225

THE ECOPHYSIOLOGY OF CANARIAN EUPHORBIA SHRUBS, FOCUSSING THE WATER BALANCE

By BRUNO A. MIES [1]

With 8 figures

ABSTRACT. The woody spurges (*Euphorbia* spp.) of the Atlantic Islands differ in their ecological potentials corresponding to their habitat preferences. The structure of vegetation, morphology, microclimate, transpiration, photosynthesis and leaf water relations have been examined to consider the ecological strategies of the species. Most of them express a 'Federbusch' type morphology, only *E. balsamifera* provides a special one. The latter stores water in the stems, the shrub canopy - adpressed to the soil - provides extensive water loss and reduces water transpiration by stomatal control. It is the most drought resistant species in the Canarian habitats. In comparison, *E. broussonetii* has no such ecological control mechanisms. *E. canariensis* and *E. aphylla* express a succulent, cactoid shape with the ability for Crassulacean Acid Metabolism (CAM). The ecological potentials are discussed in the light of environmental factors.

KEY WORDS: *Euphorbia* spurges, ecology, morphology, habitat adaptation, drought, transpiration, water economy, Canary Islands

INTRODUCTION

The genus *Euphorbia* occupies nearly all altitudinal belts and habitats of the Mid-Atlantic Islands (Fig. 1). The succulent spurges with terminal leaf rosettes (genus *Euphorbia* sect. Tithymalus) are an integral part of the paleotropical arid zone, extending from the Canary Islands to the Near East (Fig. 2A). They shed their leaves in the summer months after the annual rains have ceased, or have them only during a short period of outgrowth. In the case of *Euphorbia balsamifera*, it is a remnant of a Tertiary or even older drought-adapted vegetation type in suitable habitats of northern Africa (AXELROD & RAVEN, 1978;

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Mies 1996, Verdcourt, 1969). The species occurs throughout the African continent with a western subspecies, *balsamifera*, growing from Portugal-Morocco to the Canary Islands and the mountains of western Africa and an eastern one, ssp. *adenensis*, on the mountains of North-East Africa and Arabia (Bally 1965). Morphologically, this species differs from the others out of the leafy Tithymalus group through the hemispherical shape of the bushes adpressed to the rocky soil. All other species of the group express an umbrella-type morphology. The other species of the genus examined here are restricted to the Atlantic Islands (Macaronesia). Whereas *E. balsamifera* grows in a belt nearest to the sea on the Canary Islands (Fernandez-Palacios 1992, Rivas-Martinez & al. 1993, Fig. 2C), all other species are found higher in altitude or even in mountain locations.

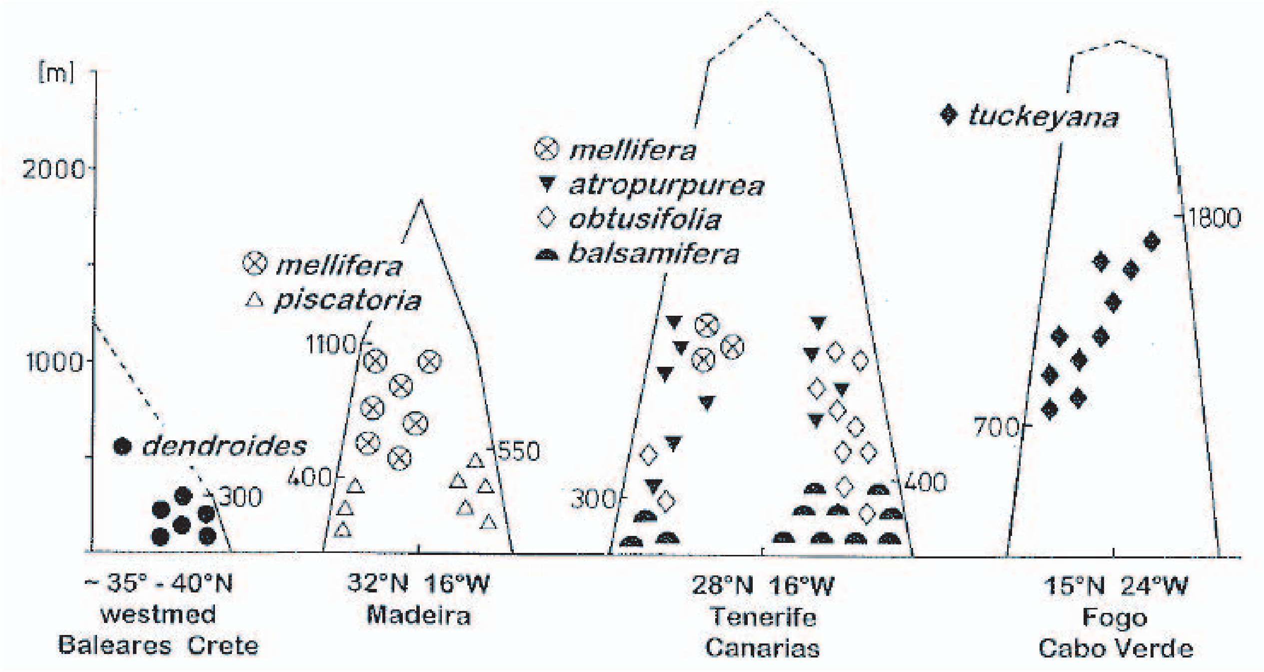

Fig. 1 - *Euphorbia* sec. Tithymalus occupies nearly all altitudinal belts and habitats of the Mid-Atlantic islands and stretches into the Mediterranean area.

On the Canary Islands the species has the potential to endure physiological dryness near the coasts, influenced by high osmotic potentials in soils caused by the sea-foam (see Mies & al. 1996). *E. balsamifera* is the dominant species of a coastal succulent shrub community accompanied by *E. canariensis, E. broussonetii* (syn. *E. obtusifolia*), *Plocama pendula* and *Campylanthus salsoloides*. The community has been described as a phytosociological subclassification of the succulent shrub belt of its own (*Periploco-*

Euphorbietum canariensis subass. *euphorbietosum balsamiferae* RIVAS-MARTINEZ & al. 1993). In the *E. balsamifera* belt all other species depend on the occurence of this dominating species with respect to seed germination and growth, growing within the hemispherical canopy or close to it (MIES in prep.). The environmentally essential morphology of this species led to a variety of ecological questions as an example. The Canary Islands, the island of Tenerife e.g., represent a model for studying the ecology of species in the northern paleotropics. This study focusses on the genus *Euphorbia*, to rely not only on ecological comparisons, but to touch also niche adaptation and perhaps phylogeny in this example. The vegetation of young lava flows and volcanic cliffs of Tenerife consists of one meter or even man-high plant species. The dominating species grow in a condensed vegetation matter, which supports the assumption that the availability of water is the main factor for the individuals to endure.

The general lowland climate of the archipelago [Fig. 2D] shows a generally Mediterranean type with a winter rain situation followed by a severe summer drought season. The air temperatures in summer exceed 30° centigrade over day. After the data of 1993 and '94 of this project the area over humidity in that diagram, exceeded by the temperatures, means drought stress to the plant. After THORNTHWAITE we have to take into account the amount of persisting and available water in the soil. Both water quantities, the direct precipitation and the stored ground water affects the time span of growth, at least for the most adapted species to aridity in the Canarian vegetation - *Euphorbia balsamifera*. These two quantities result in the annual span, having leaves for this species e.g. The Fig. 2B show the cover area of *Euphorbia balsamifera* on Tenerife at Malpais de Guimar, translated as 'bad lands of Guimar'.

After the approximation of BLANEY & CRIDDLE (1962), potential evapotranspiration can be rated to **1800 - 2400 mm a^{-1}**. This equation is an approximation to the rate of water loss per area unit depending on mean rates of insolation, humidity and temperature monthly. Besides of its character to have quite a lot of assumed and disregarded parameters on the other hand, this range is more than tenfold the quantity of loss than direct precipitation has been measured. Even ground water can only contribute minor water supply in the semi-arid belt of the islands facing that ecological pressure. Climbing the islands slopes from the succulent belt up to the mountains, those dicrepancies are less powerful. The mountain belts on the Canaries receive more precipitation through the amounts of rain, dew and mist.

But at least two factors mean drought stress to the plant in the Canaries' lowlands: At first the amount of available water and - second - there is an additional increasing factor on the island coast, the increased osmotic pressure causing an additional physiological dryness for the plant. Sea foam is blown far inland and affecting exposed, but even remote cliffs. Bear in mind, that salinic aerosol droplets are more concentrated than pure ocean water through drying out, up to blown particles of pure salt crystals. Generally, the amount of deposited salts decreases from the coast to inland localities. In my opinion, the situation of an island is comparable to more arid conditions on the mainland, on which the diffusion of underground water in a fine-pored soil leads to salinification and individual drought stress as well.

In the context of this study, providing energy for the water cyclus through insolation remains important to be enlightened. The radiation environment of various vegetation types has been intensively studied before within homogeneous, agricultural monocultures, alpine dwarf shrubs, coniferous and deciduous forests of the temperate and boreal zone, mediterranean shrublands, tropical and temperate rain forests (see MIES & ASCHAN 1995). In the regarded Canarian vegetation type, evaporation, diurnal courses of temperature and the transpiration of *Plocama pendula* (GESSNER, 1985) and *Euphorbia canariensis* have been studied already (LÜPNITZ & LADWIG 1992). HÖLLWARTH & KULL (1979) provided general climatological data and physiological response of *E. broussonetii* (under *'E. regis-jubae'*). Those investigations did not focus however on the particular vegetation aspects of energy, water balance and the ecophysiological differences of the *Euphorbia* species. However, MIES & ASCHAN (1995) investigated the radiation input and the subsequent effects on temperature and atmospheric water pressure deficit of an *E. balsamifera* bush at Guimar, Tenerife. More data are almost lacking for the succulent vegetation of any subtropical dry zone.

This article will focus on some details of the microclimatic situations, on the potential of selected species, and on a selected working spot out of several from Tenerife Island, exemplifying some basic data of semi-arid to arid habitats. In addition to MIES & ASCHAN (1995) and MIES & al. (1996), this will enable us to construct a field-supported model of water flux, production and energy balance of such an environment in an annual course in the future. In the following, this work deals with three parts: (A) Vegetational Strategies, (B) Morphological Adaptations, and (C) Ecophysiological Data and Patterns.

MATERIAL AND METHODS

The sites chosen for field studies in the Canary Islands were at Malpais de Guimar in the Southeast, at Las Carrizales in the Masca area, and at Punta de Teno at the north-western tip of Tenerife in March 1993 and continously measured from March '94 untill Jan. '95. A rainy period alternated with a pronounced dry spell, lasting in general for about six months from April to September (see HUETZ DE LEMPS 1969). Although the area received sufficient rainfall in October 1994, the winter '94/'95 proceeded to be exceptionally dry and no more rain fell. Soil moisture was determined gravimetrically in close proximity to the experimental plants at a depth of 10 cm. The water contents of the soil at Punta de Teno during '94 were 162 ±12 g kg^{-1} in March, 92 ±5 g kg^{-1} in May/June, 25 ±5 g kg^{-1} in August, 121 ±12 g kg^{-1} in October and 85 ±8 g kg^{-1} in December (in respect of dry soil weight). During the field work 1994, the apparent incipient wilting point for most herbaceous species associated with the *E. balsamifera* stands was estimated to be less than 70 - 80 g kg^{-1}. The vegetation at Malpais de Guimar was characterized in 30x30 m grids and the plant's occurences were marked on a map in 1993.

A large variety of species was examined in the greenhouse for their differential water potentials [*E. atropurpurea, balsamifera, bourgaeana, dendroides, mellifera, broussonetii, piscatoria* (Madeira), *tuckeyana* (Cape Verde)]. Plants of *E. aphylla* were examined in vivo, both in the field at Punta de Teno and under laboratory conditions, using greenhouse material in the latter (see MIES & al. 1996).

The site of the measurement of *E. balsamifera* and *E. broussonetii* is situated on a relatively young dark-coloured lava field (hauled 1704) at the Malpais de Guimar on the SE coast of Tenerife Island (28°18'30''N, 16°22'00''W, Canary Islands, Spain). There the vegetation was mapped along a transect of 30x30 m grid squares. For ecophysiological investigations, shrubs of *Euphorbia balsamifera* and *E. broussonetii* have been chosen 300 m apart from the sea-shore, at 60 m a.s.l., and in SSE exposition (Fig. 2C). The microclimatic methods are as in MIES & ASCHAN (1995) and the gas exchange methods as in MIES & al. (1996), data from these sources may be reflected and re-evaluated. Each species has been examined for its photosynthetic capabilities yielding light optimum curves and temperature tolerances. The data on the tolerable span of temperatures were obtained empirically in The Botanical Garden at Düsseldorf and from WALKER (1994). The species were grown under different temperatures over at least seven years in a greenhouse facing Central European winter's temperature in the lower extreme or being heated in a growth chamber. Diurnal courses of the ambient microenvironment of the leaves in the field, transpiration and resistance of the leaves to vapour exchange were measured by means of a LI 1600 steady state porometer (Licor, Lincoln U.S.A.). The leaf area was determined by representative sampling plots in the bushes, leading to the leaf area index (LAI, the green area index (GAI), and whole surface area including stems (SAI). The LAI was measured by an optical planimeter, GAI and SAI were measured and counted from the stem's surfaces. In March 1994 the chloride content of soil samples was determined photometrically using a Merck Spectroquant test-kit (No. 14775). Under the prevailing maritime conditions, sodium chloride (> 98%) accounted for the predominant fraction of chloride salts.

The compared species were exposed to controlled desiccation in a growth chamber (20°C over day, 16° over night, water saturation deficit 4 g/m^3 WSD and subject of dew point hygrometry. The desiccation was determined gravimetrically and the asymptotic drought point was used as the reference point for the soil drought. The water relations of three different leaves were assessed by pV curves obtained using a dew point hygrometer (Wescor, U.S.A.) to measure leaf water potential after the method of ANDERSEN & al. (1993). The given values are the means of three leaf pieces. The leaves were excised under distilled water at the end of a light period; one part was measured for the actual water potential directly, the other rehydrated for 20 h. For the subsequent procedure, drying of the leaves between ψ measurements took place on the bench and leaf water changes were determined by weighings preceding the ψ determination. Only the symplastic water potential has been examined, in pre-experiments the apoplastic water content seemed to be neglectable. By plotting 1/ψ versus the full relative water content (R=1) a curve was obtained with an initial non-linear section, where the beginning of the linear portion indicates the leaf water potential at the turgor loss point (ψ0) and to the zero turgor (R=0). At lower water contents, the turgor loss point of the curve fits into a linear portion, enabling a linear regression analysis.

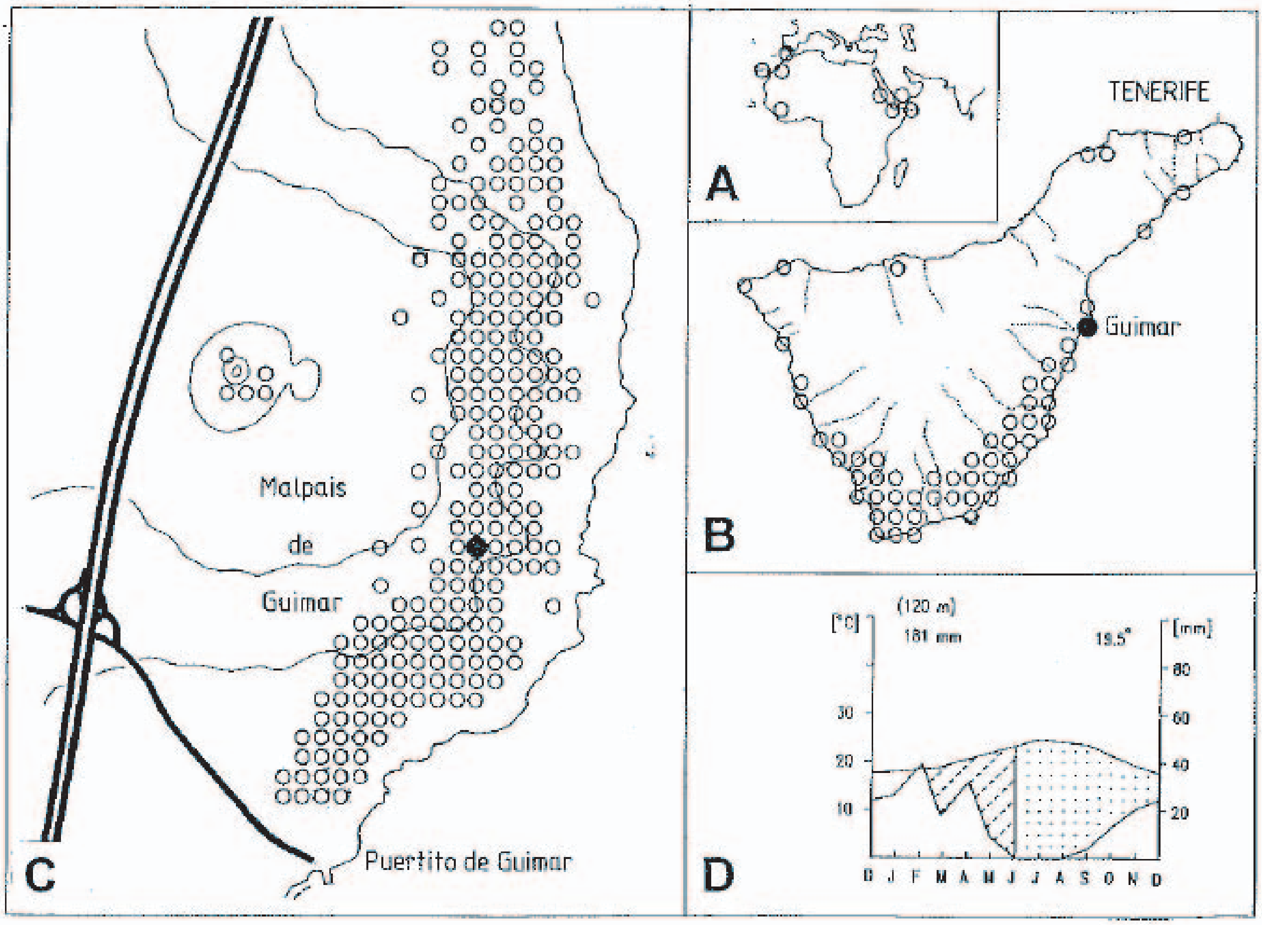

Fig. 2 - Distribution of the succulent spurge shrub *Euphorbia balsamifera* in Africa **A**, on Tenerife Island (Canary Islands) **B** and in the Malpais de Guimar **C**. In Africa and the Canaries, the western populations belong to ssp. *balsamifera* and the eastern ones to ssp. *adenensis*. On Tenerife, all grid areas are figured with dominating *Euphorbia balsamifera*. **D** The climate diagram from the nearby station Guimar (120 m) shows a semi-arid climate type with the period of available soil water for plants in dashed hachures (in the sense of THORNTHWAITE, climate data after RIVAS-MARTINEZ & al. 1993) (after MIES & ASCHAN 1995).

RESULTS

Vegetation mapping and morphological features at Malpais de Guimar

The vegetation mapping along a transect through the area of Malpais de Guimar on Tenerife - from the coast line up to the nearby volcano - segregates into 3 phytosociological zones (fig. 3):
(1) The coastal strip (relevées 1 + 2) consists of halophytic succulent herbs. The salt content of the soils is extremely high (> 20 mg/g soil).
(2) At 200 m distance from sea-shore, the cover of vegetation consists of practically one species - *Euphorbia balsamifera* - which is becoming denser inland.
(3) At 800 m distance the vegetation has changed again, in that species composition consists of man-high shrubs of the cactoid *Euphorbia canariensis* and the umbrella-shaped *E. broussonetii* as dominating species.

This is proven by three clusters in the principal component analysis of 42 relevées along this gradient (fig. 3 right). But - ecologically seen - there is an obvious change in vegetation characteristics within 200, 400, and 600 m either. If one looks at the distribution of species, the spatial patterns, all species are hidden in or closely related to *E. balsamifera* near the coast.

The fig. 3 shows already 72% of all other species or plant individua growing inside of a *E. balsamifera* canopy or even 0.5m besides in the belts between 200 to 600 m sea-shore' distance at Malpais de Guimar. Moreover, another part of 20% individua of various species grow within the 1.0m vicinity of a *E. balsamifera* bush. Only ephemeral plants like annuals, grasses and some bulbs grow totally dispersed. The vegetational pattern leads to the assumption of a dependancy of plant growth in the lava fields on the canopy of the dominating species.

There is a differentiation between the 'Balsamifera Zone' and the subsequent 'Canariensis Zone', the latter named after the other dominating species there. The fig. 4 shows the morphological shrub heights of the two dominating species, in that - near the coast - *E. canariensis* never overtops *E. balsamifera*. Moreover, specimen of *E. canariensis* often occur 'hidden in the Balsamifera-bush'. This study enlightens more aspects of this phenomenon called **Nursery Plant Effect,** notifying microclimatic influence to vegetation structure and dynamics.

Morphology and microclimate

Morphology plays an important role for the species' establishment itself and the vegetation growing in it. LÜPNITZ & LADEWIG (1992) have demonstrated it already with *E. canariensis*. The morphology of the spurges seasonally exposed to drought (with the exception of *E. mellifera* and *E. stygiana*) is hemispherical to umbrella-shaped. *E. balsamifera* expresses an ideal hemispherical canopy which is very much different from that of *E. broussonetii* for example. The ecological function of morphology for the species has to be shown.

MIES & ASCHAN (1995) measured a drastical decrease in global radiation (GR) and photosynthetically active radiation (PAR). The soil temperatures below the shrub did not exceed 25°C (LAI 0.93), whereas the lava surface outside was heated to 43°C. Lava surface temperatures about 50-60°C have been measured under summerly macroclimatic conditions. The insulating effect of the vegetation kept the soil surface cooler during the day and warmer during the night than the shrub surface. Through shading by leaves and more moderate temperatures the potential evaporation is significantly lowered inside the canopy of that species. As a result of this study, evaporation was 600 ml per m^2 and hour outside of *E. balsamifera* in March '94, whereas it ranged from 100 to 200 ml inside. In May '94, the same leafless shrub showed a microclimate nearly the same as outside, with 85 to 100 % the amount of evaporation inside (LAI 0.05). Other species do not differ as much, from which the morphological shape is not such close to the ground. The wind speed is extremely lowered, as measured at 0.5 m and at 0.1 m inside the *E. balsamifera* shrub (fig. 5). This special morphology reduces transpiration as well (see below). Moreover, a calm bubble inside a close canopy leads to litter and soil accumulation, so that the substrate beneath *E. balsamifera* significantly provides more nutrients.

Transpiration and photosynthesis

The Fig. 6 shows the temperature tolerances of the examined species and their light optimum. *E. mellifera* and *E. stygiana* are cold-adapted species with shade plant's characteristics originating from the laurel forests of the islands, whereas *E. balsamifera* takes the other extreme in an hot and arid environment.

The behaviour of the species to economize the available water in the ground and inside the plant is different. Fig. 7 exemplifies daycourses of transpiration and stomatal conductance of one *E. balsamifera* and one *E. broussonetii* shrub, growing side by side at Malpais de Guimar and transpiring under well-watered conditions in March 1994. The insolation was regularly sunny (2,100 mmol/m^{2}s on midday without clouds). *E. balsamifera* showed transpiration activities in the morning and the afternoon, reducing stomatal conductance over midday. *E. broussonetii* had no such ability. The latter transpired with less regulation of stomata width over midday; in comparison, it expressed the strategy of wasting water. *E. broussonetii* sheds leaves even earlier than *E. balsamifera*. Obviously, *E. balsamifera* is the most xerophytic species on the Canaries, other comparable species are even weaker in transpiration control. The differing transpiration patterns of for instance this two species underline their differential habitats or altitudinal belts on the Canaries.

A completely different way to face the semi-arid climate is undertaken by the stem succulents. *E. canariensis*, *E. handiensis*, and *Ceropegia* species express a regular Crassulacean Acid Metabolism (CAM), saving water over day in its fleshy stems. The assimilation rate is one seventh up to one fifth from that of C$_3$ species (LARCHER 1981). A remarkable feature on the Canaries is the adaptation of transition species between both pathways. *E. aphylla* is one example of such (MIES & al. 1996). Under drought stress, high day temperatures induced a slight CAM cycling. In winter, there was no remarkable CO_2 fixation over night. *E. aphylla* is a facultative CAM species. *Kleinia nereifolia* is expressing as such a facultative CAM cycling in its stems during the leafless period (JIMENEZ & MORALES 1987); their ephemeral leaves remain of the C_3 type.

Seven 'Federbusch'-spurges have been examined regarding the cellular water potential under the conditions of water stress to the plants. Fig. 8A shows the actual water potential of seven species of the leafy spurges (*Euphorbia* sect.Tithymalus) in a drought stress experiment. *E. broussonetii* (as *E. obtusifolia*) and *E. mellifera* responded very significantly to drought stress, whereas the other species maintained the water content. The osmotic potential at water saturation level in those two species and in *E. dendroides* can be resumed as an intracellular osmotic adjustment of the plants, to retain water similarly (fig. 8B). Only the actual water potential of *E. balsamifera* is not affected by drought stress, indicating the ability for water storage in the species with a caudex succulence (Fig. 8C).

DISCUSSION

The morphology of the species *E. balsamifera* warrants further attention, in that the ecological response is greatly influenced by canopies. Regarding the dominance of the species in those sites, the temperature can be regarded as an indicator for a variety of environmental factors selecting and promoting a special type of vegetation. The microclimate in the canopy during the day characterizes this canopy as a close system built by one plant, whereas most other vegetation types, so far examined (besides alpine dwarf shrubs), are dense interspecific canopies (e.g. laurel forest, ASCHAN & al., 1994). The canopy of *E. balsamifera* is not much affected by the strong winds in winter owing to the specific morphology of this species. The soil surface covered by the canopy is protected by the symmetrical shade. LÜPNITZ & LADWIG (1992) reported the decrease of temperature as a consequence of self-shading of individual shrubs of *E. canariensis* from Gran Canaria, but these authors did not specify the influence of the affecting winds either. Other species are less adapted to high insolation and have less temperature tolerance, occuring in even more moderate habitats or going on to the risk of severe drought injuries.

Shading, lowered temperatures, potential evaporation and wind leads to favourable conditions beneath *E. balsamifera* for germination and growth of seedlings. For this type of vegetation in addition, leaf size and total leaf area are lowered as nearer to the sea. The morphology of *E. broussonetii* e.g. and most other shrubs of this vegetation (see GESSNER, 1985 for *Plocama pendula*) differ from *E. balsamifera* in having a more or less umbrella-shaped canopy, open beneath. This allows insolation and wind to reach the stem base, thus less to reduce transpiration loss of water, not to protect the rooting area, not to accumulate debris and soil and not to improve the germination of seedlings. Protection of the canopy environment and even the area and soil - explored by own roots - is essential for a plant occuring under potential drought stress. The fine roots often lie near to the surface gaining water and nutrition rapidly after precipitation events (shallow root system: NOBEL 1989). The plants are rooted several meters deep in cracks and lava tunnels (LÜPNITZ & LADWIG 1992). Stems and especially roots are rather fleshy in all dominating species, saving water for the dry season to come.

The transpiration is lowered by thick glaucous wax layers on the leaf epidermis and the stems of all species (HEMMERS & al. 1986, GÜLZ & al. 1988). We could not observe yet a tendency to express more sclerophyllous leaves within one species or within the habitats under different water supply. *E. balsamifera* expresses C_3-type photosynthesis, because it can depend on the stored water in the caudex still.

Some species alter their ecophysiological 'behaviour' with the beginning drought, although less effective in sum. *E. broussonetii* and related species change their cellular osmotic potential to retain water e.g. Besides of *E. balsamifera*, only *E. mellifera* does not react as such. This is quite understandable in the light of habitat requirements in the latter's laurel forest zone. The examination of light optima and the temperature tolerance to the extremes gave similarly differentiated results.

The comparison of *E. balsamifera* and *E. broussonetii* unveiled two extreme strategies to face their harsh environments: The first retains water through fleshy stems and stomata control, the latter lavishes water - 'a spendthrift'. Both colonize their different environments very effectively. *E. broussonetii* colonizes a zone above the coastal strips of Tenerife. BATANOUNY & al. (1991) reported an ecophysiological gradient of *Euphorbia* species along a north to south gradient in Egypt.

The stem succulents diminish water loss through a 'niche of time' opening their stomata at night. *E. aphylla* is very effectively adapted to the different seasons on the Canaries. It reacts as a flexible CAM plant (MIES & al. 1996). African mainland species of the systematical section Tirucalli of the genus express full CAM, so that the authors suppose this feature to be an evolutionary process. BØRGESEN (1924) and BRAMWELL & BRAMWELL (1990) regarded *E. aphylla* e.g. as an halophytic species in view of the influence of salt-laden winds on its habitats. The relatively high salt content of the soil (6 - 8 mg g^{-1} DW soil) at the Punta de Teno site of *E. aphylla* for example agreed with this assumption. However, it does not apply to all natural stands of this species in the Canary Islands. Salt content of soils from stands with the best developed plants of *E. aphylla* is distinctly lower (0.2 - 1.3 mg g^{-1} DW soil, MIES & al. 1996).

Similar patterns of ecological adaptation found in related plant groups appear not to be coincidental. Evidence exists of a distinct hereditary ecophysiological pattern in the few cases hitherto examined (e.g. LÖSCH 1990). The differential abilities and strategies of the *Euphorbia* species and - regarding the nursery plant effect - the vegetation structure and possibly the vegetation dynamics of this Canarian succulent shrub belt displays the preference of a special ecological niche, on the Canaries. The presence, availability, and saving of water is essential. Developing a sketch of a model of this vegetation type in water economy, production and energy balance, we have to take into account the function of morphology, microclimate, physiology, and not at least all biotic and abiotic vegetation patterns. There is a tendency and potential to store water or even retard it from evapotranspiration. The role of wind velocity and evapotranspiration might be a new factor for modelling, e.g. in the equations after BLANEY & CRIDDLE as applied above or as in MONTHEITH equations (see SCHRÖDTER 1985). From the author's field experience, real data are essentially in need for understanding the ecology of species and vegetation. There remains a great wealth of information to obtain on ecological adaptations in semi-deserts and in the evolution of taxa of *Euphorbia* growing on the Atlantic Islands.

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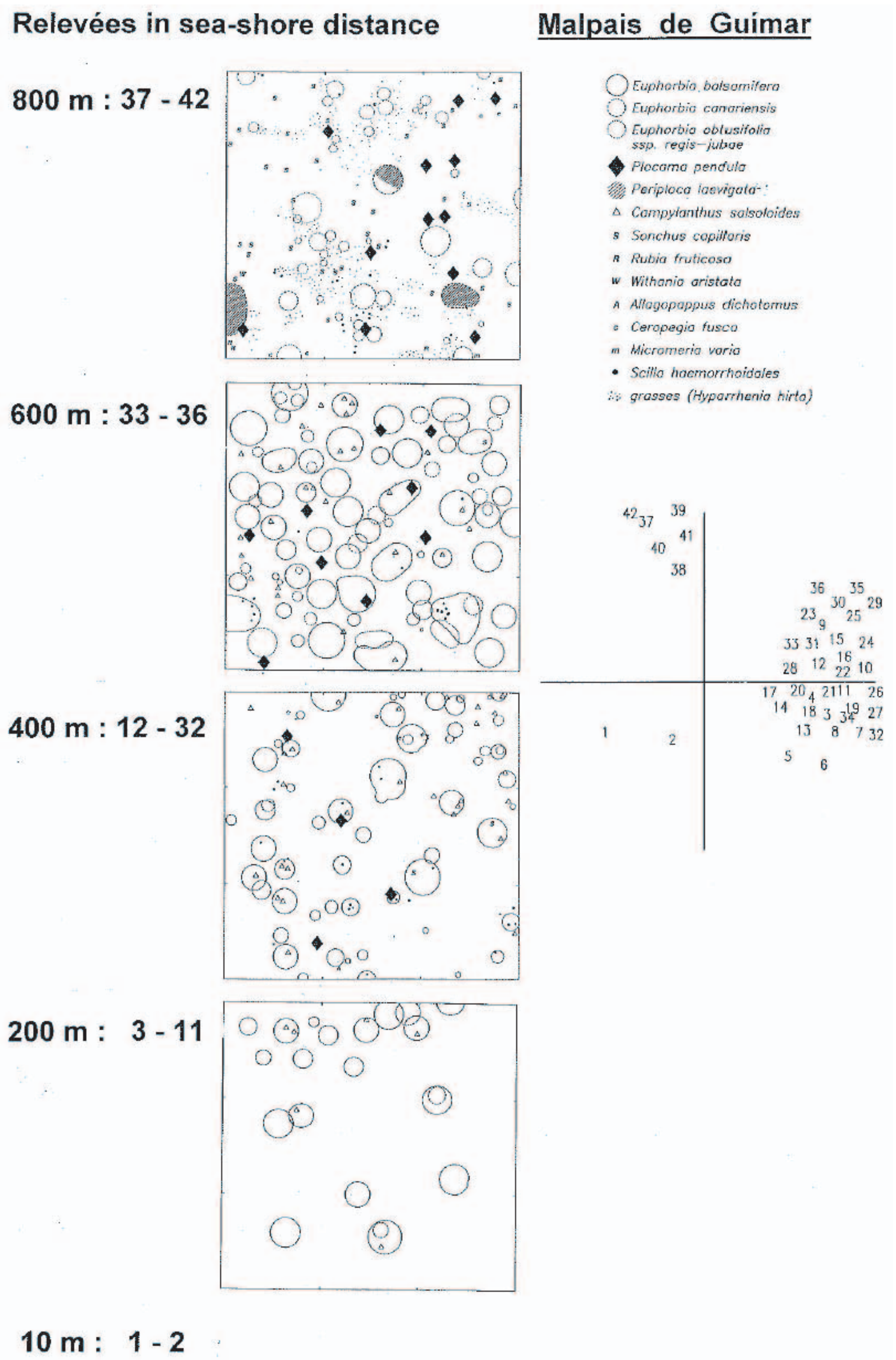


Fig. 3 - Phytosociological grids on the lava flow at Malpais de Guimar at 0, 200, 400, and 600 m distance from the sea-shore. (right) principal component analysis of 42 relevées.

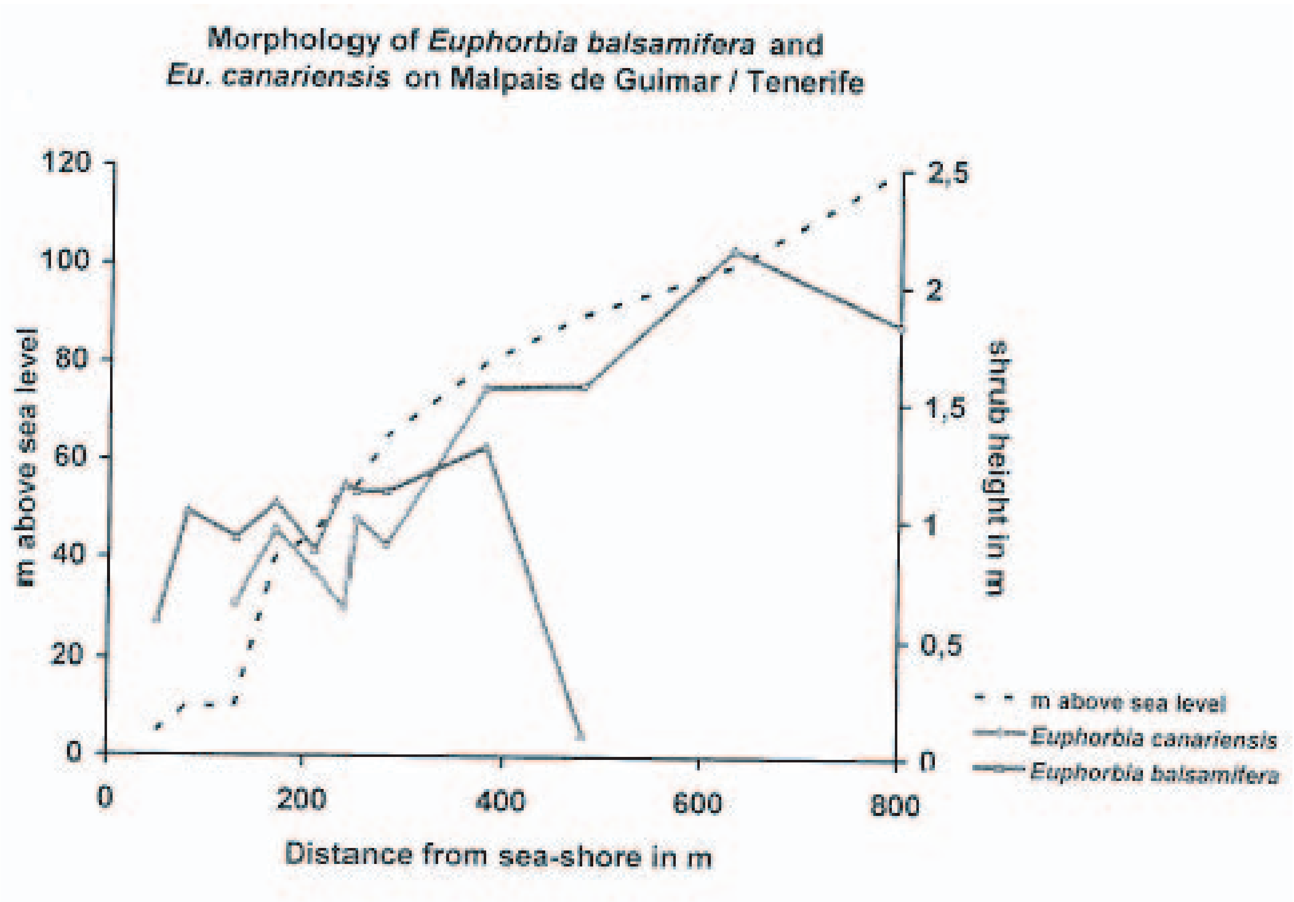
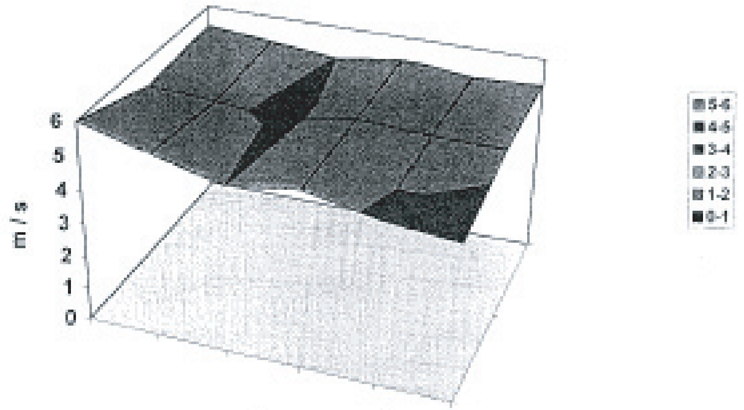
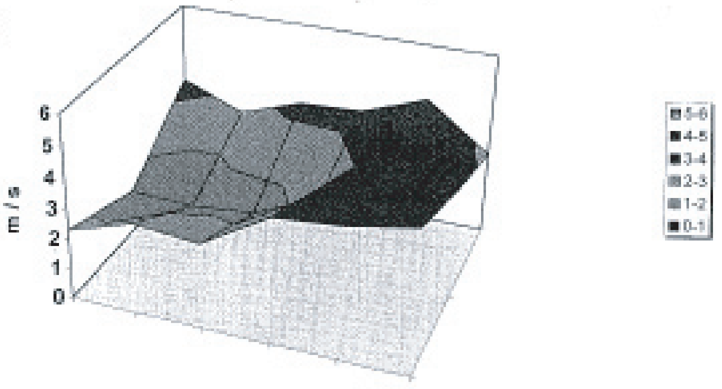


Fig. 4 - Shrub heights of *Euphorbia balsamifera* and *E. canariensis* at Malpais de Guimar in relation to the sea-shore distance.

Wind 2 m above ground and above *Euphorbia balsamifera* shrub on Malpais de Guimar 16.III.93



Wind 0.5 m



Wind 0.1 m

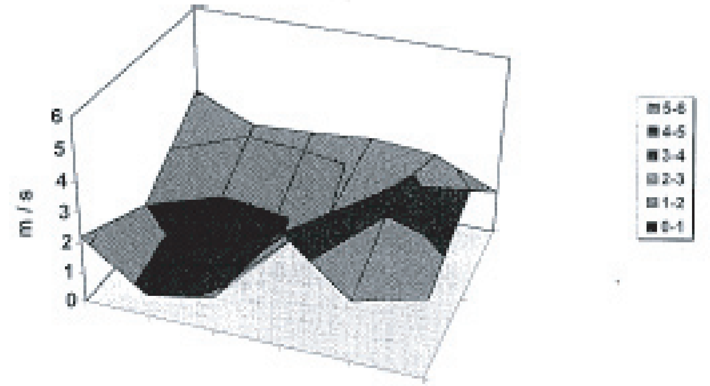


Fig. 5 - Wind speed above, within and beneath the canopy of *Euphorbia balsamifera* at Malpais de Guimar.

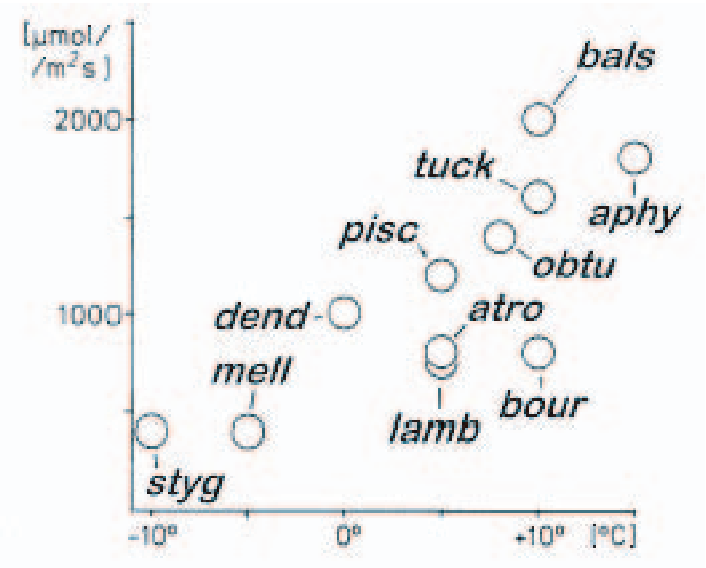
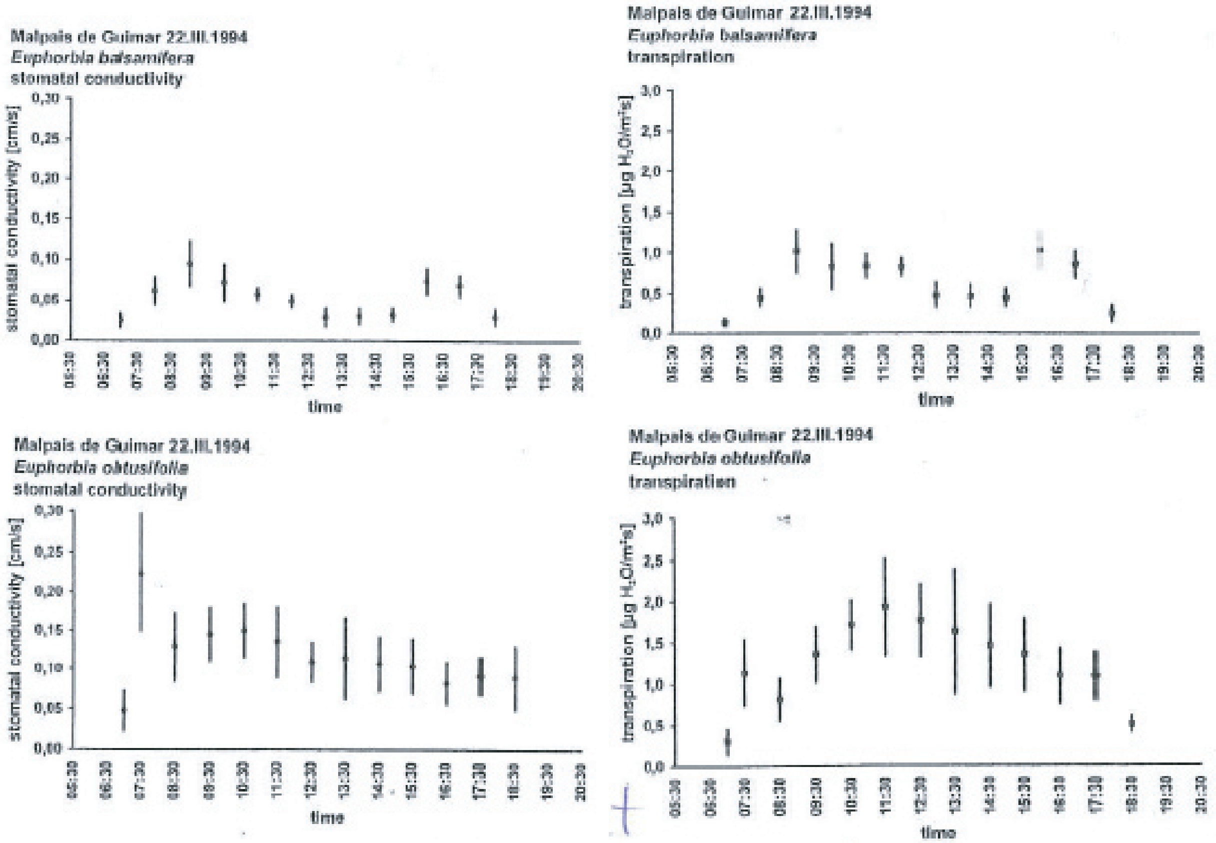


Fig. 6 - Photosynthesis and cold resistance of Atlantic *Euphorbia* species (*aphylla, atropurpurea, balsamifera, bourgeana, dendroides, lambii, mellifera, bropussonetii=obtusifolia, piscatoria, tuckeyana*).


Malpais de Guimar 22.III.1994
Euphorbia balsamifera
stomatal conductivity

Malpais de Guimar 22.III.1994
Euphorbia balsamifera
transpiration

Malpais de Guimar 22.III.1994
Euphorbia obtusifolia
stomatal conductivity

Malpais de Guimar 22.III.1994
Euphorbia obtusifolia
transpiration

Fig. 7 - Stomatal conductance and transpiration in a day course with *Euphorbia balsamifera* and *E. broussonetii* (Syn. *E. obtusifolia*) at Malpais de Guimar / Tenerife in March 1994.

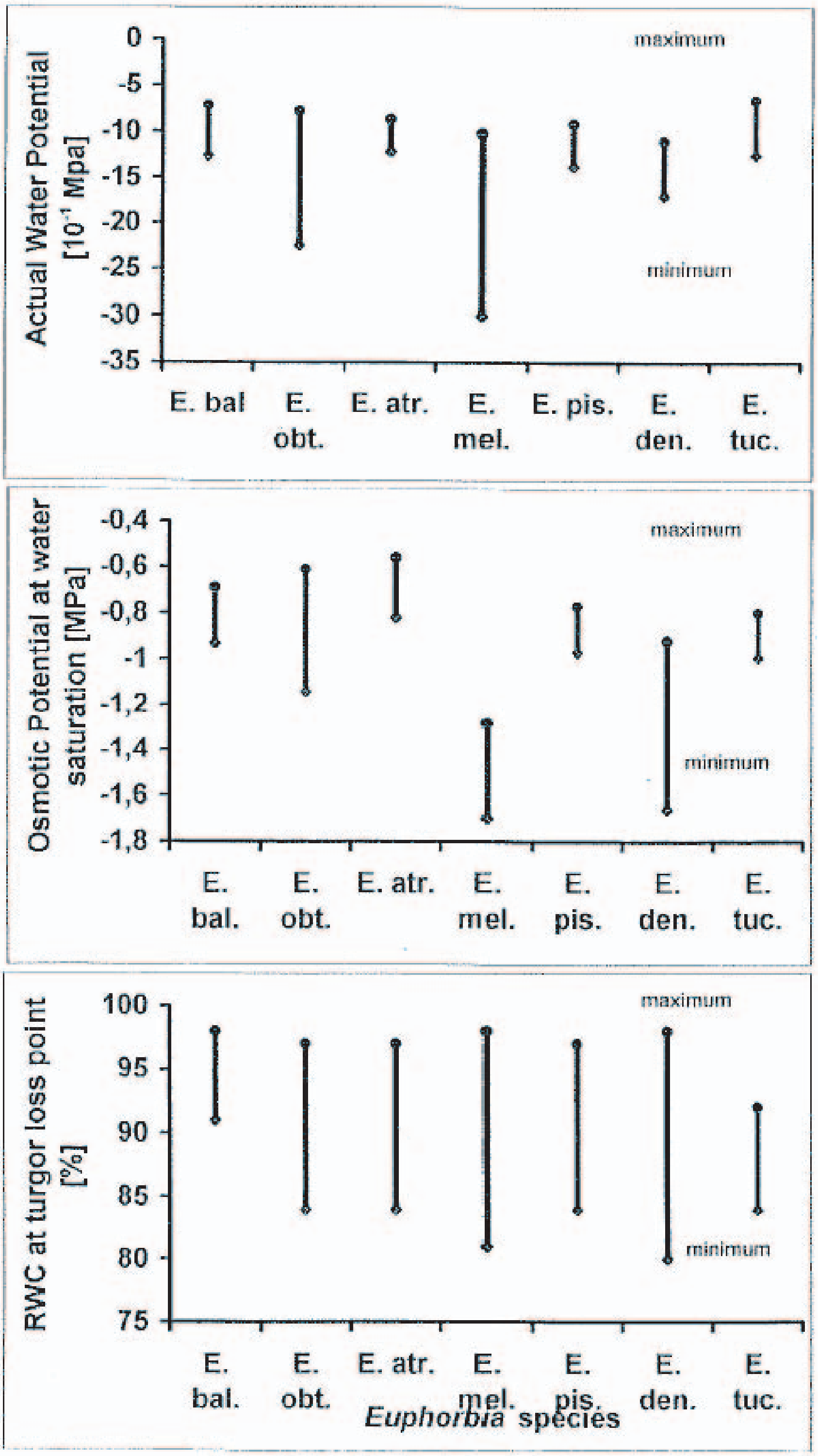


Fig. 8 - **A** Actual water potentials, **B** Osmotic potentials, **C** Relative water content at turgor loss point of seven species of the leafy spurges (*Euphorbia* sect. Tithymalus) in a drought stress experiment (*balsamifera, broussonetii=obtusifolia, atropurpurea, mellifera, piscatoria, dendroides, tuckeyana*).

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