the late Cretaceous (Mies 1996).

Environmental conditions and quality throughout the island are generally good and much better than those on the major part of mainland Yemen. The island is geologically characterized by the plutonic nucleus of the granitic Haggier Mountains located in its centre, and by two similar crystalline massifs at the eastern and western tips of the island, in places overlaid by sedimentary rocks (Beydoun et al. 1970). Two limestone plateaus probably correspond with similar layers on the nearby Somalian peninsula (Kossmat 1907). The decomposition of granites has led to the formation of rich red soils. The soils, accumulated in the valleys and plains and even along the less steep slopes, form the deepest and most fertile soil deposits. An area within the confines of the limestone plateau is dissected by gullies. Little pockets of fine, grey

clayey soil occur between rock crevices, but larger shallow soil deposits have accumulated in depressions where the gradient is slight (Popov 1957). A sufficient set of climatic data is lacking; scarce information for a few years in the 1940s and in 2000 (Pavliš 2001) is all that is available. The island generally falls into an arid tropical zone, but with a climate tempered considerably by north-east and south-west monsoons, it is less torrid than that of the adjacent mainland. Precipitation ranges between 200 mm for coastal plains and 1,000 mm (estimate includes heavy horizontal rain-fall) for the highest mountains (Popov 1957; Miller and Morris 2001).

From a biogeographical viewpoint, Socotra is evidently more closely linked with Africa than Arabia but there are also interesting affinities with other island groups such as the granitic Seychelles and even some remote Atlantic islands (White 1983). Its three main biogeographical zones can be distinguished as: (1) coastal plains, (2) limestone plateaus, and (3) the Haggier Mountains.

Species diversity projected through altitudinal vegetation zones is markedly influenced by orographical, geological and pedological variability of the habitats. The same is true on many of the Canary Islands (Sunding 1972). Some of the most dominant tree species often give the landscape a rather bizarre or prehistoric appearance (cf. Balfour 1888) with respect to their physiognomy and structure. Prosperous shrubland and woodland can be found mainly at higher altitudes and in sheltered valleys dominated by xenomorphic growth forms as a result of plant adaptation to local harsh conditions, i.e. desiccating effects of strong winds and intensive solar radiation. The most evident adaptations evolved to assist the plants' survival include the swollen and silvery trunks of *Adenium obesum* ssp. *socotranum* (Vierh.) Lav. and *Dendrosicyos socotranus* Balf., and the distinctive umbrella or mushroom-shaped canopies of *D. cinnabari* Balf. and *Euphorbia arbuscula* Balf. (Mies and Beyhl 1996).

Five to six principal vegetation tiers are consistently distinguishable on Socotra (Miller et al. 1999; Buček 2001). Although prevalent physiognomic appearance is related to shrubland category, woodland and even forest categories are also present throughout all the tiers: (1) coastal plains and low inland hills with prevailing formations of open deciduous low shrubland (widespread *Croton socotranus* Balf. and *Jatropha unicostata* Balf.), (2) highlands with woodland character (variety of *Commiphora* sp. and *Boswellia* sp.), (3) limestone plateau with semi-evergreen forests (optimal conditions for *D. cinnabari*), (4) granite mountains/higher part of limestone plateau with evergreen forest and woodland (e.g. *Euphorbia socotrana* Balf., wild ancestor of pomegranate *Punica protopunica* Balf.), and (5) alto-montane zone with both evergreen forest (e.g. *Euclea balfourii* Balf.) and dwarf cushion vegetation on the rocks.

Open forests of *D. cinnabari* can be found mainly in the submontane zone. However, its common occurrence ranges from 300 to 1,500 m alt., preferring limestone-based subsoil. This area is mainly covered by thickets of



Fig. 1 The last remnant of 'Tethys woodland'

Rhus thyrsiflora Balf., *Cephalocroton socotranus* Balf., *Allophylus rhoidiophyllus* Balf., *Boswellia ameero* Balf., *B. socotrana* Balf., *Jatropha unicostata* Balf. and *Croton socotranus* Balf. At higher altitudes, this type of thicket is intermixed with *Hypericum* shrubland. *D. cinnabari* contributes significantly to the biodiversity value of the island (see Fig. 1).

The first inhabitants, represented by south-Semitic nomadic tribes, probably came to the island some 3,000 years ago (Naumkin 1993). Over many centuries they developed a relatively balanced land management system, securing self-sufficiency in food for a scattered population. As a matter of fact, grazing practice naturally influenced plant communities and notably contributed to the contemporary distribution and structure of tree populations around the island, including endemic *Commiphora* spp., *Boswellia* spp., *Dendrosicyos socotranus* and *D. cinnabari*.

Materials and methods

Two prolonged visits to the island in 2000 and 2001 occurred in varied weather seasons in transition, February/March, October/November and August/September. Attention paid to *D. cinnabari* specimens throughout the island has brought together records on phenology, habitat features, species composition, space and age structure of *D. cinnabari* populations and details of indigenous pastoral management influencing the guild. This species analysis was conducted as a follow-up of earlier vegetation investigations on Socotra Island undertaken by several scientific teams (Mies and Beyhl 1996; Miller 1989–2001, unpublished data; Petroncinni and Ceccolini, unpublished data). With a view to elucidate growth pace and ageing of *Dracaena*, supplementary microscopic analyses were also carried out (Adolt 2001). In order to illustrate regeneration processes of *D. cinnabari* under natural conditions and to obtain reliable information on germinative capacity, germination experiments were undertaken, both in the field and in the glasshouse (Pavliš 2001).



Fig. 2 'Sausage-shaped' branch sections or orders of branches

Analyses of the age structure of natural populations of *D. cinnabari*

An indirect method based on architectural age and statistical analyses were applied to analyze age structure of *D. cinnabari* population on Socotra. Accordingly, information was collected on growth features and dimensions of particular specimens of *D. cinnabari* near Firmihin (three localities) 12°28'28"N, 54°00'54"E, altitude 440 m; and Hamadero 12°35'12"N, 54°18'9"E, 328 m altitude. A randomly situated set of 50 neighboring specimens at all four localities was recorded, including the following parameters: (1) number of swollen sections on a randomly selected peripheral branch, (2) height of tree (m), (3) girth at breast height (cm), (4) length of a stem (m), (5) crown dimensions (m) and (6) spacing of *D. cinnabari* trees (m) in order to obtain spatial structure characteristics of the localities under study. Linear measures were taken with a tape, tree heights with a hypsometer/clinometer Silva-Clinometer. Data were processed using exploratory data analysis (EDA), theory of estimation and probability distribution. Details of mensurational data of trees are not part of this paper (Adolt 2001; Pavliš 2001). At Firmihin additional sampling was also carried out, consisting of 22 dead dragon trees (most already uprooted), to obtain a reference set of the probable age of overmature trees.

For each analyzed dragon tree at the given locality, sampling age was calculated according to Eq. 2 (see below). Age sampling obtained in this way was then analyzed. It has been found that it is possible to determine normal distribution in all samplings. For testing normality the following tests were used: diagrams of normal probability, diagrams of empirical density of probability, test of the combination of sampling skewness and kurtosis and Kolmogorov-Smirnov test (Meloun and Militký 1998). According to the determined parameters of distribution (mean values and standard deviations), diagrams of probability densities and diagrams of distribution functions of dragon tree age in particular populations were constructed.

An indirect method proposed in this paper for age structure analysis is related to the search for a model reflecting relationships between the number of flowering periods and the actual age of a specimen. The relationship can be well defined through specific branching of arborescent *Dracaenas* characterized by markedly swollen branches segregated individually by narrowed sections or 'sausage-shaped' sections (see Fig. 2). These obviously relate to the growth rhythm of a tree and correspond to one period of flowering.

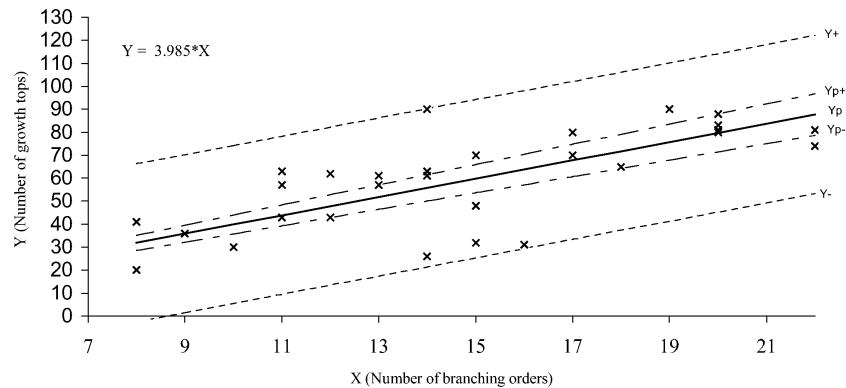


Fig. 3 The model of a relation between the number of growth tops of the crown periphery and the number of orders of peripheral branches. Lines $Yp+$, $Yp-$ depict a region where all linear models without an absolute term will occur with 95% probability. Lines

$Y+$, $Y-$ depict a region where all experimentally determined values of the number of growth tops of the crown periphery in dependence on the number of orders of peripheral branches will occur with 95% probability

This branching peculiarity was first described by Symon (1974) and Magdefrau (1975) from observations of cultivated specimens of *D. draco*. However, it was not statistically utilized for any generalization of age determination. The presented indirect method of age determination is based on the number of orders of peripheral branches of the crown distinguishable according to their characteristic 'sausage-shaped' form. Growth of the tree apex is terminated after flowering followed by branching which is often monochasial in the higher order of branches. In older branches (branches of several first orders), distinguishing the part corresponding to one flowering period may be more difficult due to secondary swelling of the branch which can result in suppression of the typical 'sausage-shaped' form of a branch section. From the vantage point of the top, after climbing a tree, it is possible to see very distinct, particular orders even in older branches—a trace after a peduncle which remains noticeable even after considerable swelling of the branch. For the purpose of developing a theory of age estimation, 30 *D. cinnabari* trees in the Firmihin area were analyzed. The number of 'sausage-shaped' sections (orders of peripheral branches of the crown) was determined (round mean value from several randomly selected branches), as well as the number of crown tops (i.e. individual 'dragon heads') on the crown periphery, the number of fruiting tops and the number of flowers on the crown periphery. Based on the data obtained, (1) a model was developed of the dependence between the number of crown tops on the crown periphery and the number of orders of peripheral branches, and (2) a relationship was derived between the number of fruiting tops of the crown periphery and the total number of tops of the crown periphery. The following considerations and preconditions were dealt with:

- In general, it is not possible to suppose that trees are in flower in all crown tops simultaneously (in the same year); evidently only part of all tops is in flower.
- There is a significant correlation between the number of tops on the crown periphery and the number of orders of peripheral branches.
- The number of branch orders of the whole crown periphery is increased in a given age by one (within a period which is equal to the ratio of the mean number of tops and the mean number of yearly flowering tops).
- The ratio is not changed if only the crown periphery is considered.
- Flowers can appear in various seasons of the year and, therefore, it is more suitable to use fruit panicles which persist on a tree for a longer time than flower panicles but not longer than 1 year.

For the given number of orders of peripheral branches it is possible, according to established models, to find:

- Average number of tops on crown periphery
- Average number of tops flowering yearly
- Average time necessary for increasing the number of branch orders along the whole crown periphery by just one order.

In this way, it is possible to estimate the age of a *D. cinnabari* crown. For the final estimate of tree age, it is still necessary to find the tree age at the time of first flowering (in the majority of cases, also of first branching). The estimate of age rate made on the basis of several non-ramified trees of known age served this purpose. An indigenous "gardener" estimated the age of one *D. cinnabari* specimen he was cultivating for ornamental purposes. However, local understanding of the passage of years is not very exact. Based on the information provided, it was supposed that in the time before the first flowering, the *D. cinnabari* stem showed a height growth corresponding to about 10 cm/year. According to the known stem length of the analyzed tree it is then possible to estimate the age when the first flowering and branching occurred. The sum of tree age in the time of first flowering and the age of the tree's crown gives the estimate of its total age. The estimate of tree age can then be expressed according to the following relation:

$$V = \int_0^x \frac{f(x)}{g[f(x)]} dx + \frac{l_{\text{stem}}}{d_{\text{year}}} \quad (1)$$

where V is the tree age, \int_0^x is the definite integral from zero to x , $f(x)$ is the function of the relation between the number of tops on the crown periphery and the number of orders of peripheral branches, $g[f(x)]$ is the function of the relation between the number of annually fruiting tops of the crown periphery and the total number of tops of the crown periphery, l_{stem} is stem length, and d_{year} is the mean annual length increment of a stem.

Based on the above mentioned conclusions, three models were constructed aimed at identifying proper relations for age assessment of *D. cinnabari*.

Model 1: a model of the relation between the number of growth tops of the crown periphery and the number of orders of peripheral branches

There is a statistically significant linear dependence (probability of invalidity of the thesis is <1%) between the variables. The correlation coefficient value amounts to 0.716 (95% confidence interval 0.479–0.855). The significance test was carried out using Ruben transformation (Meloun and Militký 1998). The linear model was accepted, the model diagram and its parameters are

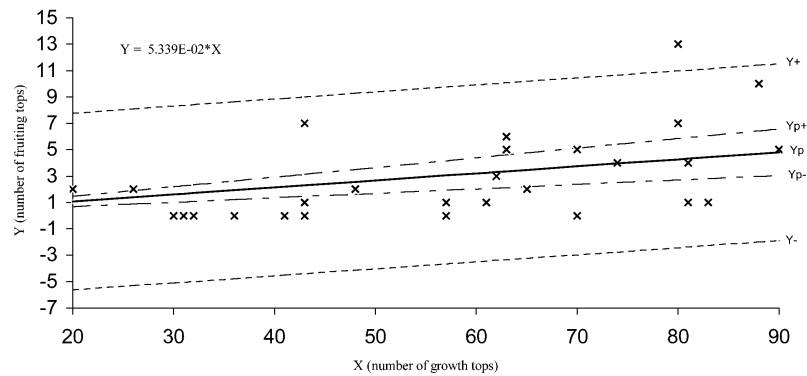


Fig. 4 The model of a relation between the number of annually fruiting growth tops of the crown periphery and the number of all growth tops of the crown periphery. Lines $Yp+$, $Yp-$ depict a region where all linear models without an absolute term will occur with

95% probability. Lines $Y+$, $Y-$ depict a region where all experimentally determined values of the number of growth tops of the crown periphery in dependence on the number of orders of peripheral branches will occur with 95% probability

given in Fig. 3. The model represents an important improvement in prediction as opposed to the use of a simple arithmetic mean of the interpreted variable which was demonstrated by a test based on the analysis of variance. The linear model is acceptable for the description of dependence, verified by a test according to Utts (1982). The model does not include an absolute term. The term was not taken into consideration because in a previous calculation, it was shown to be insignificant. The absence of an absolute term is also in agreement with the idea that with zero number of orders of peripheral branches, the number of growth tops of a crown also has to be zero.

Model 2: a model of the relation between the number of annually fruiting tops of the crown periphery and the total number of growth tops of the crown periphery

A linear correlation coefficient between the values of the variables amounts to 0.534 (95% confidence interval 0.215–0.750). The correlation coefficient is statistically significant; probability of error of the thesis does not exceed 1%. The model and its parameters are given in Fig. 4. Based on the test according to Utts (1982) the linear model was found to be acceptable for the dependence description (Meloun and Militký 1998). The regression function is statistically significant (its use for prediction is more suitable than the use of arithmetical mean of a dependent variable). The model does not include an absolute term because in a previous calculation it was shown to be insignificant. Similar to the model mentioned above, there is a logical substantiation of the absolute term insignificance. It is based on the fact that with zero number of tops on the crown periphery, the number of yielding tops on the crown periphery also has to be zero.

Model 3: a model of the relation between tree age and the number of orders of peripheral branches and stem length

Since both previous models are linear and do not include an absolute term, the general relation Eq. 1 for the calculation of tree age changes to a simpler relation:

$$V = \frac{1}{k} \times X + \frac{l_{\text{stem}}}{d_{\text{year}}} \quad (2)$$

where V is the tree age, k is the linear term of the dependence model of the number of annually fruiting tops of the crown periphery on the total number of tops of the crown periphery (a value of 0.053388), X is the number of orders of peripheral branches, l_{stem} is the stem length, and d_{year} is the mean annual length increment of a stem.

A relation $\frac{1}{k}$ in the formula corresponds to the estimate of the average time (expressed in years) necessary for increasing the number of branch orders of the whole crown periphery by just one order.

Results and discussion

Peculiarities of growth

In many respects Dracaenaceae are implicitly exceptional among monocotyledonous plants. One of the remarkable features is their secondary growth. There are even curious growth zones on parts of the stem or branch of *D. cinnabari* (Adolt 2001) resembling growth rings of a temperate zone. They are, however, of no use for age estimations due to the probability of being caused by specific crossing of vascular bundles (Razdorskij 1954; Tomlinson and Zimmermann 1969). This secondary tissue consists of scattered vascular strands, and is quite unlike that of dicotyledonous trees (Hallé et al. 1978). However, there is a close structural and developmental relationship between primary and secondary vascular bundles, according to Tomlinson and Zimmermann (1970), revealing closeness of developmental steps from primary to secondary growth.

Another distinctive feature of the arborescent *Dracaena* group is its growth habit called ‘Dracoid habitus’ (Bos 1984; Lösch et al. 1990) or coined as Leeuwenberg’s model (Hallé et al. 1978). It can be found in plants of several families, and was indeed present in extinct plants such as *Lepidodendron* sp., *Bothrodendron* sp. or *Sigillaria* sp. of the Carboniferous period (Stewart and Rothwell 1993). *D. cinnabari* bears its leaves exclusively at the end of the youngest branches arranged in clusters (‘rosette trees’) like similar ‘dracoid’ plants. The oldest leaves seem to be shed en bloc every 3–4 years with simultaneous maturing of new leaves sensu ‘leaf-exchanging-type with periodic-growth’ (Longman and Jeník 1987), influenced by incessant growth of the branch at its tip. Interestingly, some ‘dracoid’ species shed all their

leaves each year at the beginning of the dry period. In other words, 'dracoid habitus' denotes a special way of growth and ramification the details of which are further exemplified by the example of *D. cinnabari*.

There always arise more or less symmetrical branches from the upper end of a trunk, being somewhat inflected, rarely rectilinear, but branching again at their ends, to form the second, third, etc. orders (see details of the crown in Fig. 2). Branching normally occurs only when growth of the terminal bud is stopped, either by flowering or by a traumatic event. However, branches often develop only one single secondary branch at their tip, after cessation of growth, so that they look as if they had not ramified (Beyhl 1996). Large erect terminal panicles of flowers expand from the terminal bud of the youngest branches and, after it has matured, it is pushed aside as one or more axillary buds develop in the axils of the leaves immediately below the inflorescence (Symon 1974). This new shoot replaces the parental axis; growth of each swollen branch unit always ends after blooming (Bos in Kubitzki 1998). One or more buds from the nearby leaf axils will then be activated to grow and to form a new branch, although occasionally in a pseudo-dichotomous way. Branches are, therefore, characterized by pronounced swollen units segregated individually one from another by a narrowed joint obviously related to tree growth rhythm over the course of time. Each axis is, therefore, a sympodium consisting of many successive growth units (Symon 1974). The sympodium appears articulate both from the scars of the dried inflorescence stalks and from a swelling which marks each joint (Zimmerman and Tomlinson 1969). These slightly swollen units, marked by constrictions, are referred to, e.g., Byström (1960) as 'generations of branches'. Such a ramification system of branches of several orders subsequently yields a very regularly shaped, umbrella-like crown (Beyhl 1996). These swollen parts or 'sausage-shaped' sections have incomparable value for both age assessment of individual trees and whole *Dracaena* sp. populations in natural stands, since wood anatomical structure, classical dimensional characteristics as girth at breast height (g.b.h.), or tree height do not provide credible clues.

In spite of that, *D. cinnabari* flowering periods seem to differ notably on Socotra from locality to locality (even ever-flowering is probable), *D. cinnabari* blooming and subsequent fruiting always take only a certain percentage of crown 'dragon heads' during "mankind's time marker" (1 year). Fruiting assessment described in model 2 of the methodology above indicates percentage of fruiting heads as low as 5% per year (cf. Symon 1974). Notwithstanding some difficulties, a model can be deduced for crown fruiting in the course of time that brings important clues for age estimation of either trees or *D. cinnabari* populations (vide infra).

The fruits are globose, fleshy berries changing from green to black as they ripen and becoming orange-red in the last stage. Berries bear 1–3 seeds that are then eaten by birds (e.g. *Onychognatus* sp.) which function as

dispersal agents. Although berries of both species have nearly the same size (Beyhl 1996), *D. cinnabari* seeds are considerably smaller than those of *D. draco*. There are also differences in the number of seeds inside a berry. According to the present study, the quantity of 2- to-3-seeded berries of *D. cinnabari* reaches as high as 38.3%, as compared to the berries of *D. draco* that contain only one seed with 97.4% probability. *D. cinnabari* has got in 95% of cases a seed diameter between 4.13 and 4.98 mm. On the other hand, *D. draco* seeds have diameters from 6.60 mm to 8.81 mm with the same probability. Weight of the seeds also differs significantly—i.e. 1,000 seeds of *D. cinnabari* weigh only 68 g whereas 1,000 seeds of *D. draco* weigh 335 g (Adolt 2001).

Age structure of *D. cinnabari* populations

Knowledge of the tree population age structure is a key factor for determining the procedure and urgency of their early and effective conservation. However, it is a very time-consuming task to determine the age of trees, whether monocotyledonous or dicotyledonous, by their direct measurement over time. In spite of this, precise yield tables for main production tree species have been developed through generations of foresters in temperate commercial forests. Such a direct method also brought the first clues about the ageing of *D. draco* (Symon 1974; Magdefrau 1975). Nevertheless, indirect methods based on architectural age and statistical analyses (Hallé et al. 1978) seem to be more suitable for age determination of monocotyledonous trees. In that indirect way, age structure estimation of *D. cinnabari* population on Socotra was carried out.

Based on the above-mentioned model 3 of the dependence of *D. cinnabari* tree age on the number of orders of peripheral branches, the problematic nature of determining the exact age of individual trees is evident. The problem is related to the difficulty of estimating the age of a tree at the first flowering and the total crown age. The assessment of crown age is limited by a potential error in determining the coefficient k of a regression model (see Eq. 2). An error in the estimate of coefficient k shows a zero mean value and with 95% probability its absolute value does not exceed a limit of 0.0196. The average time necessary for increasing the number of orders of peripheral branches of the whole crown by just one order shows limits $\frac{1}{k+0.0196}$, i.e. 13.7 years and $\frac{1}{k-0.0196}$, i.e. 29.6 years and a mean value equal to $\frac{1}{k}$, i.e. 18.7 years. If a tree of *D. cinnabari* is considered with n orders on peripheral branches then the actual age of the crown (with 95% probability) will be in the interval $n \times 13.7$ years to $n \times 29.6$ years and a mean value will most probably be $n \times 18.7$ years. With respect to the small range of data, it is not possible to report in detail about errors of age estimate of the first flowering. It is possible to suppose only that the errors affect tree age determination less significantly than those in estimation of crown age.

Fig. 5 Diagram of probability density for age in particular populations under study. Mean age of particular populations on the age axis corresponds to curve tops

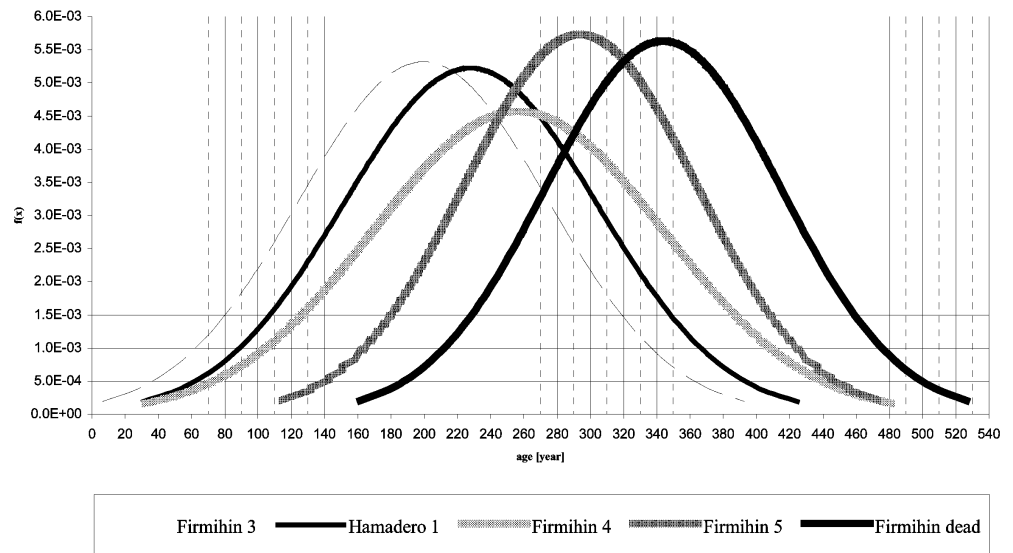
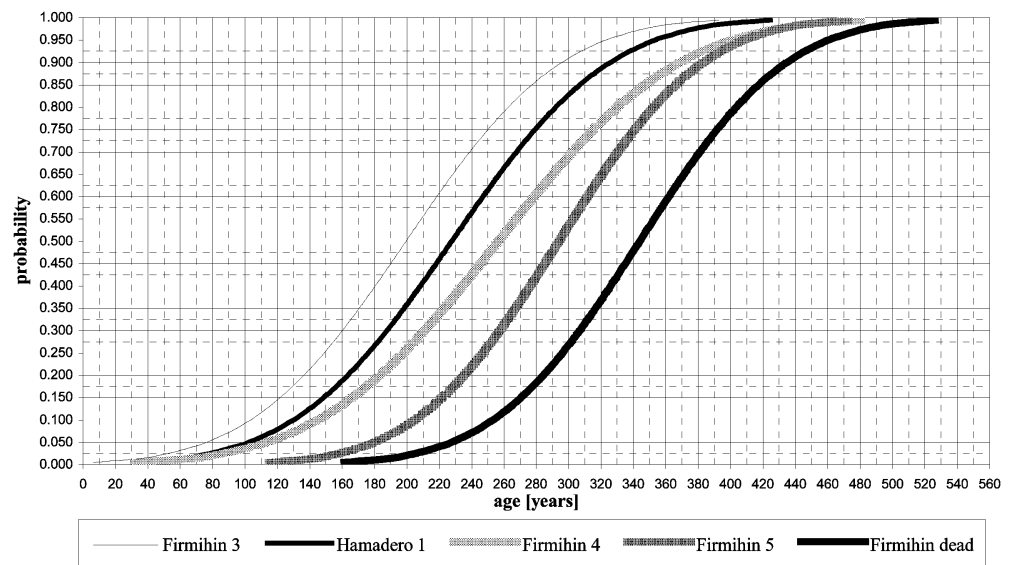


Fig. 6 Diagram of distribution functions of age for selected populations of *Dracaena cinnabari*. Probability 0.5 corresponds to the arithmetical mean of age on the age axis for the given population



The range of probable age of one ‘sausage-shaped’ section of *D. cinnabari* determined by our team thus reaches higher values, i.e. 13.7–29.6 years, than findings of Symon (1974). His findings concerning probable age of one ‘sausage-shaped’ section of *D. draco* indicate for (1) Adelaide Zoo 11 orders of constrictions, each being 9–10 years old; and for (2) Victoria Park Garden 5–6 orders, being 11–14 years old. However, our data are close to Magdefrau’s (1975) direct findings from Tenerife where he stated that age of one ‘sausage-shaped’ section ranged from 11–17 to 13–16 years. Although the authors mentioned above used the direct method of age estimation they presumably have not used statistics to estimate error probability of their findings.

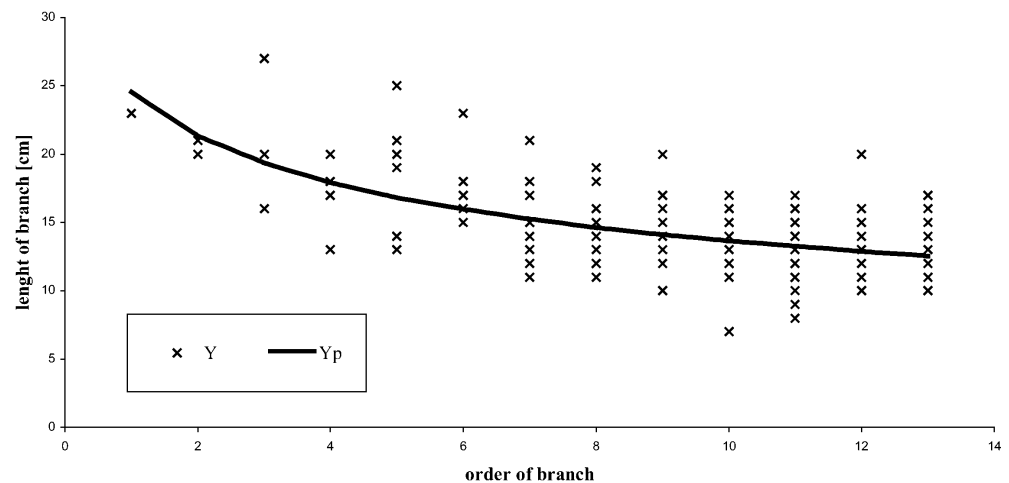
Comparisons of *D. cinnabari* populations on Socotra from the viewpoint of age, implemented by means of a

single factor ANOVA with fixed effects (Meloun and Militký 1998), brought a finding that at least two populations significantly differed in their average age probability, with the error of predication being $2.409E-13$. The Dunnett test procedure of a multiple comparison (Meloun and Militký 1998) was then applied. As a comparative group, the sample of dead dragon trees from the Firmihin area was used. Figure 5 describes the most probable age structure of analyzed natural populations of *D. cinnabari* on Socotra.

According to the position of curves for particular populations with respect to the curve of dead *D. cinnabari* trees (Fig. 6), we can deduce the amount of time needed, on average, for a given population to reach the value of average age of *D. cinnabari* death, i.e., to the stage of advanced decay (under conditions of zero regeneration of

Table 1 Mean age of *DC* populations according to localities and estimate of probable time scope to their disintegration stage

Population	Mean age of <i>DC</i> population (years)	Estimation of a probable time scope to the disintegration stage of <i>DC</i> population on Socotra Island (years)		
		The most probable estimation k	Lower 95% estimation k	Upper 95% estimation k
Firmihin 3	200	144	97	230
Firmihin 4	257	87	56	138
Firmihin 5	294	50	30	77
Hamadero 1	228	116	80	178

Fig. 7 Dependence of the length of a 'sausage-shaped' section, i.e. order of branch, on its hierarchical position in tree crown order

population). For similar analyses, however, it would be necessary to model the development of populations on the basis of known age distributions in populations, the course of *D. cinnabari* decline, seed germination and young plant mortality. The following table includes an overview of the expected stage of intensive disintegration at particular localities under analysis (Table 1).

According to the results of the Dunnett test of multiple comparisons, the mean age of *D. cinnabari* trees at all localities is lower than that of dead *D. cinnabari*; probability of invalidity of the thesis is lower than 1%.

The procedure described for age determination is based on preconditions that can be further complemented and/or specified. Most important is the fact that fruits persist for about 1 year on floral panicles so that according to the number of panicles, it is possible to determine the number of flowering tops of the crown periphery in a given year. This observation needs to be supported by further field investigations. In case of finding new facts, it would be possible to specify the most suitable time for obtaining data for the model construction. In any case, it will be useful to analyze a greater number of trees for the purpose of obtaining more precise estimates of present models (narrowing the confidence interval of coefficient k) or for possibly finding more suitable models (non-linear) describing the dependencies mentioned above.

The model of the dependence of annually fruiting tops of the crown periphery on the total number of crown tops could be non-linear. Non-linear dependence was also

found between branch order and its length. The model is depicted by the diagram below (see Fig. 7). The model is statistically significant, being constructed on the basis of crown analysis of one *D. cinnabari* tree. A decrease in the length of a 'sausage-shaped' section towards higher orders of branches is visually evident in all *D. cinnabari* trees. There is, however, a question as to what extent the dependence is related to growth dynamics and to what extent to changes in flowering frequency of particular tops in relation to age (branch order). If the dependence is a result of growth dynamics alone, the model of the number of annually flowering tops of the crown periphery, as related to the total number of tops of the crown periphery, is linear. It is, however, more probable that the dependence is affected by both factors—growth dynamics and changes in flowering frequency of particular tops over time.

The potential of natural regeneration and further seral development of *D. cinnabari* populations

In order to verify the potential of natural regeneration of *D. cinnabari* forests a controlled germination experiment was performed in a glasshouse at the Mendel University of Agriculture and Forestry (MUAFF), Brno. Results reflect generally low germination capacity of *D. cinnabari* after direct sowing on soil, after stimulation by $H_3C-COOH$; only 5% germination was reached. However, the capacity increased to 22% using 1% H_2O_2 solution.

Meanwhile, the experiment indicates that germination capacity of *D. draco* seed (used for comparison), under optimum conditions, can reach at least 77% (Adolt 2001). Even though the seed experiment in the glasshouse at MUAF was finished in April 2001 (remaining seeds were removed from blocks and discarded), pots with germinated seeds were maintained in three other glasshouses as a control. These glasshouses did not have guaranteed microclimatic conditions, but onward gradual germination was recorded (even reaching a surprising 20%) as temperature increased through the spring, summer and early autumn in 2002. It therefore seems to support the hypothesis of higher temperature as a trigger for germination of *D. cinnabari*.

There are, however, significant differences between the present results and the findings of Beyhl (1996) who mentions *D. cinnabari* germination capacity of as high as 35%. Such a divergence can naturally be caused by many factors, ranging from germination energy variation among phenotypes to different glasshouse conditions or effects of mycorrhizal requirements.

Averaging the number of branches calculated per tree (i.e., 1,056 branches per tree) and extrapolating data on the number of berries per yielding panicle, i.e. 580 berries on average (nine panicles counted), the interesting probable number of 611,000 seeds is achieved during the life span of an average tree. Comparing the data with the above mentioned ideal germination capacity of 22%, another interesting figure of about 134,000 potentially germinated seeds per tree is computed.

Seedling vitality in a glasshouse tends to be quite satisfactory as mortality rate is only about 10%. However, field observations indicate that seedling mortality rate, under climatic conditions of Socotra Island, rises up to 100% if a subsequent favorable period of rainfall does not come (also Miller and Morris, personal communication). In conformity with that, even a field experiment with 200 seeds sown inside a game-proof fence (Pavliš 2001) did not provide a single germinated seedling after 1 year.

The facts mentioned above bring some doubts about the prevalent assumption of strong browsing effects of livestock on any tree species regeneration (except poisonous plants), especially the influence of ubiquitous goats whose number reaches about 30,000 (Clarke and Dutton 2000). The presence of livestock is related to the first human habitation dating back some 3,000 years (Naumkin 1993) and revision of their land management practices confirmed prevailing sustainability within contextual birth-rate. Although leaves of *D. cinnabari* are in general unpalatable to cows and goats according to interviews with indigenous community members, our own field observations indicate that goats nevertheless do feed on fresh leaves of windfall trees. Interestingly, even though leaves are not considered palatable pasturage by herders, they themselves use a limited quantity of collected berries to feed cows in times of drought.

Although certain age uniformity of most of the *D. cinnabari* stands is remarkable, there is an interesting exception related to the occurrence of the youngest trees

and seedlings on steep and extreme cliffs (at all altitudes of *D. cinnabari* occurrence). This small-scale success of *D. cinnabari* reproductive strategy can be consequently related either to a more favorable moisture regime for seed germination inside stone pockets of those cliffs or to habitat inaccessibility to browsing animals.

The umbrella-shaped canopy of *D. cinnabari* also apparently helps seedlings to thrive better in its shadow than in full sun. This umbrella type of crown also functions as an adaptation to intercept humidity from mist, horizontal rainfall and dew, later falling down from the branches. This is of course the way to increase soil water potential below the crown. Moreover, the canopy shadow reduces soil water evaporation to values lower than elsewhere in the environment (Mies and Beyhl 1996). This favorable effect of the 'crown type' for contingent germination could presumably be the reason why many *D. cinnabari* trees grow close together, forming an interconnected crown unit, i.e., younger intermediate specimen thriving under older one growing into crown above, gradually taking over the crown space, forming finally either coexisting or competing twins.

At the same time, it is also difficult to expect that global climatic changes would be the only factor negatively influencing *D. cinnabari* regeneration, taking into account the case of the Diksam plateau (tableland below Hagghier) where, in the past, one of the largest *D. cinnabari* forests supposedly existed. At present, this area is in a stage of deep disintegration with too few scattered patriarch trees (perhaps up to 350 years old). Woodland of this area obviously started to decay more than 100 years ago.

There is, accordingly, stronger evidence for the hypothesis of a sudden mass regeneration in favorable short periods interrupting the standard long-lasting semi-arid weather pattern. However, it is still difficult to judge if this sudden mass recovery wave is caused by favorable climatic conditions or follows a decline of livestock population, i.e., recurrent animal-unfavorable deficiency of water and feed. This *D. cinnabari* reproduction strategy is slightly similar to the forest reproduction pace of natural monocoenotic overmature spruce forest of a boreal zone which regenerates over large areas following a zero event (Oldeman 1983) caused by wind, fire, or bark-beetle attack. Such a presumption of the species regeneration course is, moreover, supported by the very uniform age structure of *D. cinnabari* populations on most of the optimum habitats on Socotra.

Based on statistical analyses as well as on direct field observations, *D. cinnabari* populations on Socotra, however, do not regenerate to a great extent and their age structure generally indicates overmaturity. According to analysis of dead trees, it is evident that *D. cinnabari* populations of Firmihin die on average after reaching 17 orders of peripheral branches. Therefore, it is possible to suppose that a large part of the world's most extensive '*Dracaena* woodland' complex in area of Firmihin can be assessed from the viewpoint of age as a population in the area of locality Firmihin 5. It means that, with 95%

probability, stands here will be in the stage of intensive disintegration within 30–77 years. Such an alarming pace of likely *Dracaena* forest disappearance caused by the pressure of civilization already has some parallel with the islands of Tenerife, La Palma or Gran Canaria (Canary Islands) where forests of *D. draco* and *D. tamaranae* have not survived except for a few scattered trees currently located mainly on the most inaccessible cliffs.

Therefore, if the *D. cinnabari* woodland is to be preserved at its present extent, it is most urgent to start monitoring its natural regeneration, since we may already be at the 11th hour. Also, there is still a strong hope that the rich and unique biodiversity of Socotra—unrivalled in the Indian Ocean and in the Arabian region—will be maintained through the successful conservation and wise developmental efforts of national and international agencies.

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