

## PHENOTYPE EXPRESSION OF EPIPHYTIC GESNERIACEAE UNDER DIFFERENT MICROCLIMATIC CONDITIONS IN COSTA RICA

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**Abstract.** The phenotypic expressions of four species of epiphytic columnneas (Gesneriaceae) were analyzed in the premontane rain forest of the Reserva Biológica Alberto Brenes in Costa Rica. These expressions were correlated with the microclimatic conditions of the individual growing site, and two spheres with particular microclimatic environments were identified within the canopy. The variance in annual shoot length, age of apical meristem and ramification of each species was up to 100% from the mean. This variance in phenomorphology can be explained by the different microclimatic conditions between each growth site. Rare and unpredictable high saturation deficits that occur in the air sphere between big branches, where mostly hanging epiphytes like *Columnnea oerstediana* and *C. microphylla* grow, led to a reduction in apical meristem activity and, thus, to higher ramification rates and shorter apical meristem age. By contrast, microclimatic amplitudes in the sphere around the branches are mitigated by the epiphytic vegetation, the accumulation of organic matter and their specific water buffer capacity. Therefore, microclimatic influence is less severe for plants growing closer to the branches, like *C. lepidocaula* and *C. verecunda*. As phenotypic expression in the canopy has been observed to correspond to these spheres, their existence allows for the creation and definition of the terms "ramosphere" and "aerosphere".  
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**Key words:** *Canopy, Columnnea, Costa Rica, epiphytes, Gesneriaceae, microclimate, phenotype expression.*

### INTRODUCTION

Vascular epiphytes are one of the most distinct features of tropical rain forests. In premontane or montane rain forests they may cover more than 100% of the branch surface (Johansson 1974, Freiberg 1996). Although a first look at the distribution of epiphytic species may lead to the assumption that their occurrence shows no stratification (Richards 1952), several attempts have been made to demonstrate its existence. Schimper (1888) sorted epiphytes according to their habitat, distinguishing three parts of the phorophyte: the stem, the branches and the twigs. More recently, the division into five geometrical zones (Johansson 1974) has been widely accepted. Johansson pointed out that it should be possible to characterize these zones by their microclimate and that microclimatic differences between them might partly explain epiphyte occurrence or preferences within the canopy.

Research approaches to epiphyte ecology, primarily distribution on the phorophyte, have been treated differently from author to author. Study has focused on species diversity (Yeaton & Gladstone 1982, Bennett 1986, Catling *et al.* 1986, Catling & Lefkovich 1989), biomass (Nadkarni 1984, 1986; Nadkarni & Matelson 1992, Hofstede *et al.* 1993, Ingram &

Nadkarni 1993), cover on the branch (Johansson 1974, 1975; Freiberg 1996), sum of individuals (Sanford 1968, Valdivia 1977, Kelly 1985, Zimmerman & Olmsted 1992), closest neighboring plants (Hietz & Hietz-Seifert 1995), successional stages and distribution of plant size (Dudgeon 1923, Benzing 1980, 1990; Catling & Lefkovich 1989), or phytosociological units (Went 1940, Wolf 1993a, b). The phenomorphology of an individual plant is unique for a specific growing site. A comparison of phenomorphological variability between sites can thus help to detect the importance of different growth conditions. However, this possibility has mostly been neglected for epiphytes.

The phenomorphology of four epiphytic *Columnnea* species (Gesneriaceae) was analyzed in this study. In a parallel investigation, microclimatic measurements were carried out to characterize the growing sites of the epiphytes in greater detail (Freiberg 1994). The microclimatic influences on epiphyte growth, especially annual shoot length, age of apical meristem and ramification rate, are presented. Comparison of microclimate and epiphyte growth gave some clues in explaining phenotype expression. Possible implementations in further phorophyte subdivisions are discussed.

## METHODS

The investigations were carried out between January 1991 and June 1992 near the biological station of the Reserva Biológica Alberto Brenes (former Reserva Forestal de San Ramon), Alajuela province, Costa Rica, Central America. The station is located 84° 35' 50" W, 10° 13' 15" N in the valley of the Rio San Lorenzo river at 875 m above sea level.

The climate was humid throughout the year and perhumid between April and December, with annual rainfall of about 4000 mm. The mean monthly temperature was between 18.0°C and 20.8°C. The average relative humidity reached more than 95% during 320 days of the year. A detailed climatological description of the station is given in Freiberg (1994), a description of species diversity in Wattenberg & Breckle (1995) and Gomez Laurito & Ortiz Vargas (1991).

The epiphytes were reached by using rope-climbing techniques (Perry 1978; Perry & Williams 1981). In total, 318 specimens of the most abundant species of the genus *Columnnea* (*C. oerstediana* Klotzsch ex Oerst. (55 specimens), *C. microphylla* (Klotzsch) Hanst. ex Oerst. (81), *C. verecunda* Morton (149), and *C. lepidocaula* Hanst. (34)) growing on 12 *Ficus* trees (*F. jimenezii* Standl., *F. cervantesiana* Standl. & Williams, *F. colubrinae* Standl., and *F. crassineriosa* Burger) were studied.

Two steps were necessary to make a complete phenomorphological analysis. In the first, 30 specimens of all species were marked on a *Ficus jimenezii* tree and subsequently studied during a 14 month period to determine the rate of shoot growth and branching in different seasons. These data revealed a periodicity of internode length (Fig. 1), which could be used in the second step, which was to analyze backwards the plant sections older than 14 months and had been taken as herbarium specimens. Dried material preserved all necessary information and was used for phenomorphological analysis of all specimens.

Information on internode length, apical meristems, flowers, fruits, leaves and roots was gathered in digitized growth-form schemes (see reduced schemes in Fig. 2 to 4) and was available for statistical analyses (Freiberg 1994). Data on internodes and shoot meristems are presented here. The mean annual shoot length of a plant is the average of the added lengths of all internodes produced by each apical meristem of a plant during one year. The

average age of the apical meristems of a plant was determined by calculating the time lapse between the first and the last internode produced by an apical meristem. The age of every internode was determined with help of internode periodicity (Fig. 1). The ramification rate of a plant is the percentage ratio of the potential to the actual ramification points. If the apical meristem of a shoot dies every year, the ramification rate is 100%. A plant with ramification rate of 0% possesses only one apical meristem. Geometrical aspects of a growing site (e.g., branch inclination, diameter) are mentioned if they helped in explanation.

During a one year period, the three-dimensional microclimate of a *Ficus jimenezii* tree was recorded at 14 sites with 80 sensors at different distances from the forest floor and the crown periphery (Freiberg 1994). The climate data were interpolated for every epiphyte site on that particular phorophyte using a conventional spline-function (Locher 1992). Hemispherical photographs (Rich 1989) were taken at every epiphyte position. The product-moment-correlation coefficient was applied to correlate phenomorphology and microclimate (Sokal & Rohlf 1981, Sachs 1992). Only data on adult plants were used for correlation.

## RESULTS

The red-flowering, positively geotropic *C. oerstediana* and *C. microphylla* can be opposed to the yellow-flowering, negatively geotropic *C. verecunda* and *C. lepidocaula*. The phenomorphological variability in each species was within a range of up to 100% from the mean.

Only certain days showed the strongest correlations between phenomorphology and microclimate. These days occurred randomly throughout the year and featured rare events of exceptionally dry climate (event days). In the highest part of the canopy the relative humidity could be less than 60%. The absolute minimum (57%) was measured on May 28 at 2 p.m.. At the same time the temperature gradient between treetop and forest floor was 5°C (Freiberg 1994).

While there was no significant correlation between relative irradiance of a site, determined by hemispherical photographs, and any phenomorphological aspects of *C. verecunda*, *C. lepidocaula* or *C. oerstediana*, the shoots of *C. microphylla* were longer at darker sites (Fig. 2). The average internode length

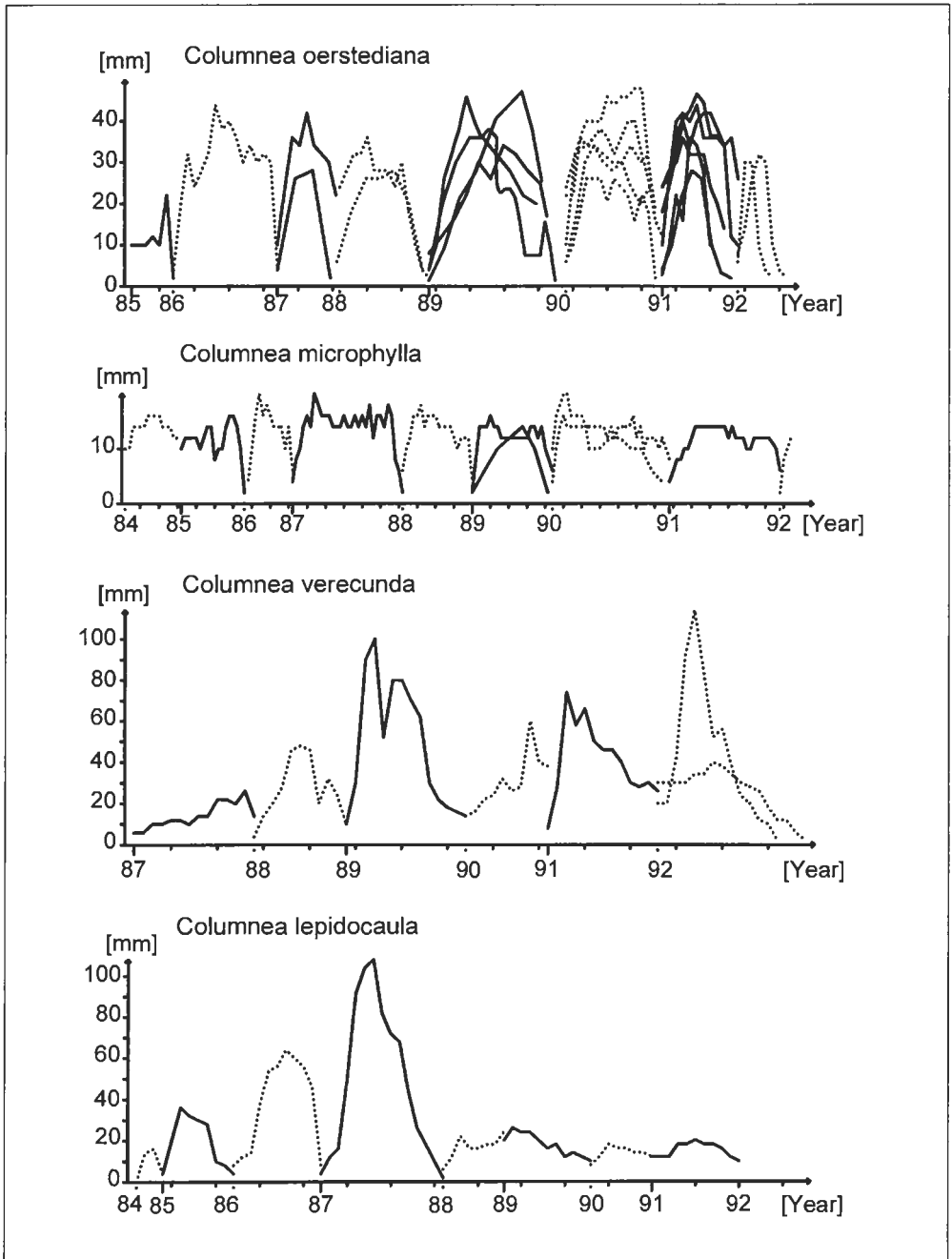


FIG. 1. Periodicity of the internode length for the four *Columnnea*s, shown for one specimen per species. Ordinate: Internode length [mm]. Abscissa: Consecutive internodes starting with hypocotyl. Minor scale steps equal 5 internodes. The position of a new season is superimposed below the internode scale by numbers 84 to 92, indicating year of origin. Coordinates of internodes originating from the same apical meristem are connected with each other (Troll 1935).

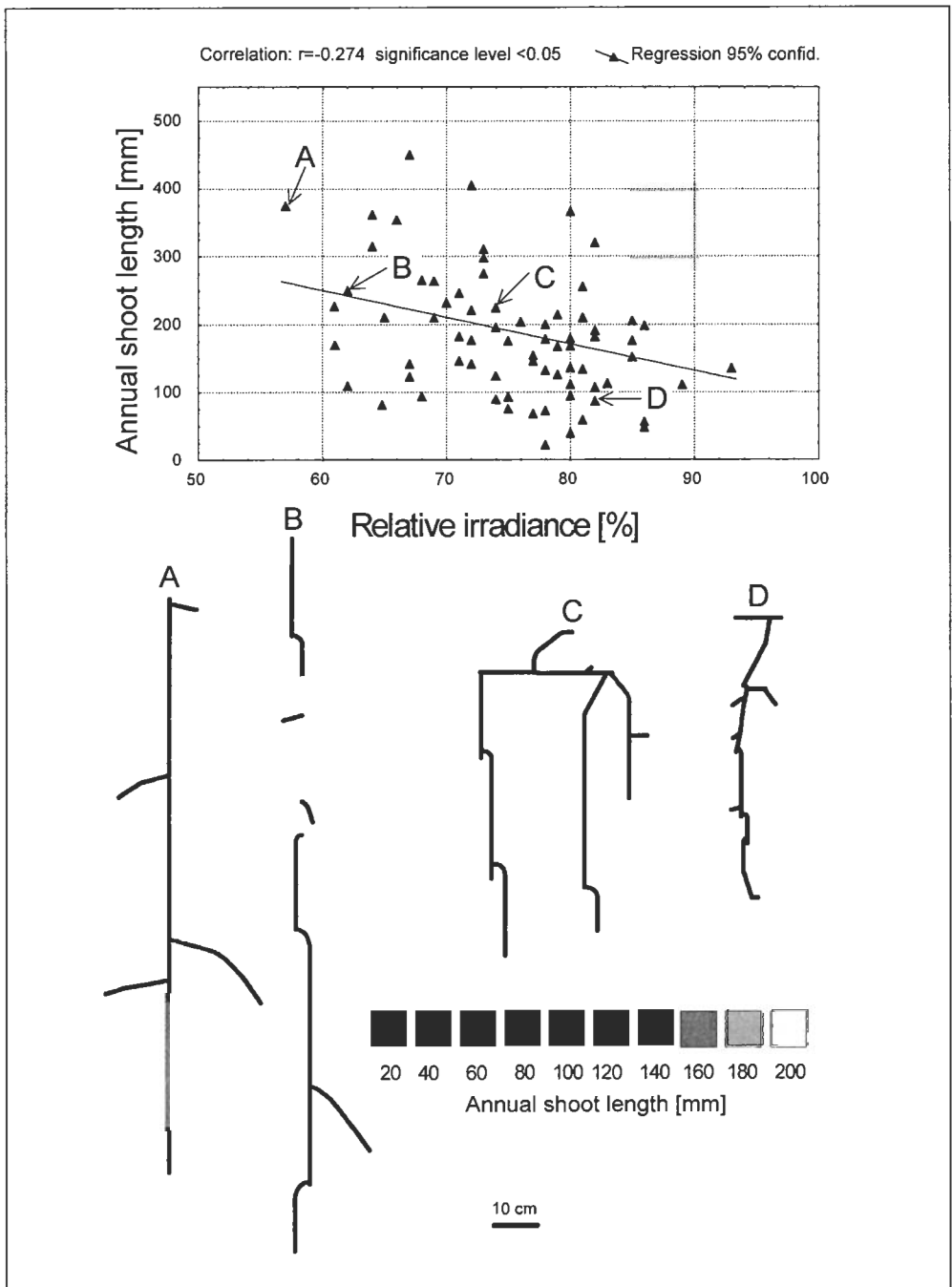


FIG. 2. Scatter diagram showing the correlation between relative irradiance calculated with help of hemispherical photographs and annual shoot length of *C. microphylla* (top). Simplified growth-form schemes showing the annual shoot length in different plant sections are given below for 9-year-old plants.

of all plants was independent of microclimatic conditions.

The age of the apical meristems of *C. verecunda*, *C. lepidocaula* and *C. microphylla* was not correlating with microclimate or any other factor analyzed. In contrast, those of *C. oerstediana* became older on steeper branches as well as on darker sites. Moreover, the meristem age of *C. oerstediana* correlated significantly with humidity and temperature on event days (Fig. 3). Average life span of the apical meristems of all *columneas* was independent of the age of the plant, but significantly negatively correlated with ramification in all *columneas*. Herbivory or injury accounted for less than 1% of all ramifications and could be neglected.

Relative height above the ground was positively correlated with ramification in *C. oerstediana*. Other geometrical aspects of the phorophyte were not significantly correlating with ramification in *C. oerstediana* nor in the other *columneas*. Ramification was independent of age and size of the epiphyte, but increased significantly with temperature and decreased with saturation deficit or relative humidity (Fig. 4) on event days. While there was no evidence of a correlation between ramification and microclimate for *C. verecunda* and *C. lepidocaula*, there was a statistically insignificant tendency for *C. microphylla* to show the same dependency as *C. oerstediana*.

## DISCUSSION

The phenotype of an individual species of the *columneas* analyzed varied considerably. Many of the phenomorphological differences between *C. verecunda* and *C. lepidocaula*, e.g., parameters like average internode length, correlated with internal factors like plant size and age (Freiberg 1994). These differences reflect the genotypes of the species or are "fixed in the symmetry of a species", as earlier proposed by Troll (1935). However, the variability of other phenomorphological aspects within the same species, especially the activity of the apical meristem, was independent of these internal factors, but was correlated with the external factors of the environment especially the microclimate. Particularly, this was the case for the positive geotropic or hanging plants of *C. oerstediana* and *C. microphylla*.

A loss of meristem results in reduced growth, reduced reproduction or even death of the plant. Under the perhumid conditions of a premontane rain forest in Costa Rica, the activity of the apical meristem

within the same species varied sufficiently with seasonality, thus determining a periodicity in internode length (Fig. 1). During event days, some locations were even dry enough to stop apical meristem growth permanently (Fig. 3). The dying of the apical meristem initiated sprouting of meristems in older leaf axes and thus produced more vegetation points, which led to a more extensive ramification (Fig. 4). Earlier studies already pointed out that in montane rain forests relatively low saturation deficits create stress, even for xerophytic plants (Buckley *et al.* 1980).

It was shown that the average life span of the apical meristems of *C. oerstediana* was higher at darker, wetter and cooler sites than at lighter, dryer or warmer sites (Fig. 3). This interrelation could not be shown for *C. lepidocaula* and *C. verecunda*, growing negatively geotropic off the branches. Despite the similarity in habit between *C. oerstediana* and *C. microphylla*, the ramification of the latter species did not correlate with the microclimate on event days. This can be explained by the two types of *C. microphylla* shoots: one type hangs down the branches producing flowers and fruits, while the other type, shoots that rarely produce flowers, creeps along the branches only within the boundaries of the bryophyte mats. The microclimatic amplitudes within these boundaries are reduced, especially during event days. Therefore only a proportion of *C. microphylla* shoots are affected but all the shoots of *C. oerstediana*. Growth experiments under controlled conditions should clarify these differences. Additionally, the limitation of shoot elongation in dark environments in *C. microphylla* (etiolation) is explained by the ambivalent shoot types of this species.

The amplitudes of the microclimatic factors in the canopy may be decreased by humus- and water-storing epiphytes like bromeliads, basket epiphytes or bryophytes (Biebl 1964, Klinge 1966, Pócs 1980, Nadkarni 1984, Freiberg 1994). The microclimatic conditions in the air layer close to the branches and within the substrate are therefore significantly different from those in the free air space between the branches. These ecological differences prompt the creation of the terms "ramosphere" (ramus lat.: branch, sphaera gr.: sphere) and "aerosphere" (aer gr.: air, sphaera gr.: sphere) in the canopy.

The ramosphere contains the substrate itself (inorganic accumulations, dead organic matter, bryophytes) and the area clearly influenced microclimatically by the substrate on the branch. Its bounda-

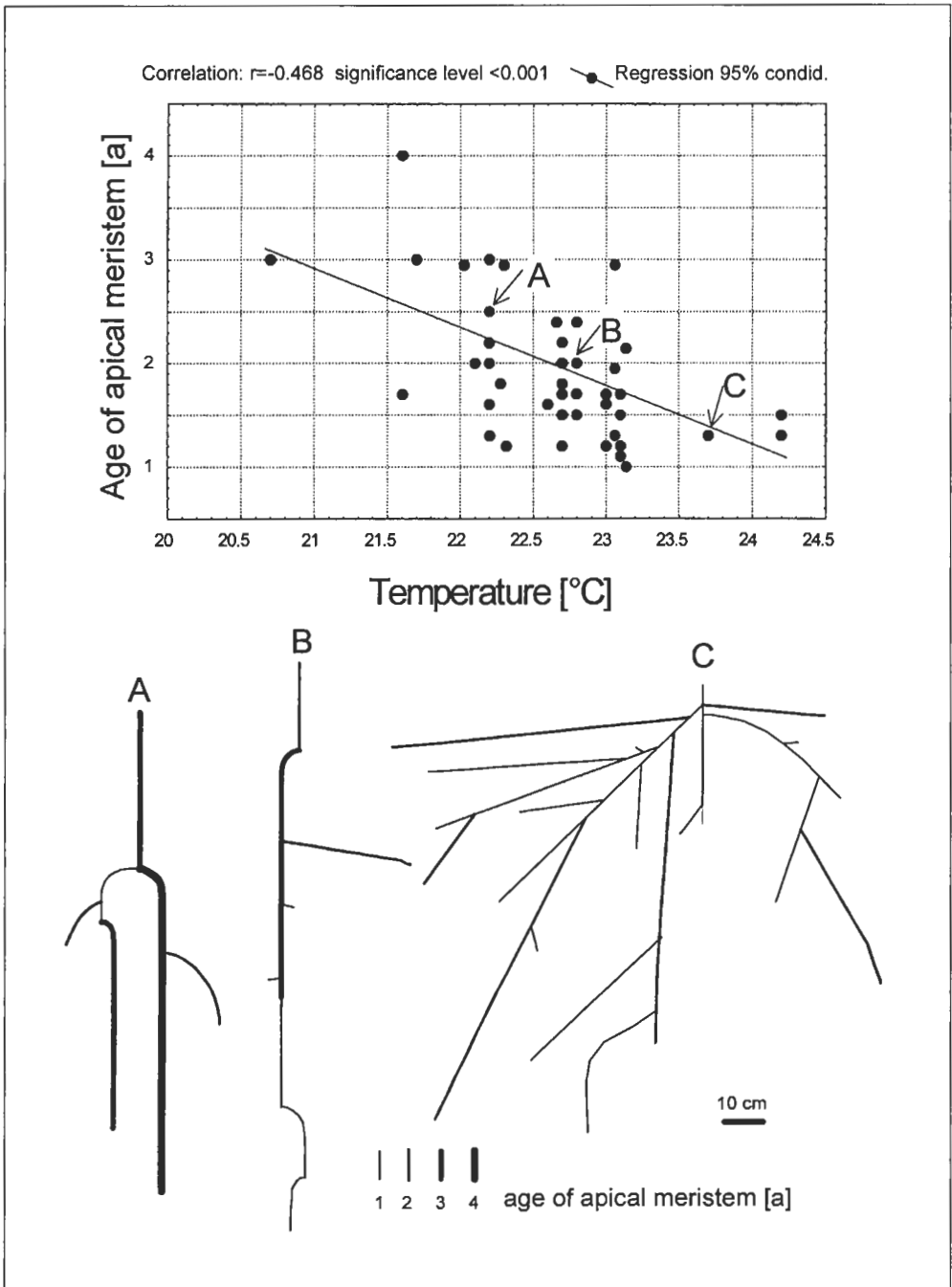


FIG. 3. Scatter diagram showing the correlation between air temperature and average age of the apical meristem of *C. oerstediana* (top). Simplified growth-form schemes of 7-year-old plants below provide information on meristem ages by line width in the graphs.

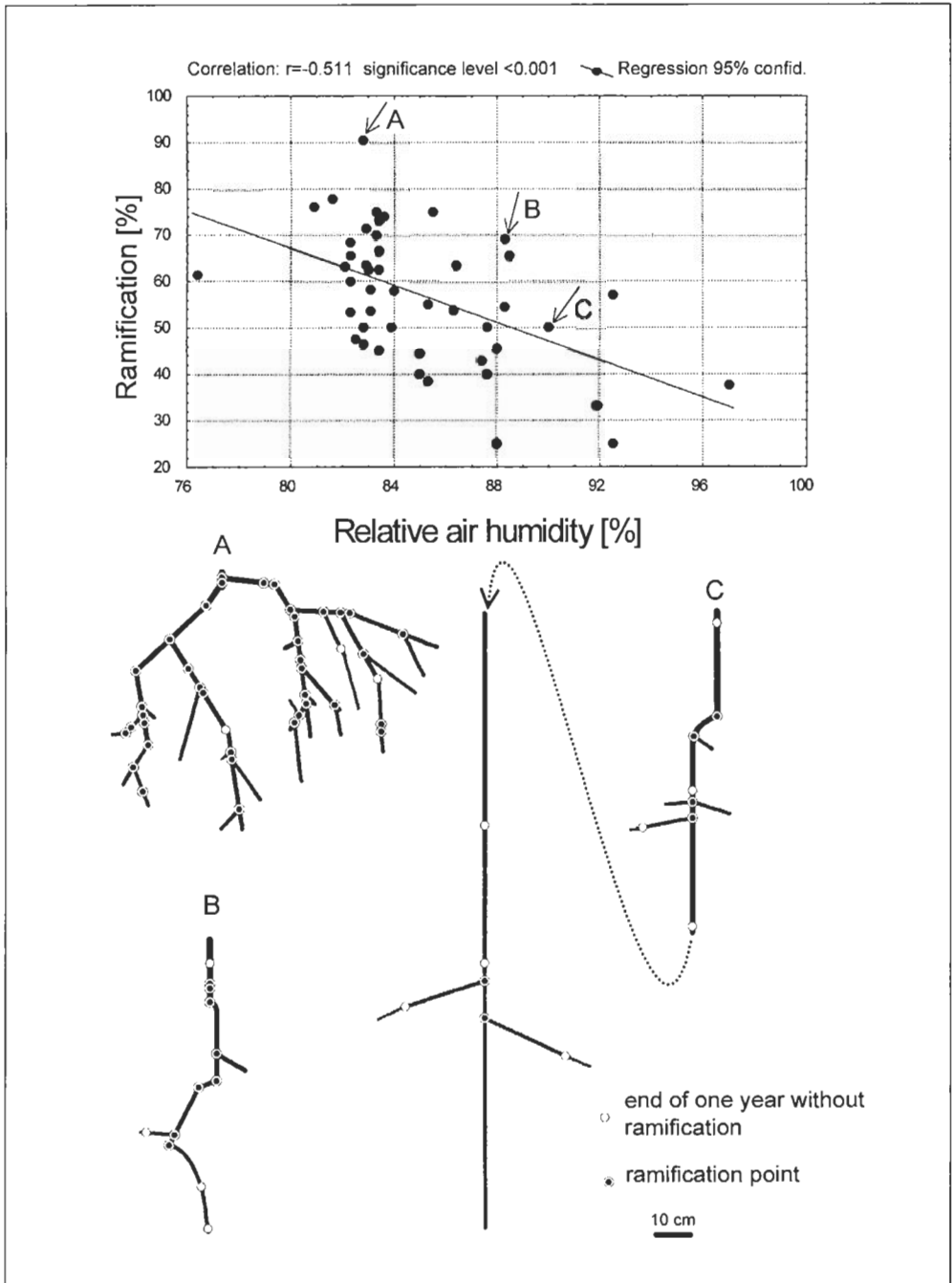


FIG. 4. Scatter diagram showing the correlation between relative air humidity and ramification rate of *C. oerstediana* (top). Some examples of growth-forms are given below for 8-year-old plants in simplified drawings focusing on ramification. Stem width is not drawn to scale.

ries depend on the volume of humus and bryophyte mats as well as on the size and growth form of predominating epiphytes. Especially lawn-type growing epiphytes (e.g., *Peperomia* and *Stelis*) will have a considerable influence (Hosokawa 1943). A well developed ramosphere mitigates microclimatic amplitudes and maintains a self-sufficient environment in drought periods until the arrival of precipitation. A prolonged drought might consume the ramosphere's stored water completely, certainly leading to a rather quick change in the special microclimatic environment of the ramosphere.

The aerosphere contains the remaining volume of the canopy, excluding the leaf surface (phyllosphere) and the stem and bark surface without accumulations of humus and vascular epiphytes (caulosphere). The aerosphere is only partly influenced by the buffering effect of the substrate. To avoid the microclimatic influences of the ramosphere, meteorological measurements, with the help of towers, were mostly done in the aerosphere (e.g., Allen *et al.* 1972, Moli6n 1987).

The ramification rate of *C. verecunda* and *C. lepidocaula* correlated with neither temperature nor humidity. This may be due to the basitonic ramification type of both species compared to the mesotonic ramification of *C. oerstediana*. While the apical meristems of *C. oerstediana* are fully exposed to the aerosphere, new branches of *C. verecunda* and *C. lepidocaula* only develop at the base of the shrub. The base, however, is protected within the ramosphere on top of the phorophyte branches. Only severe drought might initiate ramification at the base, while affected meristems in the aerosphere die without initiating ramification.

It can be assumed that the differences between the ramosphere and aerosphere are most distinct during event days and probably rather negligible during most of the time in the rainy season (Freiberg 1994). Further detailed measurements are needed to analyze the internal schematics within each sphere and the relationship of these spheres to each other. A boundary between these spheres clearly exists and is evidenced by the fact that the apical meristems of *C. oerstediana* became older on steeper branches than on more horizontal ones: relative to the geometry, vertically hanging sections of *C. oerstediana* growing on steep branches do not even grow into the aerosphere.

Phenotype expression could not be explained by a single environmental or internal factor. Moreover,

the influence of the factors on the species are very complex and only poorly understood. This study, however, revealed that these differences in the phenotype between individuals of these species can partly be linked to the peculiarities of their environment and are adequate to clarify epiphyte ecology and canopy structure.

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