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Laurel Forests in Tenerife, Canary Islands: The Vertical Profiles of Leaf Characteristics.

By

MORALES D.*), GONZALEZ-RODRIGUEZ A. M.*), CERMAK J.**) and

JIMENEZ M.S.*)

With 5 Figures

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Summary

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Different anatomical and physiological parameters were determined in leaves of three tree species of a laurel forest in which the dominant trees were *Laurus azorica* (Seub.) Franco, *Persea indica* (L.) Spreng. and *Myrica faya* Ait. Samples were taken at different layers from the top down to the lower part of the canopy. The specific leaf weight, leaf thickness, and water potential (in absolute values) decreased down through the canopy and also the chlorophyll content expressed by unit leaf area, on the contrary the leaf area increased. These features together with the change in the chlorophyll a/b ratio, denote the adjustment of the leaves to the different microclimatic conditions in every layer. Differences among the species are also shown. These changes should be taken into account for the interpretation of other physiological parameters not only at leaf level but also at the level of stand.

*) D. MORALES, A. M. GONZALEZ-RODRIGUEZ and M. S. JIMENEZ, Dpto. Biologia Vegetal, Universidad de La Laguna, 38207 La Laguna, Tenerife, Spain.

**) J. CERMAK, Inst. Forest Ecology, Mendel University, Zemedelska 3, 64400 Brno, Czech Republic.

Zusammenfassung

MORALES D., GONZALEZ-RODRIGUEZ A. M., CERMAK J. & JIMENEZ M. S. 1996. Lorbeerwälder in Teneriffa, Kanarische Inseln: Vertikalprofile von Blattcharakteristika. – Phyton (Horn, Austria) 36 (2): 251–263, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Verschiedene anatomische und physiologische Parameter wurden in Blättern von drei Baumarten des Lorbeerwaldes bestimmt. Hier waren die dominierenden Baumarten *Laurus azorica* (Seub.) Franco, *Persea indica* (L.) Spreng. und *Myrica faya* Ait. Proben wurden aus verschiedenen Höhen, von der Oberkrone bis in die unteren Bereiche, entnommen. Das spezifische Blattgewicht, die Blattdicke und das Wasserpotential (als Absolutwert) nahmen von oben nach unten ab, desgleichen auch der Chlorophyllgehalt bezogen auf die Blattfläche; im Gegensatz dazu stieg die Blattfläche an. Diese Merkmale gemeinsam mit einer Änderung im Chlorophyll a/b-Verhältnis kennzeichnen die Anpassung der Blätter an die verschiedenen mikroklimatischen Bedingungen in den einzelnen Schichten. Unterschiede zwischen den Baumarten werden aufgezeigt. Die Änderungen sollten bei der Interpretation physiologischer Parameter nicht nur auf Blattniveau sondern auch auf Bestandesniveau berücksichtigt werden.

Introduction

The Canarian laurel forest is a luxuriant vegetation with a diverse structure of trees, shrubs, herbs, climbers, ferns, mosses, lichens, and fungi. About 20 tree species belonging to different families are present in this evergreen forest, the majority of them are Canarian Macaronesian endemics and relicts of a now virtually extinct tertiary Mediterranean flora that occupied southern Europe and North Africa about 20 millions years ago (GONZALEZ HENRIQUEZ & al. 1986, SANTOS 1990). Trees may reach more than 20 m in height but the average is about 10 to 20 m. The distribution of tree species is not uniform, it varies according to microenvironmental conditions and their optimal autecological characteristics. They generally have broad leaves, always green and glossy. These forests have the typical appearance of a cloud forest (HOLLERMANN 1981) and are restricted mainly to the most humid section of the northern (windward) slope in the middle elevations where there is an almost permanent cloud belt.

Recently, ecophysiological studies have been initiated (LARCHER & al. 1991, MORALES & al. 1991, 1992, LÖSCH 1993, ASCHAN & al. 1994, ZOHLEN & al. 1996, KÖHL & al. 1996, JIMENEZ & al. 1996). An experimental plot was established in the Agua García mountains, Tenerife, Canary Islands, to study in detail the structure, growth and other living processes of laurel forest species at the leaf, tree and stand levels (MORALES & al. 1996 a, b).

Forest canopy structure is the result of interactions and feedbacks between vegetation and environment (CAMPBELL & NORMAN 1989). It is known that leaves are highly plastic in response to their growth conditions.

Morphological and physiological features of leaves vary with canopy depth as the result of microenvironmental variations mainly light attenuation. Knowledge of these variations over time and space is required for investigations ranging from studies of intracellular components up to studies of whole canopy physiological processes (JURIK 1986).

The aim of this study is to know the vertical profiles of some morphological and functional characteristics, in order to have a better understanding of general canopy features of this forest which at the moment is the focus of very much scientific interest.

Materials and Methods

This study was carried out in Tenerife (Canary Islands) in the Agua García mountains (28° 27′32″ N, 16° 24′20″ W). The site covered by laurel forest, situated at an altitude of 820 m was established on the slight slope (12) facing NNE. The natural mixed hardwood forest was composed of six tree species: *Laurus azorica* (Seub.) Franco, *Persea indica* (L.) Spreng., *Myrica faya* Ait., *Erica arborea* L. and two species of *Ilex (I. platyphylla* Webb & Berth. and *I. canariensis* Poivet.). The climate of the site is humid mediterranean with annual precipitation of 755.6 mm, mean annual air temperature of 13.6 °C and mean air humidity of 82.1 %. The leaf area index (LAI) of the stand was 7.8, the tallest trees reached an average of 17.4 m in height and the leaves were concentrated mainly in a relatively thin layer of the canopy (5.5 m thick) with a high density of 1.4 m^2 m^{-3}. The total basal area of the experimental plot was 33.7 m^2 ha^{-1}. A detailed study of the site stand structure and stand leaf area distribution can be found in MORALES & al. 1996 a, b. See also ASCHAN & al. 1994.

A 20 m height scaffolding tower was built and fully expanded leaves in the first year of life were sampled in 0.5 m increments from the top down to the lower part of the canopy in the more representative tree species *Laurus azorica, Persea indica* and *Myrica faya*. Samples at soil level (1 m) were also taken in seedling of the three mentioned species.

The leaf area was measured using a leaf area meter LI 3100, (LI-COR, Lincoln, USA); blade thickness between main veins in the central part of the leaf with an outside micrometer (Mitutoyo J15 b7502, Japan); chlorophyll content in 80% acetone extract on a spectrophotometer (UV-160A Shimadzu, Japan), using equations of Arnon for calculation (ARNON 1949); water potential was monitored at midday on detached leaf samples using the pressure chamber (PMS Instr. Co. USA). The specific leaf weight (SLW) was calculated as the ratio leaf dry weight/leaf area (g m^{-2}) and the relative water content (RWC) as the ratio actual water content/water content at saturation and expressed as percent. All the measurements were made on clear days in winter. At midday the temperature at the top of the canopy ranged between 16 and 18 °C and the relative humidity between 60 and 65 %, the maximum photosynthetic active radiation was 1700 µmol photon m^{-2} s^{-1}.

Results

Mean SLW of the three studied species decreased continuously from the top (16.5–18 m high) of the canopy. Values at the bottom of the tree canopy layer (11.5–12 m) were 35.6, 42.1 and 69.2 % of those at the top in

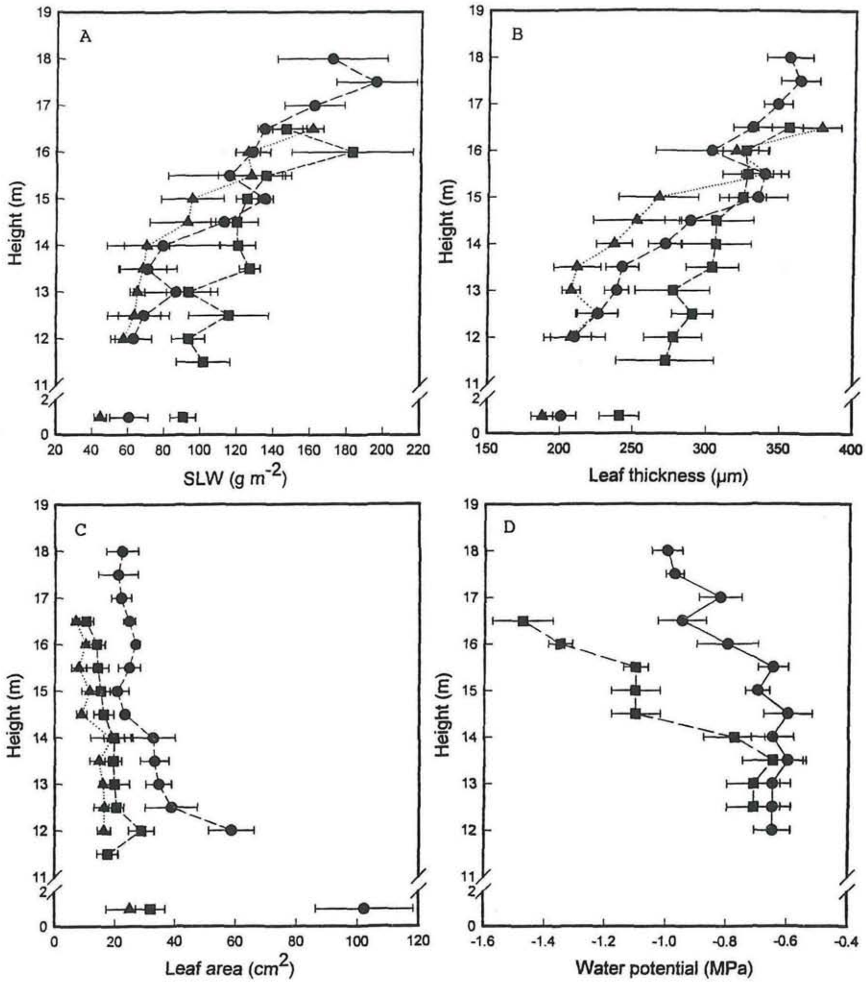

Fig. 1. – Vertical profiles of leaf characteristics through the laurel forest canopy: A) Specific leaf weight (SLW), B) leaf thickness, C) leaf area and D) leaf water potential (measured at midday) as a function of height in the canopy in ● *Persea indica*, ■ *Laurus azorica*, ▲ *Myrica faya*. Every point is the mean of 15 measurements (9 for the water potential) with standard deviations. All measurements were made in winter.

Myrica faya, *Persea indica* and *Laurus azorica* respectively. The SLW of the seedlings (1 m) was only 27.8, 40.6 and 61.8 % of those at the top respectively for the same sequence of species names (Fig. 1, A).

Mean leaf thickness varied greatly through the canopy mostly in *Myrica faya* in which the maximum value was 377 µm at the top and the

Table 1

Variations in Chl a/b and Chl (a+b) content per leaf dry mass and leaf area unit at different canopy sampling intervals in laurel forest tree species. In brackets standar deviation.

		Chl a/b	Chl a+b ($g\ kg^{-1}$)	Chl a+b ($g\ m^{-2}$)
	P. indica	2.57 (0.07)	4.03 (0.71)	0.617 (0.16)
Upper	*L. azorica*	2.75 (0.19)	4.45 (0.38)	0.621 (0.04)
(18–15 m)	*M. faya*	2.10 (0.25)	4.97 (0.77)	0.661 (0.26)
	P. indica	2.36 (0.08)	5.44 (1.00)	0.541 (0.60)
Middle	*L. azorica*	2.66 (0.17)	5.02 (0.51)	0.626 (0.67)
(15–13 m)	*M. faya*	1.98 (0.18)	6.66 (0.22)	0.553 (0.54)
	P. indica	2.25 (0.20)	5.83 (0.92)	0.414 (0.28)
Lower	*L. azorica*	2.43 (0.11)	5.13 (0.70)	0.559 (0.88)
(13–11 m)	*M. faya*	2.08 (0.20)	6.87 (0.09)	0.290 (0.15)

minimum 207 µm at the bottom of the tree canopy layer (representing 54.9 %). These values were 355 µm and 210 µm in *Persea indica* (59.1 %) and 355 µm and 271 µm in *Laurus azorica* (76.5 %). In the seedlings the mean leaf thickness was of 188, 201 and 241 µm in *Myrica faya*, *Persea indica* and *Laurus azorica*, representing 49.8, 56.6 and 67.9 % of the maximum values (Fig. 1, B).

Mean leaf area reached a maximum at the bottom of the tree canopy (14.2, 58.6 and 28.6 cm^2 in *Myrica faya*, *Persea indica* and *Laurus azorica*). Values at the top were 6.9, 25.4 and 10.3 cm^2 representing a 48.6, 43.4 and 35.9 % of those at the bottom respectively (Fig. 1, C). In the seedling the values were of 25.1, 102.3 and 31.2 cm^2 (27.4, 24.9 and 32.1 %).

There was a general increase in total chlorophyll content per leaf dry mass down through the canopy, chlorophyll b increased more with respect to chlorophyll a, decreasing chl a/b ratio (Table 1). When the chlorophyll content was expressed by unit leaf area, it decreased according to canopy depth.

The mean values of water potential at noon showed significant differences between *Laurus azorica* and *Persea indica* leaves exposed to the sun in the upper canopy (more negative values were found in the former one than in *Persea indica* –1.5 and –1.0 MPa respectively). In the lower canopy, where the microenvironmental conditions are more constant, the values were similar in both species ranging between –0.6 and –0.8 MPa (Fig. 1, D).

The leaf RWC increased down through the canopy, although its variation (ranging from 92 to 98 %) was not very impressive, when we

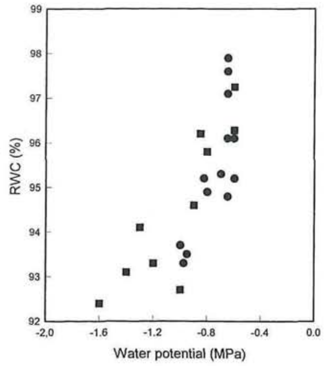

Fig. 2. – Leaf water potential (WP) as function of leaf relative water content (RWC). ● *Persea indica* , ■ *Laurus azorica*. Every point is the result of one individual measurement. Measurements were made at midday.
Regression equation: RWC = 103.45 + 14.136 WP + 4.68 * WP^2,
$r^2 = 0.69$; $p < 0.001$.

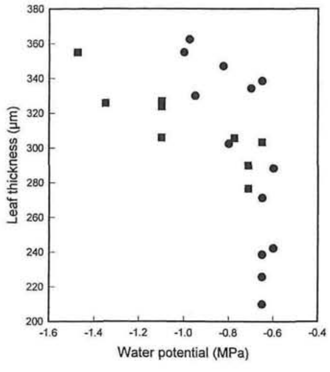

Fig. 3. – Leaf water potential (WP) as function of leaf thickness (Thick). ● *Persea indica*, ■ *Laurus azorica*. Every point is the result of one individual measurement. Measurements were made at midday.
Regression equation: Thick = 34.803 – 495.98 * WP - 197.72 * WP^2,
$r^2 = 0.461$; $p < 0.001$

plotted its values versus that of leaf water potential we got a good correlation (Fig. 2). The leaf water potential also correlated very well with their leaf thickness (Fig. 3).

Discussion

The SLW values of the three main broad-leaved species in the Agua García forest showed no significant differences among them, only in the lower part of the canopy *Laurus azorica* leaves showed values significantly higher than the other two species (Fig. 1, A). The values found are in accordance with values done by MEDINA & KLINGE 1983 for montane tropical forests. These authors point out that evergreen species have higher SLW values than deciduous species and the higher biomass investment per unit area in the former can be compensated by a longer leaf duration.

In a previous study, no variation in SLW was found along the year in mature leaves of the same species. Changes were only significant when young leaves developed to mature ones. Larger variation was found in the SLW values through the forest canopy, decreasing very much with depth ranging approximately between 210 and 50 g cm^{-2} (40 if we include the seedling strata). The decrease in the leaf dry weight per unit area with the canopy depth was also found by other authors in other forests types (e.g. MILLER 1967, KIRA & al. 1969, COYNE & VAN CLEVE 1977, SCHULZE & al. 1977, HUTCHISON & al. 1986, JURIK 1986, HOLLINGER 1989), and it has been interpreted as a way to maximize canopy photosynthesis for a given investment in foliage mass (GUTSCHICK & WIEGEL 1988), the shade tolerant species presenting the largest variation (CEULEMANS & SAUGIER 1991). Our findings indicate the great shade tolerance of the studied species. This is extremely important in the cloudy environment where they live. Although this characteristic is mainly influenced by the light environment where the leaves develop, we must also consider the genetic factor and in this respect *Laurus azorica* would be the less shade tolerant.

The decrease in SLW with increasing canopy depth in the three studied species of laurel forest is due to the variation of leaf thickness, which decreases very much down through the canopy, and to the increase in leaf area. A positive correlation between SLW and leaf thickness has been found in the studied species (Fig. 4). This correlation had been registered previously in two *Persea* species (MORALES & al. 1992) and also in amazonian species (SOBRADO & MEDINA 1980), in different categories of sun and shade leaves of *Quercus ilex* (WAGNER & al. 1993) and, in high and low mountain species (KÖRNER & al. 1989). However, CAVELIER & GOLDSTEIN 1989 did not find this correlation in elfin cloud forest tree species nor TANNER & KAPOS 1982 in species of Jamaican upper mountain rain forest trees. The former authors attributed this lack of correlation to an increase in water and air space rather than an increase in the dry weight of the tissue per unit leaf area.

The great decrease of the leaf thickness in the three laurel forest species through the canopy depth indicates a substantial plasticity for adaptation to changing environmental conditions. In order to better quantify the thickness variation as an indicator factor of shade tolerance, CARPENTER & SMITH 1981 defined the plasticity index (sun leaf thickness – shade leaf thickness / sun leaf thickness). They found a maximum value of

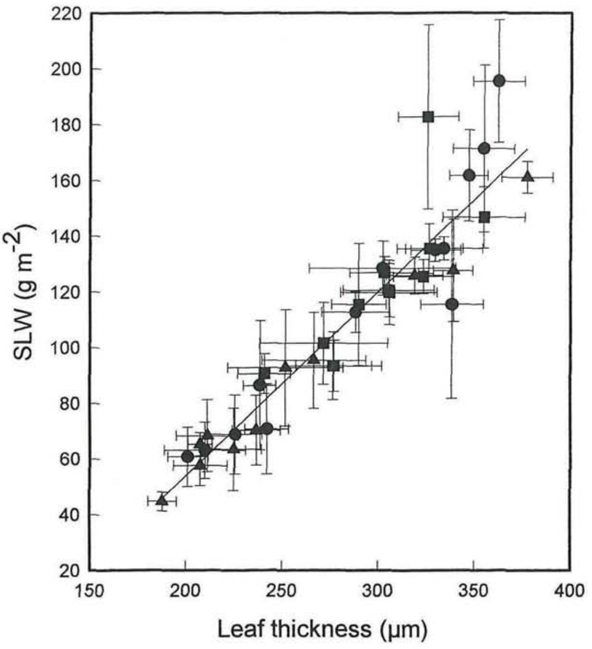

Fig. 4. – Specific leaf area (SLW) as function of leaf thickness (Thick). Data points as in Fig. 1. ● *Persea indica*, ■ *Laurus azorica*, ▲ *Myrica faya*. Regression equation: SLW = – 78.31 + 0.66 * Thick, $r^2 = 0.879$; $p < 0.001$

0.29 in Appalachian deciduous hardwoods. If we calculate this index using the mean values found in the upper sampling interval (18 to 15 m high) as sun leaf values, and the mean values found in the lower sampling interval (13 to 11 m high) as the shade leaf ones for *Myrica faya*, *Persea indica* and *Laurus azorica* we obtain, a plasticity index of 0.38, 0.34 and 0.17 respectively, again indicating a high shade tolerance in the three species, slightly lower in *Laurus azorica*.

Persea indica has the biggest leaf area followed by *Laurus azorica*, having *Myrica faya* the smaller leaves. The leaf area in the three species increased down the canopy, increasing more in *Persea indica* than in the other two species. This is a well known phenomenon registered in numerous types of forest (Hollinger 1989).

The chlorophyll content present in the three laurel forest species is in the range of shade plants, as well as the chl a/b ratio (Boardman 1977, Lichtenthaler & al. 1981, Givnish 1988). The increase in total chlorophyll content per leaf dry mass (from 4.03 to 6.87 g kg^{-1}) and the decrease when it is expressed in unit leaf area (0.62 to 0.29 g m^{-2}) through the canopy depth, are comparable with the findings by MASAROVICOVA & STEFANCIK 1990 and LICHTENTHALER 1981, 1983 in sun and shade leaves of beech trees and in different canopy layers in a hardwood forest (ELIAS & MASAROVICOVA 1985). This makes the photosynthetic machinery adapt better to the shadier conditions in the lower part of the canopy and the general decreasing of total chlorophyll per unit area depends on the decrease of leaf thickness through the canopy (BOARDMAN 1977).

The values of leaf RWC during the winter days in which the measurement were made showed very high values (ranging from 98 to 92 %) which indicated that trees were not under a big water saturation deficit (only 2 to 8 %), with enough water in the soil. Under these conditions the water potential was not very negative, nevertheless we could find very marked differences between *Laurus azorica* and *Persea indica* leaves exposed to the sun in the upper canopy with more negative values in *Laurus azorica*. Only small differences could be found in the lower canopy, where the environmental conditions were always more uniform, with values between –0.6 to –0.8 MPa (Fig. 1, D). When we plotted the leaf water potential versus RWC we found a good correlation, and the leaf water potential also correlated very well also with their leaf thickness (Fig. 3).

The enormous variations in the morphological characteristics and pigment content through the canopy, found in this forest are related to the strong light attenuation which was found (ASCHAN & al. 1994); only 2 % of incident photosynthetic active radiation reaching the soil level. That means that on clear days, leaves at the top of the canopy are exposed to very high radiation levels while leaves in the lower part of the canopy are in very shady environments, so only species which can modify their morphology to adapt to these changing conditions are able to grow in this dense forest, buffering the strong contrast in light intensity with a photohomeostatic effect (LARCHER 1995).

Light attenuation is also related to the cumulative leaf area index LAI (JONES 1992, CERMAK 1989). In a previous paper we found a LAI of 7.8 in this experimental site (MORALES & al. 1996a). If we plot SLW values as function of total LAI above the midpoint of each sampling interval, we can observe that the specific leaf weight declines with increasing cumulative LAI, and the regression equation (Fig. 5) is highly significant.

We can conclude that the leaves of the laurel forest species studied here can change their morphologic characteristics very much according to changes in the microenvironmental conditions where they develop in the very dense canopy. Although many of the trends found in this study seem to be general characteristics of forests, it is important to be aware that the canarian laurel forest follows this general pattern. The leaf characteristics

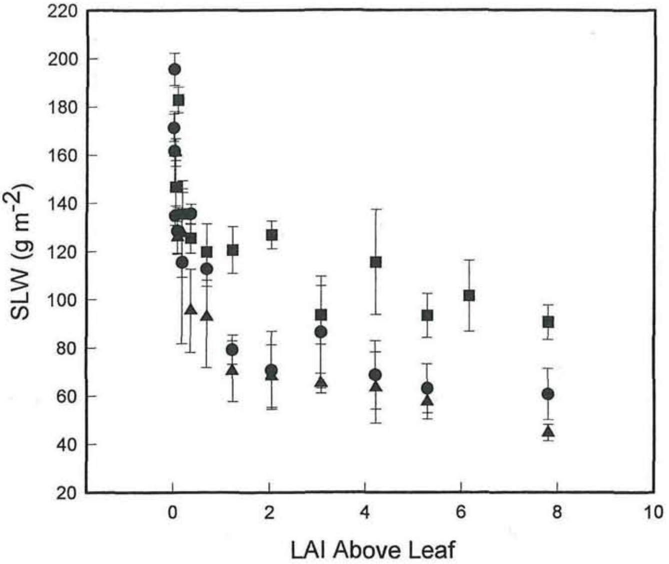

Fig. 5.- Specific leaf weight (SLW) of ● *Persea indica*, ■ *Laurus azorica* and ▲ *Myrica faya* in each sampling interval versus total leaf area index (LAI) above the midpoint of the sampling interval.
Regression equation: $SLW = a * LAI^b$
a = 93.76, b = –0.118, for *Pesea indica*
a = 119.75, b = –0.1015, for *Laurus azorica*
a = 80.484, b = –0.218, for *Myrica faya*
$p < 0.001$ for all species

shown here should be taken into account when other functional studies are performed in this forest.

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Recensiones

Wulfenia. Mitteilungen des Botanischen Gartens des Landes Kärnten, 4. – 8°, 71 Seiten, zahlreiche Abbildungen; brosch. – Botanischer Garten des Landes Kärnten, A-9020 Klagenfurt.

Von den sechs wissenschaftlichen Beiträgen gilt einer der Geschichte eines Gärtleins im Zentrum von Klagenfurt in der Zeit von ca. 1821–1861, das als ein Vorläufer im Hinblick auf die spätere Errichtung eines Botanischen Gartens gesehen werden kann. Die weiteren Artikel behandeln Vorkommen von *Aceras anthropophorum*, eine geschlitztblättrige Grauerle (*Alnus incana* f. *angustissima*, Koralpe), *Bolboschoenus maritimus*, *Botrychium multifidum* und *Leucocoprinus brinbaumii* in Kärnten. Ein populärwissenschaftlicher Aufsatz stellt die Sukkulentensammlung des Botanischen Gartens vor. Das Heft ist auf gutem Papier und drucktechnisch sehr gut hergestellt.

H. TEPPNER

PRESSER Helmut 1995. Die Orchideen Mitteleuropas und der Alpen. Variabilität, Biotope, Gefährdung. – Lex. 8°, 222 Seiten, ca. 550 Farbbilder; Ln. – ecomed Verlagsgesellschaft, D-86899 Landsberg. – DM 78,–. – ISBN 3-609-65600-X.

Schon wieder ein Orchideenbuch! Wenn die Entwicklung in Europa so weitergeht, hat bald jedes Bundesland bzw. jede Provinz eine eigene Orchideenflora, dazu kommen noch die überregionalen. So viel an neuer Information – um diese Flut