Environmental Physiology of wild *Ricinus communis* L. in Sri Lanka

by

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A dissertation submitted to the Graduate Faculty of Biology in partial fulfillment of the requirement for the degree of Doctor of Philosophy, The City University of New York

1995

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

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Ecophysiological experiments were performed on wild castor (*Ricinus communis* L.) with the goal of understanding ecotypic differentiation and phenotypic plasticity in this tropical weed. Field and laboratory studies were performed on castor from self-perpetuating wild populations in three Sri Lankan ecosystems: dry shrubland (DS), lowland tropical rainforest (LTR) and wet coastal halophytic zone (WCH). In the field, measurements were made of net photosynthetic rate (P_{net}), leaf specific mass (LSM), and leaf stomatal density. Average values for P_{net} were 26.6, 23.5, and 21.1 μmol $m^{-2}s^{-1}$ for castor leaves in the DS, LTR, and WCH sites, respectively. Net photosynthesis was significantly different ($F = 57$, df=2,362, $P < 0.0001$, R-sq. = 0.14) among the three ecosystems in two-way analysis of covariance with site and time-of-day as main effects and photosynthetically active radiation, air temperature and vapor pressure deficit entered as covariates. Leaves in each ecosystem had similar diurnal trends for P_{net}. There was no midday stomatal closure and stomatal density was conserved about a grand mean of 202 mm^{-2}. Leaf specific mass was significantly different among the sites, varied over 3-fold, did not overlap between DS and WCH leaves, and averaged 48.9, 39.6, and 27.2 μg dry weight mm^{-2} of adaxial leaf surface area for DS, LTR, and WCH, respectively. Average P_{net} increased with increasing LSM.

Photosynthetic rates for plants in the common garden in New York, averaged 23.2 μmol $m^{-2}s^{-1}$ for DS, 20.9 for LTR and 17.7 for WCH plants; trends

comparable to field data. Leaf chlorophyll content of WCH plants (19.5 $\mu g/cm^2$) was significantly lower on average than for DS plants (21.2) and LTR plants (22.4). Photosynthetic light curves for these plants revealed genetically determined differences among the plants from the three ecosystems. Leaf specific mass of LTR plants (26.8 $\mu g\ mm^{-2}$) was significantly higher than DS (20.6) and WCH plants (22.5) but LSM was homogeneous between plants of DS and WCH. Results from drought experiments indicate a possible physiological trade-off among wild castor from different ecosystems for carbon gain under optimal conditions versus under drought conditions. In the glasshouse, xylem water potential was not statistically significantly different among the plant types (pre-dawn mean -0.25, midday -0.77 MPa) but temporary wilting point was different at -0.93 for DS, -1.1 for LTR, and -1.2 MPa for WCH plants. This study provides substantial evidence to classify wild castor from the three ecosystems as ecotypes.

Dedicated

to

My Parents

Acknowledgement

I am deeply indebted to my mentor, Prof. Dwight T. Kincaid for his most invaluable support, guidance and criticism through all phases of my research and in the writing of this thesis.

I am thankful and obliged to all the members of my committee: Dr. Amrita de Soyza, Dr. Barbara Meurer-Grimes, Dr. Richard Stalter, Dr. Dennis Stevenson and Dr. Jack Valdovinos for their valuable advice given to me for my research and the writing of this thesis.

I sincerely thank Professors Thomas Jensen, Dominick Basile and Eleanore Wurtzel for allowing me to use their laboratory facilities without which some of my research would not have been possible.

My sincere thanks go to Mora Mullane and David Cain for their assistance with the care of my plants in the green house. Furthermore, I specially thank Michael Baxter for his assistance in scanning electron microscopy.

The staff of the Rubber Research Institute of Sri Lanka are gratefully acknowledged for their valuable assistance during my field work. I specially thank Mr. Piyatissa Godahena for his help during my field measurements and seed collections in Sri Lanka.

I sincerely thank all my colleagues and the staff of the Department of Biological Sciences, Lehman College for all the support, friendship and for the stimulating work environment provided.

I gratefully thank my parents and parents in-law for their encouragement and support. I thank my wife Manoji and my daughters Ranitri and Eresha for their love and the sacrifices made to accommodate my studies.

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Introduction

The castor bean plant (*Ricinus communis* L., Euphorbiaceae) hereafter referred to as castor, is cultivated in the tropics and subtropics for its valuable seed oil. Castor is native to eastern Africa. It has escaped from cultivation and now occurs worldwide in the tropics and subtropics. It grows in the wild across a variety of environmental conditions including xeric, mesic, halophytic, and altitudinal range. Castor is primarily grown in non-industrialized nations where, in some cases, the seed is hand harvested from wild plants. Cultivated varieties have larger seeds, and often, smaller plant size than do wild-type plants. It was banned as a crop in the USA in 1977 because of its toxicity.

The oil contains 90% of its fatty acids as ricinoleic acid, which is "among the world's most versatile natural products and has hundreds of industrial uses that include synthesis of nylon - 11, lubricants, hydraulic fluids, plastics, cosmetics and other materials" (Somerville and Browse 1991). Even the famed toxicity of the ricin molecule (Lewis and Lewis 1977) may find use in the natural control of leishmaniasis (Kolberg 1994).

What accounts for the pantropical ecological success of wild plants of castor? Obviously, wild plants of castor are able to survive in varied environments through accumulated genetically based ecotypic differentiation, through phenotypic plasticity or, most likely, through a combination of these mechanisms. My thesis is that there are genetically based leaf gas exchange (carbon exchange rate and water relations) and plant morphophysiological strategies behind the ecological success of wild castor.

There has been relatively little modern scientific work on the physiological ecology of cultivated castor and none that we know of on wild castor. However, the ability of wild castor to thrive in a wide range of environments and its

economic importance make it an ideal candidate for an investigation of the relative importance of ecotypic differentiation versus phenotypic plasticity. Field measurements were made in Sri Lanka. This provided a basic characterization of leaf gas exchange in wild plants from different ecosystems. Based on these results, I then conducted "common garden" experiments to investigate the physiological, morphological, and growth characteristics of the plants under controlled conditions in the glasshouse and outside the glasshouse in New York. In addition, comparative studies were carried out on diurnal gas exchange, gas exchange under drought, photosynthetic responses to light, reflectivity of leaves, leaf chlorophyll concentration and leaf epidermal characteristics.

The island nation of Sri Lanka (65,610 sq.km, ca. 432 km x 224 km) lies off the SE coast of the Indian subcontinent at 7^{O} Latitude N and 81^{O} longitude E, and with altitudes ranging from sea level to 2340 m, it displays a microcosm of the environmental conditions in which castor thrives worldwide both as a crop and as self-perpetuating wild populations (Figure 1). Although high population density and cultivation have altered the Sri Lankan landscape, montane tropical rainforests, seasonally dry montane forests, wet and dry coastal halophytic regions, dry shrublands, and lowland tropical rainforests exist as biome remnants.

Adult plants of castor are reported to be tolerant to drought and consequently may have a great potential for cultivation in drought affected areas (Shankanarayanan 1983), especially in the face of diminishing water supplies and competition (human and agriculture) for existing water resources. Pearcy and Harrison (1974) report several instances where plant species have adapted successfully to changed environmental conditions by plastic adjustments of morphology and physiology, e.g., *Atriplex lentiformis* growing in coastal and desert habitats had similar photosynthetic gas-exchange characteristics despite the large differences in habitat and temperature, but had thermal optima for

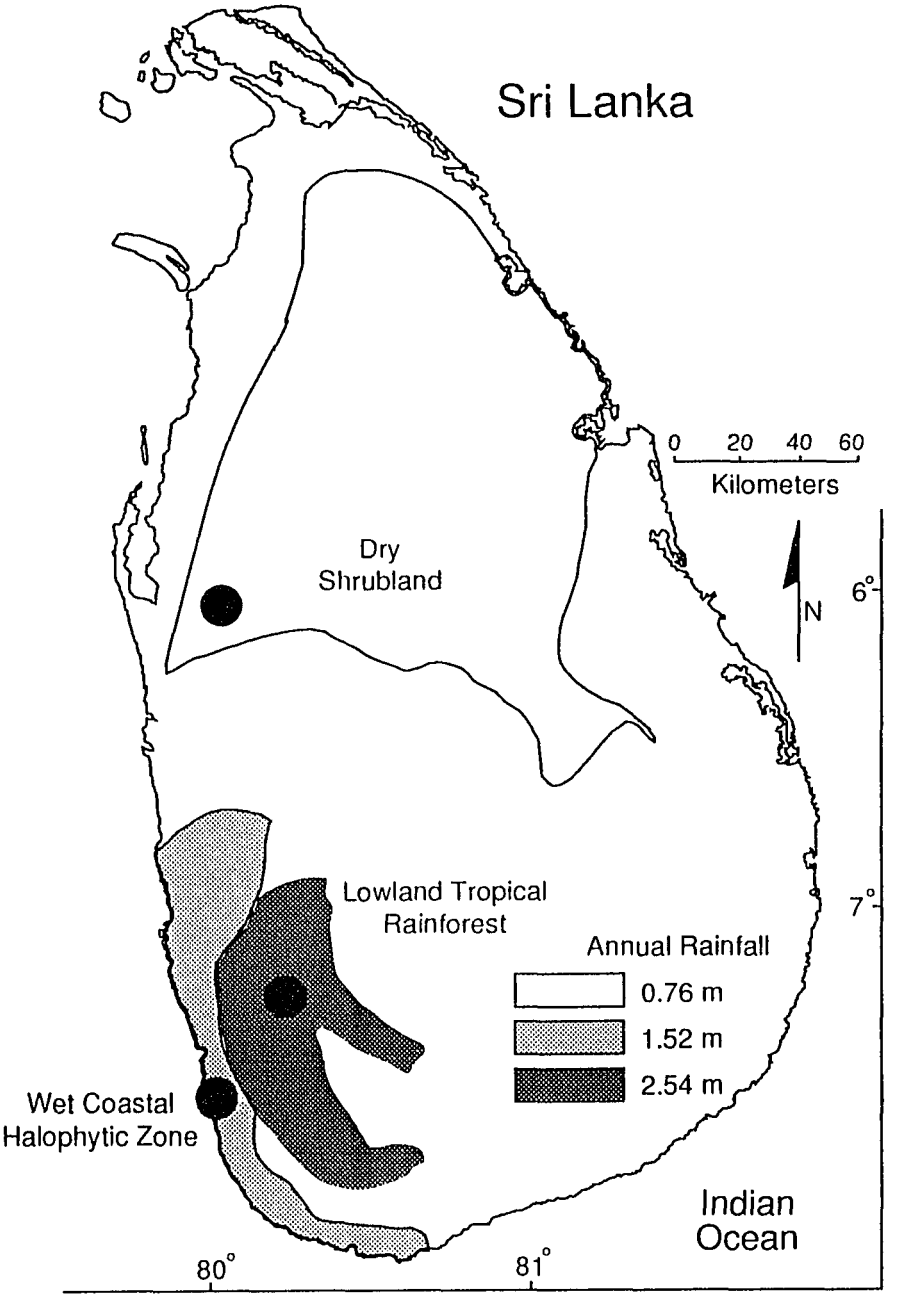

Fig 1. Map of Sri Lanka. Solid circles locate our study populations of wild Castor in DS, LTR and WCH ecosystems as shaded in relation to average annual rainfall. Map adapted from "Map of Agroecological regions of Sri Lanka" Produced by the Land Use Division, Department of Agriculture, Sri Lanka.

photosynthesis of 32°C and 42°C respectively. Mooney (1980) has shown that successful adaptation of *Heliotropium* to drier, warmer desert habitats in California was to due to the ability of the plant to change its photosynthetic thermal optimum. Similarly, Roy and Mooney (1987) have shown how photosynthesis, water relations and morphology converge to maintain high photosynthetic rates in a hot environment. Clausen et al. (1940) conducted the most famous common garden experiments of all time by growing plants from different populations of the same species collected from contrasting ecosystems. They demonstrated that within a plant species there is adaptation to the local environment often through genetic differentiation of local populations as they occur across different ecosystems.

If plants of a species adapt to different environments entirely by changes in plastic characteristics, then when returned to a common environment, they will converge in morphology and in physiology. However, if some genetic ecotypic differentiation has occurred, some physiological and morphological differences exhibited in the natural environments will persist in the common garden. Also, common garden experiments, following ANOVA (e.g., F-tests and calculation of R-squares) provide statistical evidence concerning the relative importance of "genetically fixed" and "phenotypically plastic" characteristics within and among populations of the same species.

Development of drought tolerant and salt tolerant crops is a major goal of agricultural research worldwide. Desertification due to drought and due to increasing levels of salinity is a recurring problem in many developing countries, often intensifying the problems of poverty and malnutrition. If the fundamental mechanisms which adapt the wild members of a crop species to adverse environments can be understood, these adaptations can be enhanced using genetic techniques and selection procedures which are often limited by the lack

of this kind of knowledge (Boyer 1982, Engels and Hawkes 1991). For instance, "The genes in wild species and old varieties have incalculable value to plant breeders looking for natural resistance to disease and pests" (Gene Saari as quoted in Rhoades 1991).

While in basic ecological research there are no guarantees of practical conservation outcomes, my identification and quantification of diversity in the gas-exchange mechanisms of wild castor could be a step in the development of drought and salinity tolerant varieties by conventional techniques. This can be achieved by the use of genotypes from wild castor, by selective breeding, or if appropriate, by using molecular technology. The availablity of stress tolerant genotypes would be of significant economic importance to small acreage farmers in Sri Lanka and to other growers worldwide. This information could also help to conserve valuable resources by suggesting the minimal levels of agricultural inputs required for optimization of yield, even with existing genotypes. Furthermore, drought resistant ecotypes of wild castor may have potential as agroforestry "alley trees" ameliorating the microclimate and soil conditions for dry season row crops on unirrigated uplands.

Background

Botanical classification of castor

Linnaeus in 1753 described the genus *Ricinus* L. It was originally described as three species, but now is recognized as one species *Ricinus communis* L.; the common castor. Systematic placement of the genus in the family Euphobiaceae was done by Argovskii in 1866 (see Moskin 1986). It is now placed under the subtribe Ricininae Griseb. of the tribe Acalyphoideae Aschers (Webster 1975).

Morphology

Castor is a shrub of about 6-10 meters in height and grows in tropical and subtropical regions. It has a life span of about 8-12 years. Castor growing in moderate climates produces seed and dies during winter (Mason and Mason 1986). The stem of castor is geniculate, branching and produces a terminal raceme-spike. Male and female flowers occur in the same spike and do not have petals. Fruit is three locular with a seed in each locule. Seed is mottled, smooth and ellipsoidal (Mason and Mason 1986; Moskin 1986).

Arrangement of leaves is alternate with 2/5 phylotaxy. Leaves are generally large and range between 20-50cm when mature and possess a long petiole. The leaf blade is palmate with 7-11 lobes and the edges are serrated. Leaf color may be dark green, brown or violet. Sometimes a whitish waxy coating occurs on the stem and the underside of the leaves (Moskin 1986). In young plants the veins of leaf blades, petioles and stems contain functional nectar glands. Generally, the length of the tap root varies from 1.5 -3m, and the lateral roots spread to 1m (Moskin 1986).

General plant ecophysiological characteristics

Gas Exchange

Cultivated castor has high rates of photosynthesis compared to tobacco and maize (Dai *et al.*, 1992). Dai *et al.* suggest that this high net photosynthesis (P_{net}) is due to a high level of photosynthetic components such as chlorophyll content, RUBISCO protein and total soluble protein per leaf area. In experiments with cultivars castor maintained high photosynthetic capacities at high humidities, and P_{net} was sensitive to vapor pressure deficit (VPD) and declined with increasing VPD (Dai *et al.*, 1992). The possibility for inhibition of some component of the photosynthetic process under either low humidity or water stress was suggested from a study using eight plant species (Sharky 1984). He observed that, at a given intercellular CO_2, plants under low humidity or water stress had lower photosynthetic rates.

Within a plant species variations in P_{net} could occur due to adaptive responses of the population to the environment. Variations in biochemical and morphological factors such as the amounts or activities of specific proteins and pigments, differences in leaf structure, cell size, or stomatal frequency may cause differences in P_{net}. Differences in photosynthetic performance among pea cultivars have been attributed to differences in chlorophyll content (Mahen and Hobbs 1981).

Changes in leaf form and orientation can have dramatic effects on leaf energy budgets (Gates 1965,1980; Vogel 1983) and perhaps on the gas exchange characteristics of the plant. It is reported that leaf greeness is highly correlated to chlorophyll and leaf nitrogen content (Marquard and Tipton 1987; Yadava 1986; Evans 1983; Peng *et al.*,1993). Light colored leaf surfaces increase reflectivity and

reduce absorptance (Barbour *et al.*, 1987; Ehleringer and Björkman 1978b; Mooney *et al.*, 1977). This important feature of plant survival in xeric environments reduces leaf temperature, transpiration and metabolic rate (Ehleringer 1981). Mooney *et al.* (1977) demonstrated that the desert holly (*Atriplex hymenelytra*) increases reflectance by morphological adaptations such as having glands which dry out to increase surface reflectance. Stevenson and Shaw (1971) found that vertical leaves of soybean had higher stomatal conductances than did horizontal leaves, apparently because vertical leaves had lower leaf temperatures and lower water vapor pressure gradients between leaf and air. The optical properties of castor leaves (Lee and Patel 1987) are typical of many plants (Ehleringer 1981). Lee and Patel in 1987 observed that the absorptance (1-[transmittance + reflectance]) of photosynthetic photon flux density (400-700nm) in castor leaves was 0.88. At 350-1100nm reflectance rather than transmittance accounts for a greater proportion of light not absorbed by the leaf (Lee and Patel 1987).

Jeschke and Wolf (1988) observed in castor that NaCl salinity above 40 mol m^{-3} severely affected development as shown by suppressed branching, reduced size and epinasty (the downward curvature of leaves) of leaves. However they also found that castor has the ability to survive and produce viable seeds even at 160 mol m^{-3} NaCl salinities. In *Lupinus alba* (a salt sensitive species) salinities as low as 40 mol m^{-3} inhibited reproduction (Jeschke *et al.*,1986). Reduction of growth rate due to salinity was observed in castor by El-Shourbagy and Missak (1975). The retardation of growth in saline environments disqualifies castor as a halophyte but certainly it can survive in halophytic environments. Thigmotrophic effects such as the shortening of stem and internodes induced by gentle mechanical stimuli have also been observed in castor (Jaffe 1973). Thigmomorphogenesis in castor probably functions as protection from mechanical stresses of high winds. In a

study of another aspect of leaf orientation in castor, Jeschke and Wolf (1988) suggested that in epinasty in castor could be an adaptation to reduce transpiration. This reduced demand for root water absorption may serve to reduce excessive import of Na^+ and Cl^- into the shoots, a factor of obvious survival value. It has also been shown in *Helianthus* (Rawson,1979; Rawson and Woodward 1976) that leaves in a vertical position have a higher water-use efficiency (WUE - ratio of grams of carbon fixed in photosynthesis per gram of water lost in transpiration) than do leaves in a horizontal position, because in a vertical leaf, photosynthesis is less reduced than is transpiration. Therefore, whereas wilting may seem to be a final step of a droughted leaf towards senescence, paraheliotrophic movements in response to water stress are far from a terminal action. However it should be noted that high WUE can be achieved at severely depressed photosynthetic rates provided that transpiration is even more severely depressed, so any consideration of WUE as a factor in plant adaptation should also take into account the P_{net} at which it is achieved (pers. comm. de Soyza, 1994).

Often, variation in a plant's anatomy may play a role in survival in dry environments. For example, Crombie *et al.* (1985), using an acoustic detection method, observed cavitation[2] in tomato (at 0.4 MPA sap tensions) and cultivated castor (at 0.8 MPA) when grown under environmental conditions which would be barely sufficient to initiate cavitation in the xylem of woody species such as *Rhododendron, Fraxinus* and *Eucalyptus*. This propensity towards cavitation in castor is causally related to the physics of having large diameter vessels in the xylem. Cavitation and subsequent refilling of the xylem columns by root pressure may occur diurnally in some plants thereby enhancing survival in xeric environments (Milburn and McLaughlin,1974).

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[2] breakage of xylem water columns such that air bubbles are introduced, thereby blocking the flow of water.

Phenotypic plasticity is the ability of an individual organism to alter its physiology/morphology in response to changes in environmental conditions (Schlichting 1986). Phenotypic plasticity may reduce genetic influences on phenotypic expression which may reduce micro-evolutionary change (Bradshaw 1965; Levin 1988) but allow the generation of suitable phenotypes for changing habitats. Absence of a morphological response to the environment does not necessarily mean that a plant lacks plasticity (Bradshaw 1965). Species which are light demanding seem to demonstrate a larger morphological plasticity than those which are shade tolerant (Bazzaz 1979, 1984). Oliva *et al.* (1993), working on *Festuca pallescens* (Poaceae), found that phenotypic plasticity allows for diverse habitat colonization. They also found that larger plants are characteristic of humid habitats. Plants from xeric and saline habitats were characterized by fewer and larger spikelets per panicle than found in plants from humid habitats.

Plants growing in xeric or high light environments typically produce leaves with less leaf area (Geeske *et al.*, 1994; Kubiske and Abrams 1992; Mooney *et al.*, 1977) but with greater thickness and greater leaf specific mass than the leaves of plants growing in mesic or shaded environments (Carpenter and Smith 1981; Abrams and Kubiske 1990; Kubiske and Abrams 1992). Kubiske and Abrams (1992) measured leaf area and leaf thickness in seedlings of *Quercus rubra* in xeric and in mesic natural habitats as well as in the common garden. Leaves were smaller and thicker in seedlings from xeric sites, both in the field and in the common garden. This indicates that in *Quercus rubra* this morphological difference is genetically modified and does not exhibit phenotypic plasticity. It was also observed that the xeric seedlings had higher net photosynthetic rates and higher stomatal conductances compared to mesic seedlings. In contrast Mooney *et al.*, (1977) observed that the desert holly (*Atriplex hymenyletra*) changes leaf characteristics during the year. They found that the leaves produced during the

cool dry season are nearly twice the size of leaves produced during summer, a clear example of phenotypic plasticity. For a particular plant species, LSM may change in response to nutrient availabilty and water stress (Mooney *et al.*, 1978; Jurick *et al.*,1982; Shaver 1983).

As stated by Slatkin (1987) "Populations of a species that occur in diverse habitats exhibit differing physiological and morphological characteristics which reflect the predominant stresses imposed by the environment." When leaves are subjected to water stress, it is often observed that P_{net} is decreased while intercellular CO_2 is held constant (Tenhunen *et al.*, 1984; Wong *et al.*, 1985). Renou *et al.* (1990) reported that the decrease in photosynthesis rate during water stress can be attributed to the decrease in chloroplastic CO_2 concentration in spite of constant intercellular CO_2.

During water stress, decrease in photosynthesis could occur by stomatal limitation (due to increased stomatal resistance) and/or by non-stomatal limitation (due to limitations in the photosynthetic apparatus). In *Quercus rubra*, it was observed that the non-stomatal factor is generally lower in xeric plants than mesic plants (Kubiske and Abrams 1992). This suggests that the photosynthetic apparatus of xeric seedlings has a greater tolerance for leaf water deficit compared with mesic seedlings. It was also shown that the sensitivity of these two types of processes may differ considerably between species and genotypes (Grieu *et al.*,1988; Guehl and Aussenac 1987).

A study done by Kloeppel *et al.* (1993) working on *Quercus prinus, Quercus velutina, Sassafras albidum* and *Acer rubrum*, suggested that the seasonal variations in P_{net} and leaf conductances were significantly correlated with each other and with leaf specific mass. They concluded that these species display very similar adaptations in response to varying light and water availability. Leaf

shedding during drought is an adaptation used by some plants to avoid desiccation.

A number of studies show that some species are physiologically more sensitive to water stress than others as indicated by differences in water potentials at stomatal closure (Miller and Poole 1979). There is some evidence that the degree of physiological tolerance to drought is correlated to the rooting depth, with shallow rooted shrubs tending to have tissue with greatest physiological tolerance to drought (Poole and Miller 1975, 1978). Shallowly rooted shrubs tend to have the most xeromorphic leaves. It was observed by Davis and Mooney (1986) that chaparral shrubs of California have a suite of morphological and physiological adaptations to withstand the prolonged summer droughts.

Several authors have described physiological differences between drought tolerent evergreen plants versus drought avoiding evergreen plants (Hinckley *et al.*,1983; Davis and Mooney 1986; Wright *et al.*, 1992). "Tolerants" maintain more negative osmotic potentials and larger conductances than avoiders. Seasonal changes in conductance and leaf tissue properties also contribute to drought acclimation in tropical rainforest plants. Dry season drought may cause ontogenic changes in leaf tissue properties making an important contribution to dry season turgor maintenance (Fetcher 1979; Robichaux *et al.*,1984; Wright *et al.*,. 1992).

Kolb and Davis (1994) observed that the ability of *Salvia melifera* (coastal Sage) to inhabit drier sites than *Ceanothus megacarpus* (chaparral) may be due to the drought deciduousness in summer and high growth rates in spring which results in rapid construction of xylem and leaf tissues. It has been shown that plants physiologically adjust to water stress by stomatal closure, osmotic adjustment and turgor maintenance, and that these physiological adjustments play an important role in drought tolerance (Davis and Mooney 1986, Saruwatari and Davis 1989).

Many plants reduce water consumption by stomatal closure during drought (DePuit and Caldwell 1975, Cambell and Harris 1977, Miller 1988). Shedding of leaves and thereby reducing the total leaf area of the plant helps survival in drought (Branson *et al.*,1976). Although physiological activity is greatly reduced by water stress, desert evergreens such as *Larrea tridenta* may survive even at water potentials less than -7.0 MPa (Franco *et al.*,1994). In contrast, the textbook value of permanent wilting point of field crops is - 1.5 MPa.

Materials and Methods

Field Studies

Field measurements were taken from June to August 1992 in three contrasting ecosystems in Sri Lanka using wild, self-perpetuating populations of castor. As shown in Fig. 1, these are -- dry shrubland (DS)(North Western Province), lowland tropical rainforest (LTR)(Sabaragamuwa Province) and a wet coastal halophytic region (WCH)(Western Province). These sites are low altitude (0-15m) with undulating terrain. Annual rainfall increases over three-fold from DS to LTR (Fig. 1). WCH and LTR receive two seasons of monsoonal rainfall (South-West monsoon from May through August and North-East monsoon from October through December) and scattered inter-monsoonal rainfall. In contrast, DS receives rainfall mostly by the North-East monsoon.

Wild castor has much smaller seeds than castor cultivars. Wild castor has dehiscent capsules which eject seeds, as opposed to cultivars which have been selected for nondehiscent capsules to allow harvesting (Moskin 1986). The study plants were chosen as being wild plants on these bases, among other criteria, including the knowledge of local land use history. Plants are derived from seeds; reproduction by ramets does not occur in this plant which is a perennial in the tropics. Twenty castor plants were selected from each of the three ecosystems and net photosynthetic rates (P_{net} -- μmol $m^{-2}s^{-1}$, CO_2 fixed per unit leaf area per time) of the most recently fully expanded leaves were measured using an infrared gas analyzer-based portable photosynthetic system (Model LI 6200, LI-COR Inc., Lincoln, Nebraska, USA) on clear days at 4 time intervals (10:30am, 12 noon, 1:30 pm, and 3:00pm solar time).

Leaf specific mass (LSM, μg dry weight per mm^{-2} of leaf area, one side) was measured for leaf discs extracted with a calibrated hole punch, avoiding major leaf veins. Fifty discs from each of 10 plants at each site were dried to constant weight at 70°C. Fifteen leaf discs were rehydrated in a detergent solution, critical point dried, gold-coated and 90 scanning electron micrographs were taken at 250X. Abaxial stomatal density was measured in six fields-of-view per leaf disc representing five plants per site.

For statistical analysis, StatView (Feldman and Gagnon 1986), JMP (ver. 2.0.1; SAS Institute Inc.), and programs written for approximate randomization analysis (Noreen 1989) were used on Macintosh computers. Stomatal density and LSM were analyzed by single classification ANOVA. The null hypothesis, that there were no differences among the ecosystems for mean P_{net}, was tested when the means were "adjusted" in two-way analysis of covariance (ANCOVA) in an attempt to eliminate the influence of different values at the time of gas exchange measurement for photosynthetically active radiation (PAR), air temperature, and vapor pressure deficit (VPD), these three variables being entered as multiple covariates. Diurnal trends of P_{net} among the three ecosystems were diagnosed by the F-test for interaction in this two-way ANCOVA. Especially given the large sample sizes, it was demonstrated that data transformation was not necessary to meet the assumptions of ANCOVA. In addition, co-linearity among covariates was not a problem.

The approximate randomization tests proceeded as follows. The raw data set was in a 365 row by 6 column layout, with rows representing leaves, and columns defined as the classification and measurement variables. Three hundred random shufflings of the column containing the response variable (P_{net}) were generated while maintaining the original arrangement of the other 5 columns (habitat, time of measurement, PAR, air temperature and VPD). This generated 300 random datasets under the null hypothesis that the particular arrangement of

P_{net} in the raw data matrix represents only one of a very large number of equally likely random datasets. The two-way ANCOVA model was applied to each of these 300 null datasets and F statistics were tallied for each main effect and contrast that was examined when the model was applied to the raw data. P-values are calculated as (NGE+1) / (NP+1) where NGE is the number of F-statistics greater than or equal to the F being tested for significance, and NP is the number of permutations, 300 in this case (Noreen 1989).

Common Garden Experiments

Common garden experiments were carried out at Lehman College, New York under glasshouse conditions and outside the glasshouse on the roof of Davis Hall. Seeds collected from all three sites were planted in pots for controlled studies of the physiological variables mentioned above and, in addition, to study water relations, growth characteristics, responses to stress and diurnal physiological trends under common environmental conditions.

The gas exchange variables measured are listed below.

Variable	**Units**
Net photosynthesis (P_{net})	(μmol $m^{-2}s^{-1}$)
Stomatal conductance to water vapor (g_{wv})	(mol $m^{-2}s^{-1}$)
Transpiration (E)	(mol $m^{-2}s^{-1}$)
Intercellular CO_2 (C_i)	(ppm)
Relative humidity (RH)	(0-100%)
Leaf temperature	(^oC)
Air temperature	(^oC)

Photosynthetically active radiation (PAR)	(μmol $m^{-2}s^{-1}$)
Vapor pressure deficit (VPD)	(mb)

Vapor pressure deficit is the difference between the water vapor pressure of bulk air at a specific temperature and at 100% RH, minus the vapor pressure of the air at its current humidity, and at the same temperature. It is the best measure of the drying power of the air.

Leaf xylem water potential measurements were made done using a Scholander pressure chamber (Soil Moisture Inc., Santa Barbara, California).

Plant material and growth conditions

Seeds of castor were collected from populations in the three ecosystems in Sri Lanka. In New York, these seeds were germinated in a soil mixture containing top soil, vermiculite and sand in a 1:1:1 ratio in pots of 16 cm diameter x 17.5 cm high. For each experiment seedlings were selected for uniform size and one plant was maintained per pot. Plants were watered every day and were supplemented with a commercial fertilizer solution (Peters N:P:K: 20:20:20). The plants were sprayed with a miticide/soap mixture on a regular basis.

Experiment 1 - Gas exchange and water relations in the glasshouse

Five plants each of all three plant types were planted using pots and the common soil mixture mentioned above. All 15 pots were placed according to a completely randomized design in the glasshouse. Gas exchange and leaf water potential studies were carried out using these plants.

The gas exchange measurements were started when the leaf lamina was large enough to completely cover the 2.5 x 4 cm measurement port used in the

1000ml leaf chamber. Gas exchange was measured fortnightly at midday (± half hour) unless otherwise noted.

Plants were watered to field capacity before measurement and their positions within the matrix were changed after every measurement. During gas exchange measurements a 1000 watt metal halide lamp was used to obtain full sunlight intensities (PAR of 2000 mol $m^{-2}s^{-1}$, 400-700 nm) during Fall, Winter and Spring of 1992 and 1993.

Pre-dawn and midday leaf xylem water potential measurements were made on the fully matured, fourth youngest leaf, using the pressure chamber. Plants were watered to field capacity the evening before measurements were made.

Experiment 2 - Evaluation of physiological characteristics and water relations (outside the glasshouse)

This experiment was done outside the glasshouse during summer 1993. It was conducted according to a completely randomized design having 10 replicates of each plant type. The plants were seeded in the glasshouse during March 1993. When three weeks old they were transplanted into pots of 30cm diameter by 25cm height. These plants were transferred outside to the roof adjacent to the glasshouse in early May and were measured throughout the summer. Gas exchange measurements were made five times during the summer of 1993.

Experiment 3 - Diurnal gas exchange

Diurnal effects on gas exchange were assessed using the plants from Experiment 2. The plants were well watered the previous day and all readings were taken in clear sky. The measurements were made five times beginning at 8:30am, 10am, 11:30 am, 1pm, and 3:30pm. Time taken to complete all the plants

of the experimental design was 45 minutes to 1 hour. The plants were randomly picked for measurements.

Experiment 4.- Comparative growth and biomass allocation

Seeds were planted in February 1992. Ten seedlings from each ecosystem were selected and transplanted into pots of 30 cm in diameter by 25cm height. After 16 months the plant heights and the number of leaves were measured and the plants were uprooted. At harvest, leaf area and dry mass of plant leaves, petioles, roots, and shoots was determined. Plants were dried in a convection oven at 70^{o}C to a constant weight (approximately after 4-6 days depending on the plant part). Before uprooting, 20 leaf discs were obtained from each plant using a number 10 cork borer having an area of 13.5 mm^{2}. These leaf discs were used for the calculation of total leaf area (Watson and Watson 1957) and LSM (µg dry weight per mm^{-2} of leaf area). Comparisons of growth characteristics were made using the above measurements (Hunt 1978).

Plants from Experiment 2 were used to measure plants heights starting from the 12th week to 24 weeks.

Experiment 5 - Photosynthetic response to light

When the plants reached five months in age, gas exchange was measured at four *PAR* levels averaging, 196, 650, 1315, 1792 mol m-^{2} s-^{1}. The light source used was a 1000W metal halide lamp. These light intensities were obtained by placing layers of wire mesh (acting as neutral density filters) between the light source and the plant. The set of plants used in Experiment 1 was used for this experiment.

Experiment 6 - Leaf reflectivity

This experiment was carried out using the plants of Experiment 1. Measurements of P_{net} were taken to compare the differences of the adaxial and abaxial surfaces of the leaves with regards to reflectivity. This was done by first measuring leaf gas exchange with the leaf positioned in normal fashion, adaxial surface towards the light. The relevant portion of the blade was then rotated 180° in the cuvette with the abaxial suface placed towards the light, taking care not to kink the midrib or petiole, and gas exchange was measured.

Experiment 7 - Gas exchange under drought

In October 1993 the plants used in Experiment 2 were placed in a completely randomized block design (3 x 10) in the glasshouse. The plants were subjected to drought by totally withholding water until the leaves wilted. During drought gas exchange characteristics were measured daily.

At temporary wilting point the midday leaf water potential was measured and the plants were re-watered.

Experiment 8 - Chlorophyll concentration

The plants from Experiment 2 were used for this experiment. A leaf disc from each of the 30 plants was obtained using a number 8 cork borer. The discs were cut into thin strips with a scalpel. These strips were soaked in 95% ethanol in small tightly sealed vials in a dark incubator at room temperature until no green specks were observed on the strips. The absorbance of the supernatent was measured using a Varian 634 series spectrophotometer at 649, 654 and 665 nm.

The following expressions were used to calculate the chlorophyll concentrations:

Total Chlorophyll = 1000 x A654 / 39.8 µm/ml (single wave length method)

Chlorophyll a = 13.70 x A665 - 5.76 x A649

Chlorophyll b = 25.80 x A649 - 7.60 x A665

Chlorophyll a+b= 6.10 x A665 + 20.04 x A649 (dual wavelength method)

The chlorophyll contents were corrected for dilution and leaf area using the following expressions:

Chlorophyll a = Chlorophyll a x 5ml (ethanol) / 1.62 cm^{-2} (area of leaf disc)

(The source of the above method - Wintermans and Mots 1965).

Experiment 9 - Leaf epidermal studies

Leaf surfaces (upper and lower) were studied using a scanning electron microscope (Amray, model1830). Field and glasshouse leaf samples were processed. All three plant types were used in replication, to study stomatal and cuticular structures and other observable epidermal features. Leaf squares measuring approximately 0.5cm x 0.5cm were cut from five plants of each plant type. These were critical point dried using a Samdri-790 (Tousimis Research Corporation, Rockville, Maryland) and received a 100 Å thick layer of gold using a Hummer 2 sputter coater. Stomatal counts were made at six random locations at x250 magnification using the scanning electron microscope. Photographs were made using 1900 magnification to compare stomatal morphology among the plant types.

Data Analysis

Gas exchange, plant tissue water relations, plant growth analysis, stomatal counts and chlorophyll contents were each analyzed using analysis of variance (ANOVA). Tests for pairwise differences were performed using Fisher's least significant difference (LSD) following a significant, overall ANOVA.. Other methods such as principle component analysis (PCA), regression, discriminate

function analysis, logistic regression analysis, multivariate analysis of variance (MANOVA), and analysis of covariance (ANCOVA) were performed as needed. All analyses were done using a Macintosh computer using Statview, Systat and JMP(SAS) programs.

Results

Field Experiment

The results are summarized in Table 1 as descriptive statistics. Average values of P_{net} for the raw data were 26.6, 23.5, and 21.1 μmol $m^{-2}s^{-1}$ for castor leaves in the DS, LTR, and WCH ecosystems, respectively. Midday stomatal closure did not occur. A discriminant function analysis of PAR, VPD, and air temperature logged at the time of P_{net} measurements in the three ecosystems is seen in Fig. 2, showing that the three sites have significantly different multivariate means for these microclimatic variables (Wilks' Lambda, F = 48; 6, 712 df, P < 0.0001).

Net photosynthesis

The 365 P_{net} measurements were cross-classified by the 3 ecosystems and by 4 diurnal time intervals and analyzed by two-way ANCOVA with PAR, air temperature, and VPD entered as multiple covariates (Damon and Harvey 1987). Figure 3 displays both the raw means and the means adjusted in ANCOVA and graphed against time-of-day. This model generated an explained sum of squares of 0.51 (R-square). Each effect in the model was significant except for the ecosystem by time interaction, and overall statistical power[1] was so high (ca. 1.0) that only N = 32 leaves would have generated a significant result. The means over all diurnal time intervals, for P_{net} as adjusted in ANCOVA, were highly significantly different (F = 33.6; 2,361 df; P < 0.0001; R-square = 0.46) at 25.3, 25.8 and 20.8 μmol

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[1] Power analysis was done using SAS (JMP), specifying a type I error of 0.05, and using the sample size, root mean square error, and effect size of the raw data (Cohen 1977).

Table 1. Descriptive statistics of field data for wild castor growing in the three ecosystems of Sri Lanka.

Variable	DS	LTR	WCH	F (df)	P	R-square
Net Photosynthesis (μmol m^{-2} s^{-1})	26.6 (±5.33)a	23.5 (±6.31)b	21.1 (±4.77)c	38.6 (2,362)	0.0001	0.02
Leaf Temperature	33.5 (±1.15)a	33.8 (±1.29)ab	34.1 (±1.10)b	9.0 (2,262)	0.0002	0.05
PAR(mol m^{-2} s^{-1})	1820 (±356)a	1331 (±467)b	1497 (±342)c	46.9 (2,358)	0.0001	0.21
Air Temperature	33.9 (±1.13)a	34.3 (±1.10)a	34.8 (±1.25)b	24.6 (2,362)	0.0001	0.12
Relative humidity	74.0 (±3.53)a	70.8 (±9.03)b	76.7 (±5.00)c	27.6 (2,362)	0.0001	0.13
VPD(mb)	13.8 (±2.18)a	15.8 (5.22)b	13.2 (3.54)c	14.2 (2,362)	0.0001	0.07
N	133	73	159			
Leaf Specific Mass (N=10) (μg mm^{-2})	48.92 (±6.76)a	39.63 (±4.16)b	27.243 (±3.15)c	48.6 (±2,27)	0.0001	0.78
Stomatal Density (N=30) (no. mm^{-2})	200.0 (±16.9)a	202.5 (±22.6)a	204.3 (±19.0)a	0.36 (±2,87)	0.6962	0.01

Means (±SD) followed by different letters denote statistical dissimilarity ($P<0.05$, using Bonferroni pairwise comparisons)

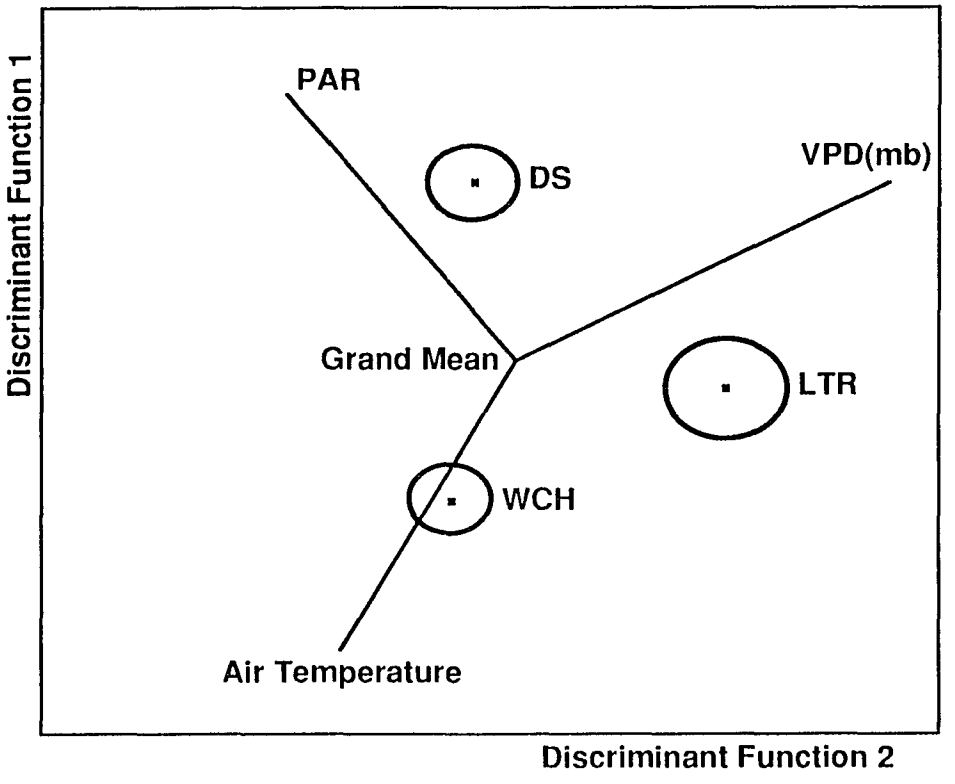

Fig. 2. A discriminant function analysis separates the 3 castor study sites by their values on 3 microclimatic variables -- PAR, air temperature, and VPD. Centroids with 95% confidence regions are given for 3 sites on 2 discriminant functions. Rays show direction and contribution (ray length) of the original microclimatic variables in discriminant space.

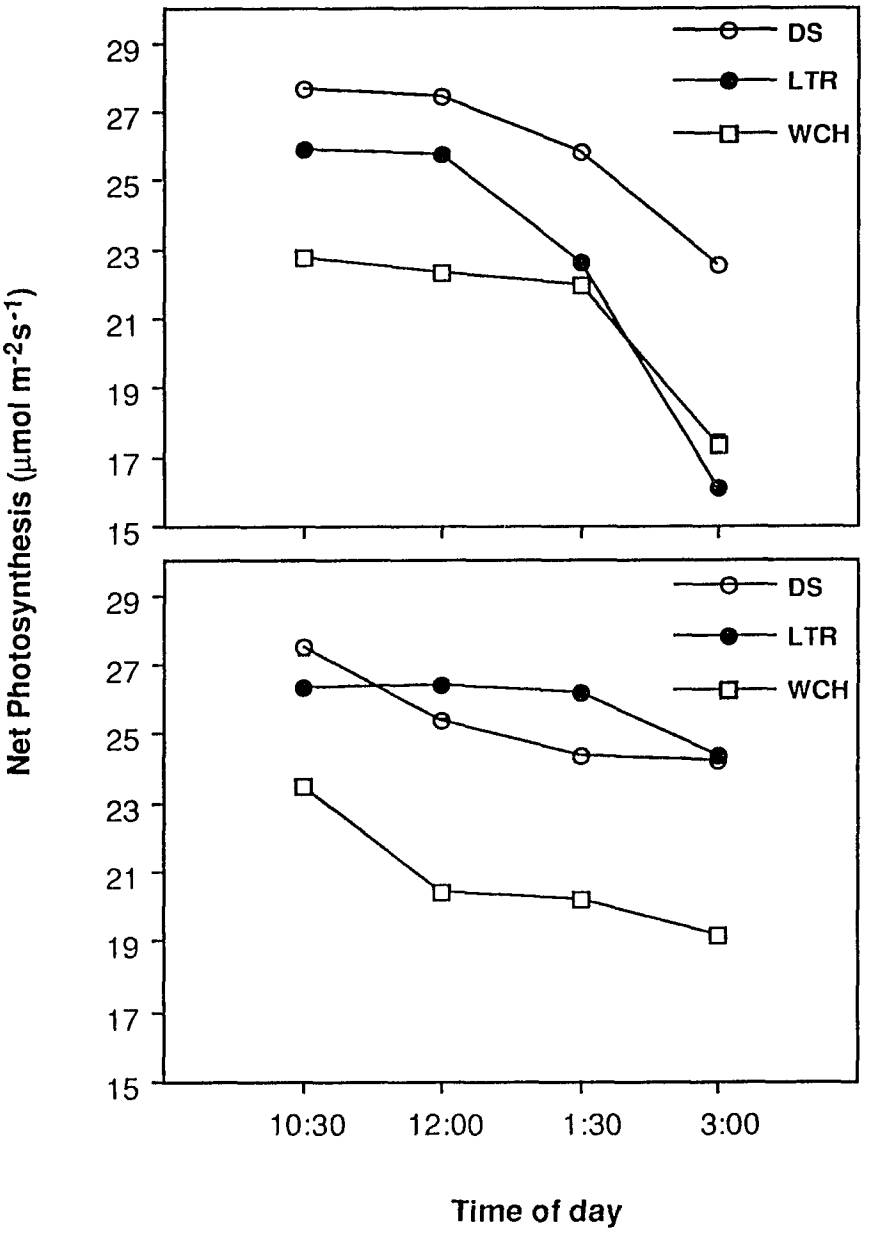

Fig. 3. Diurnal path of mean *Pnet* at each study site. Upper graph -- the raw means. Lower graph -- means adjusted in two-way ANCOVA using PAR, air temperature, and VPD as covariates.

$m^{-2}s^{-1}$, for DS, LTR, and WCH, respectively. This F-test for ecosystem type as a main effect on P_{net} had high statistical power (ca. 1.0).

Decomposing, by contrasts, the sum of squares due to ecosystem differences agreed well with the visual impression of the lower panel of Figure 3 -- average P_{net} was not significantly different between the DS and LTR ecosystems (F = 0.403; P = 0.53) but P_{net} over all time intervals, was clearly lower in the WCH than it was in the other two ecosystems (e.g., for DS vs. WCH, F = 46; P < 0.0001).

The time-of-day by ecosystem interaction was not significant (F = 0.92; P = 0.48; R-sq. = 0.007) indicating that castor leaves in each ecosystem had similar diurnal trends for P_{net} (curves somewhat parallel in the lower panel of Fig. 3).

Data were also analyzed using single classification ANCOVA at each time of day with PAR, air temperature, and VPD entered as multiple covariates. Figure 4 displays both the raw means and the means adjusted in ANCOVA, graphed against time-of-day. Adjusted data did not show significant differences among LTR and DS in all four time intervals. However, the adjusted means of WCH were significantly different with both DS and LTR during all 4 time intervals (P<0.05).

Leaf specific mass

LSM varied over 3-fold across the ecosystems (Fig. 5); and showed no overlap between DS and WCH leaves. Leaves in the DS had the highest average LSM at 48.9 µg dry weight mm^{-2} adaxial surface area, while LSM declined to a low of 27.2 at the WCH zone (Table 1). Figure 6 presents the relationship I found between the average rate of net photosynthesis and average leaf specific mass for the 3 study sites. Mean P_{net} (with 95% confidence intervals) is graphed against mean LSM. Average P_{net} increased with increasing LSM.

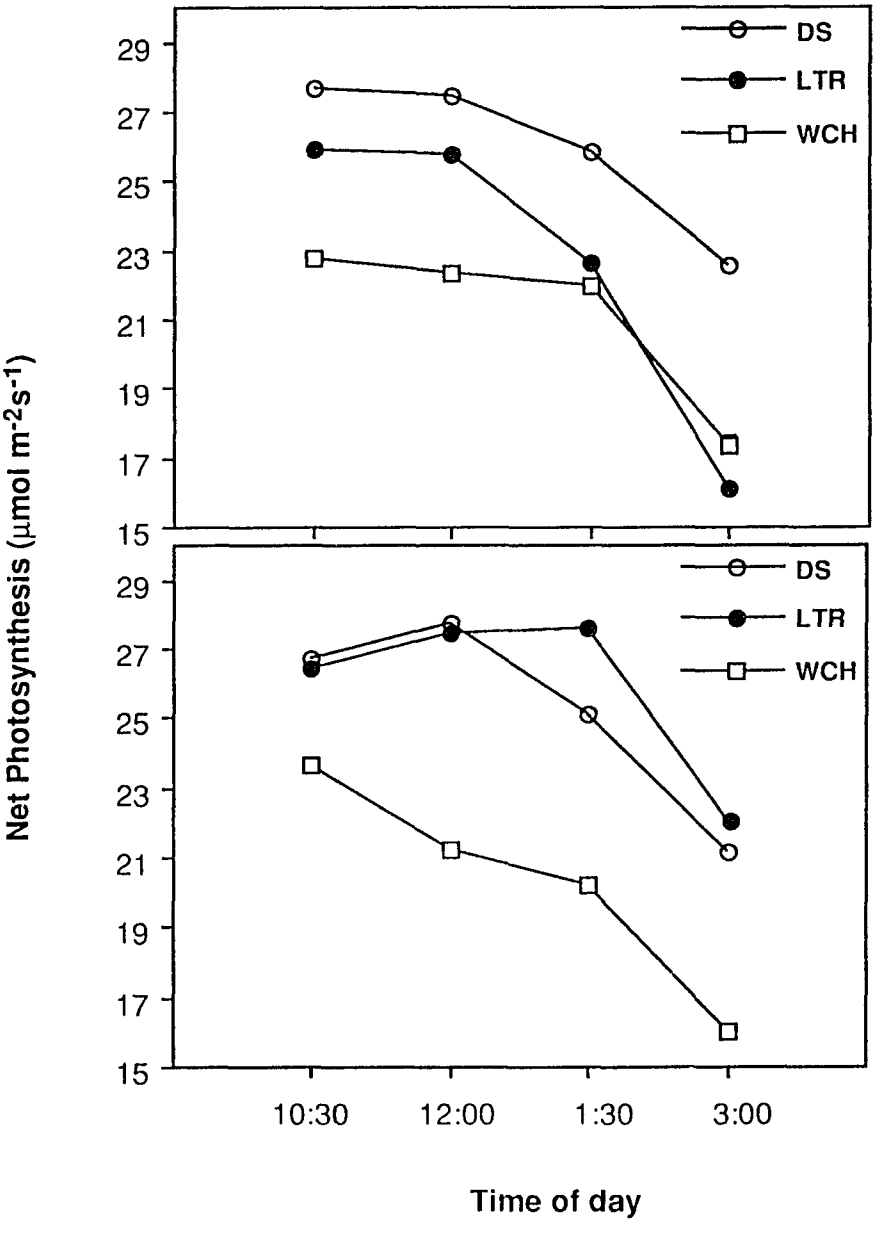

Fig. 4. Diurnal path of mean P*net* at each study site. Upper graph -- the raw means. Lower graph -- means adjusted in one-way ANCOVA at each time of day using PAR, air temperature, and VPD as covariates.

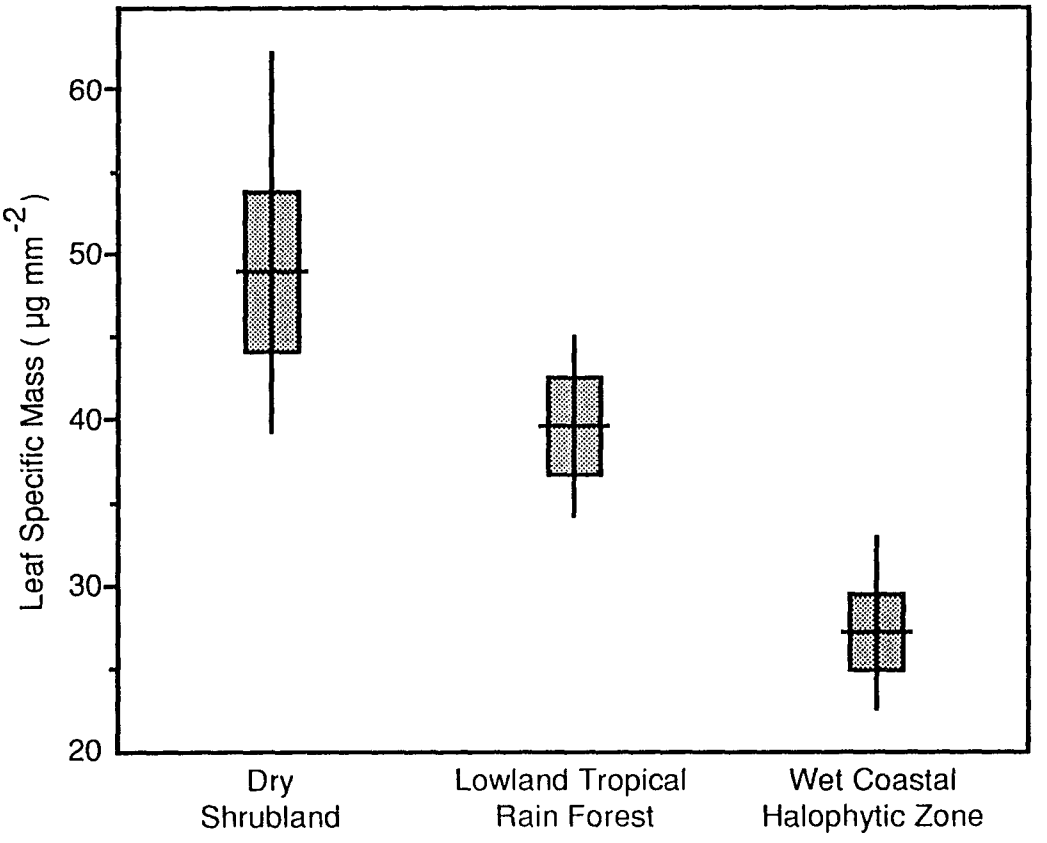

Fig. 5. Leaf specific mass of the three plant types. Box plots indicate the 95% confidence limits of the mean and ranges.

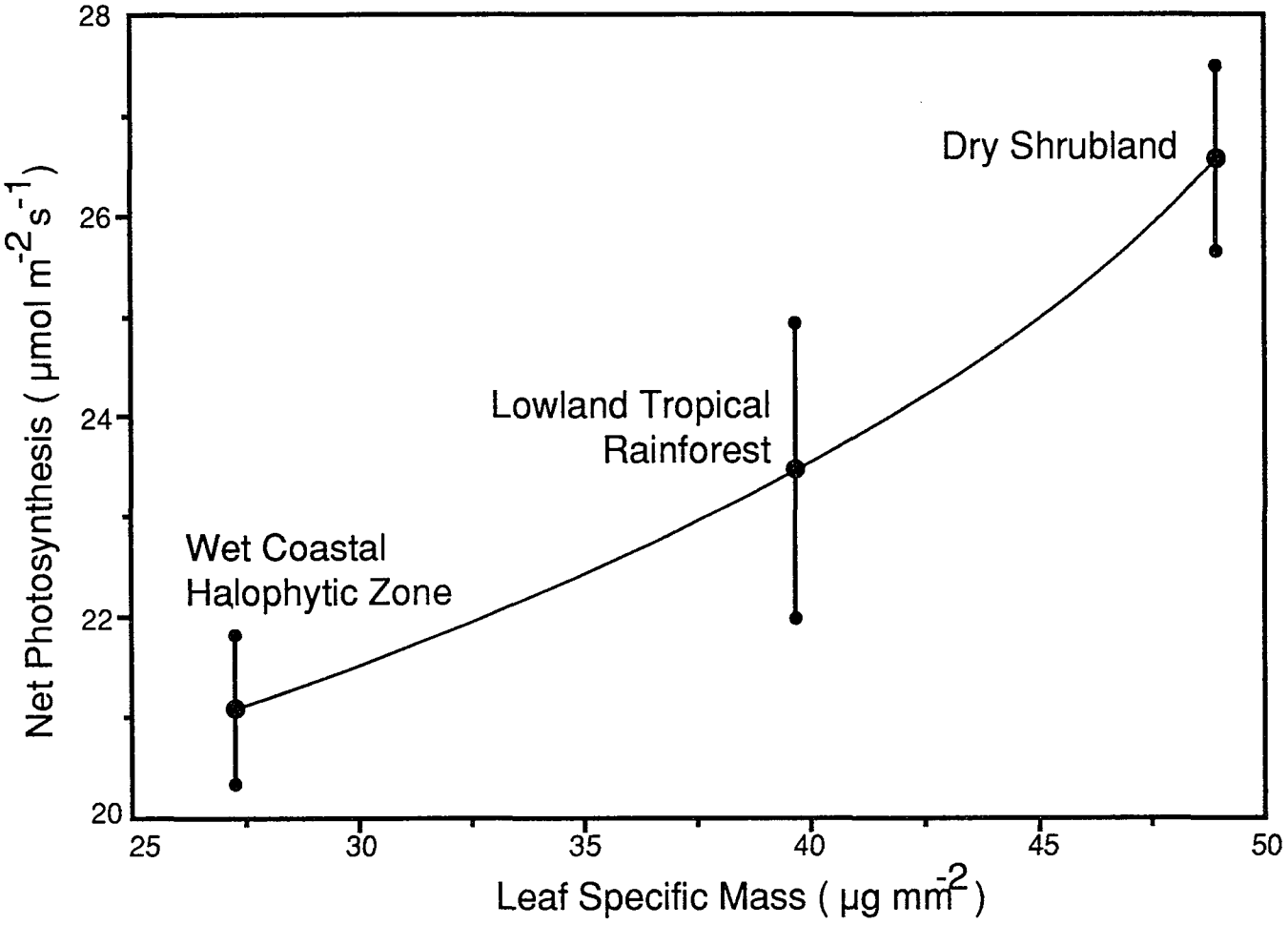

Fig. 6. Mean P*net* with with 95% confidence limits, graphed against mean LSM. Points connected by cubic spline.

Vapor pressure deficit

The range of VPD encountered in the field at the time of gas exchange measurement was 6 to 27 mbars. There was no statistically significant relationship between P_{net} and increasing VPD for all leaves merged from the three ecosystems -- r was not significantly different from zero (r = 0.015, P = 0.77, N = 365 leaves). Figure 7 presents this scatter plot with the 90% prediction ellipse of the points (Sokal and Rohlf 1981).

Within each ecosystem P_{net} was only weakly related to increasing VPD (Fig. 8). In DS P_{net} showed no correlation with increasing VPD (P = 0.247, R-square = 0.01). However, in LTR P_{net} declined with VPD (P = 0.0002), but the R-square value was weak at 0.17. In WCH, P_{net} was significantly positively correlated (P = 0.0001) with VPD, but again, with low R-square (0.15).

Stomatal density

Mean stomatal density was statistically homogeneous among the plants from the three ecosystems in one-way ANOVA (2,87 df; F = 0.36; P = 0.70). It averaged 200.0, 202.5, and 204.4 stomata per square mm of abaxial surface area for DS, LTR, and WCH, respectively (Table 1).

Common Garden Experiments

External morphological observations

The most outstanding morphological difference observed in the common garden was that the leaf adaxial surfaces of the DS plants exhibit a glossy appearance compared with the other two plant types (LTR and WCH) which have dull adaxial surfaces (Fig. 9).

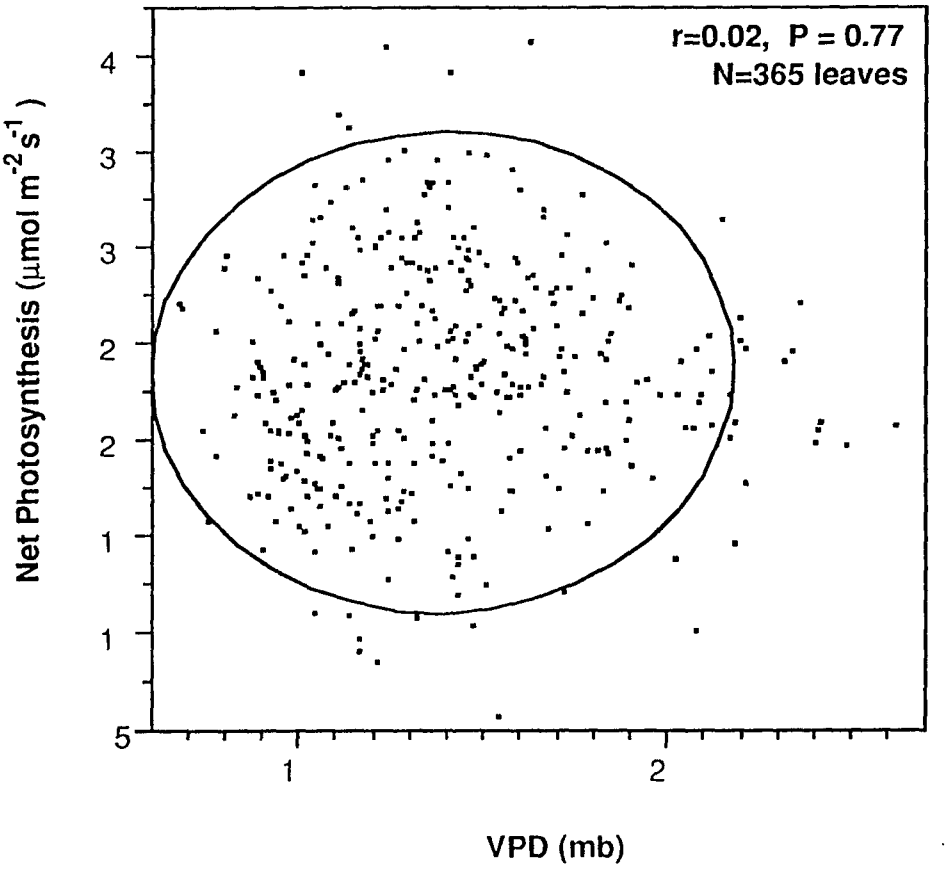

Fig. 7. Scatter plot and correlation analysis for P_{net} versus atmospheric VPD, graphed with the 90% prediction ellipse of the points merged from the three ecosystems. There was no statistically significant relationship between P_{net} and VPD in wild castor -- r was not significantly different from zero

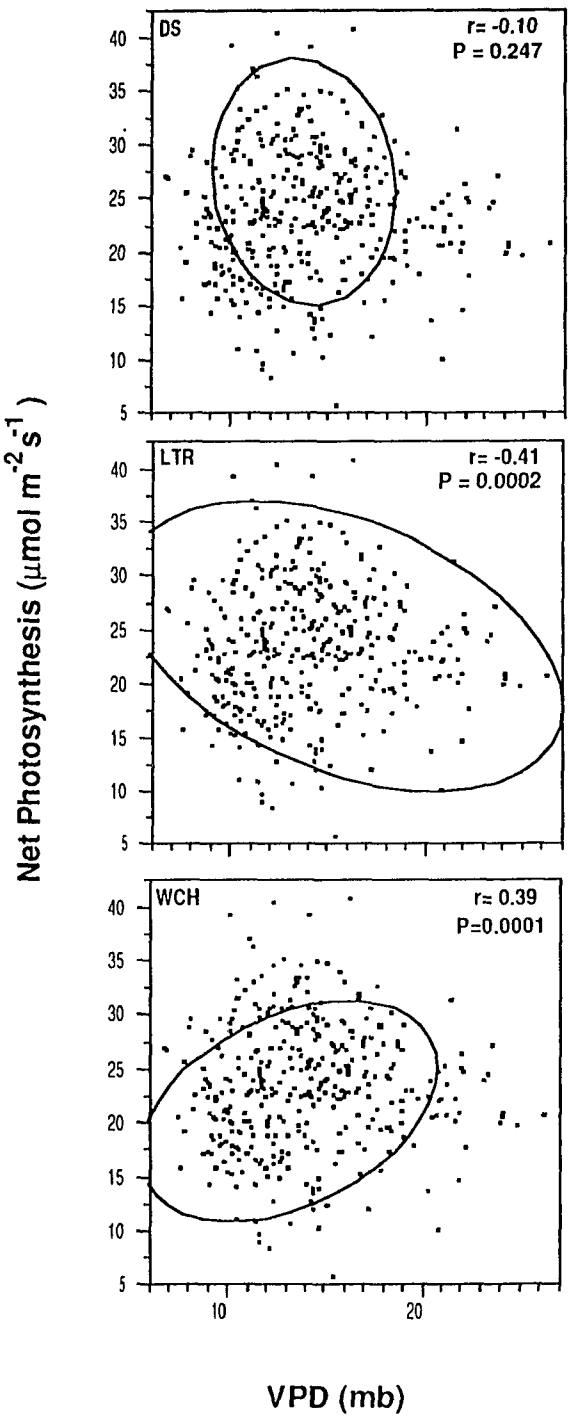

Fig. 8. Scatter plots and correlation analysis for P_{net} versus atmospheric VPD, graphed with the 90% prediction ellipses of the points.

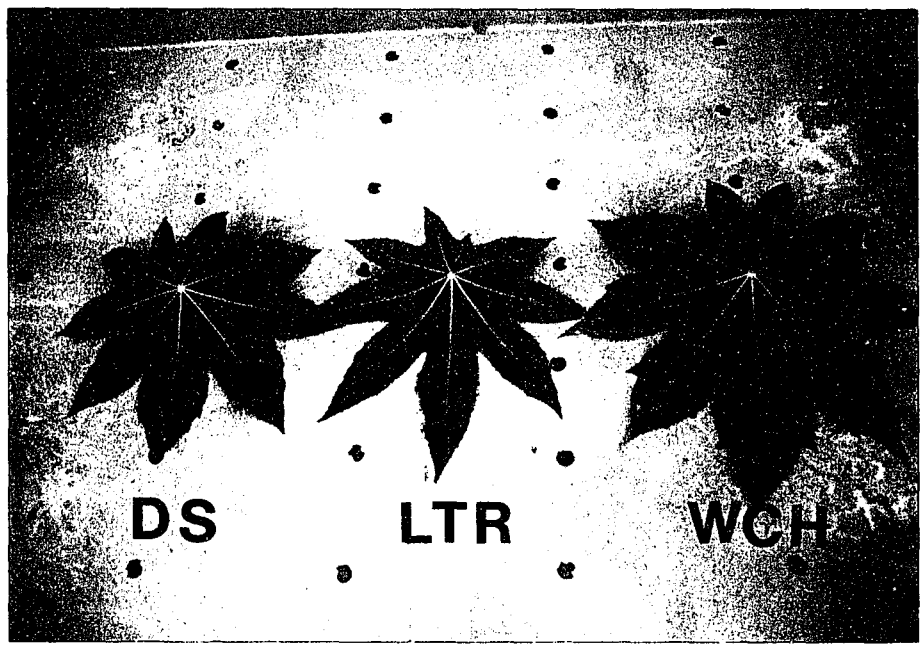

Fig. 9. The adaxial leaf surfaces of the three plant types.

The leaf abaxial surface and the stem of the DS plants also exhibited silvery white waxy surfaces compared to the dull green surfaces on the other two plant types (Fig. 10). Plants of the WCH were shorter than DS and LTR plants.

Experiment 6 was carried out in an attempt to evaluate the probable differences in light reflectance due to the above mentioned leaf morphological differences. The differences of P_{net} (upper minus lower) of the upper and the lower photosynthetic surfaces were statistically significant. DS plants had the greatest reduction in P_{net} when compared with LTR and WCH plants ($P>0.01$)(Table 2).

Cuticular and stomatal morphology

Observations with the scanning electron microscope revealed differences among the three plant types in the epicuticular wax on the leaves. DS plants maintained a smoother cuticle while WCH and LTR plants had a rougher and undulating cuticle (Fig. 11). These characteristics are also reflected by the external appearance of the leaves. It was also observed that the stomata of all three types were covered with a cuticular arch forming a stomatal ante-chamber. In WCH and LTR plants the two guard cells of the stomata were visible when viewed from above the cuticular pore of the ante-chamber. The guard cells of the DS plants were not visible through the cuticular pore as they are located much deeper within, exhibiting a deeper stomatal ante-chamber space although this was not quantified (Figs. 12 and 13).

Leaf chlorophyll concentrations

Total chlorophyll concentrations of WCH leaves were significantly lower when compared with DS and LTR leaves ($P<0.01$)(Table 3). Chlorophyll a (*chl a*)

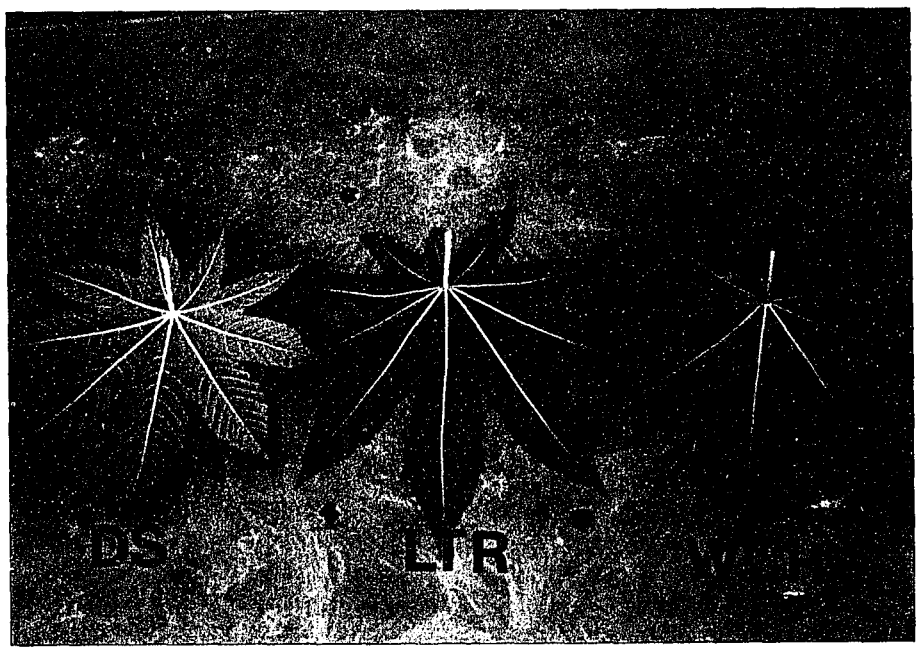

Fig. 10. The abaxial leaf surfaces of the three plant types.

Table 2. Difference between the net photosynthetic rates (upper minus lower), measured by exposing abaxial and adaxial surfaces of the leaves to light under glasshouse conditions. Each of the column variables was subjected to one-way ANOVA.

		Net photosynthesis (μmol/sq.m/s)			
Ecosystem	**N**	**Upper (U)**	**Lower (L)**	**Difference (U-L)**	**%difference (L/Ux100)**
DS	10	19.85 (±3.85)a	10.44 (±1.27)a	9.40 (±3.61)a	53.8a
LTR	10	15.03 (±2.10)b	9.32 (±0.887)a	5.71(±1.60)b	62.5b
WCH	10	16.55 (±2.68)b	10.02 (±1.56)a	6.54 (±2.64)b	61.4ab
F		6.89	2.01	5.01	2.74
P		0.004	0.154	0.014	0.082
R-square		0.34	0.13	0.27	0.17
PLSD (P<0.05)		2.72	1.16	2.24	8.34

Means followed by different letters denote statistical dissimilarity between ecosystems (P<0.05, using Fisher PLSD)

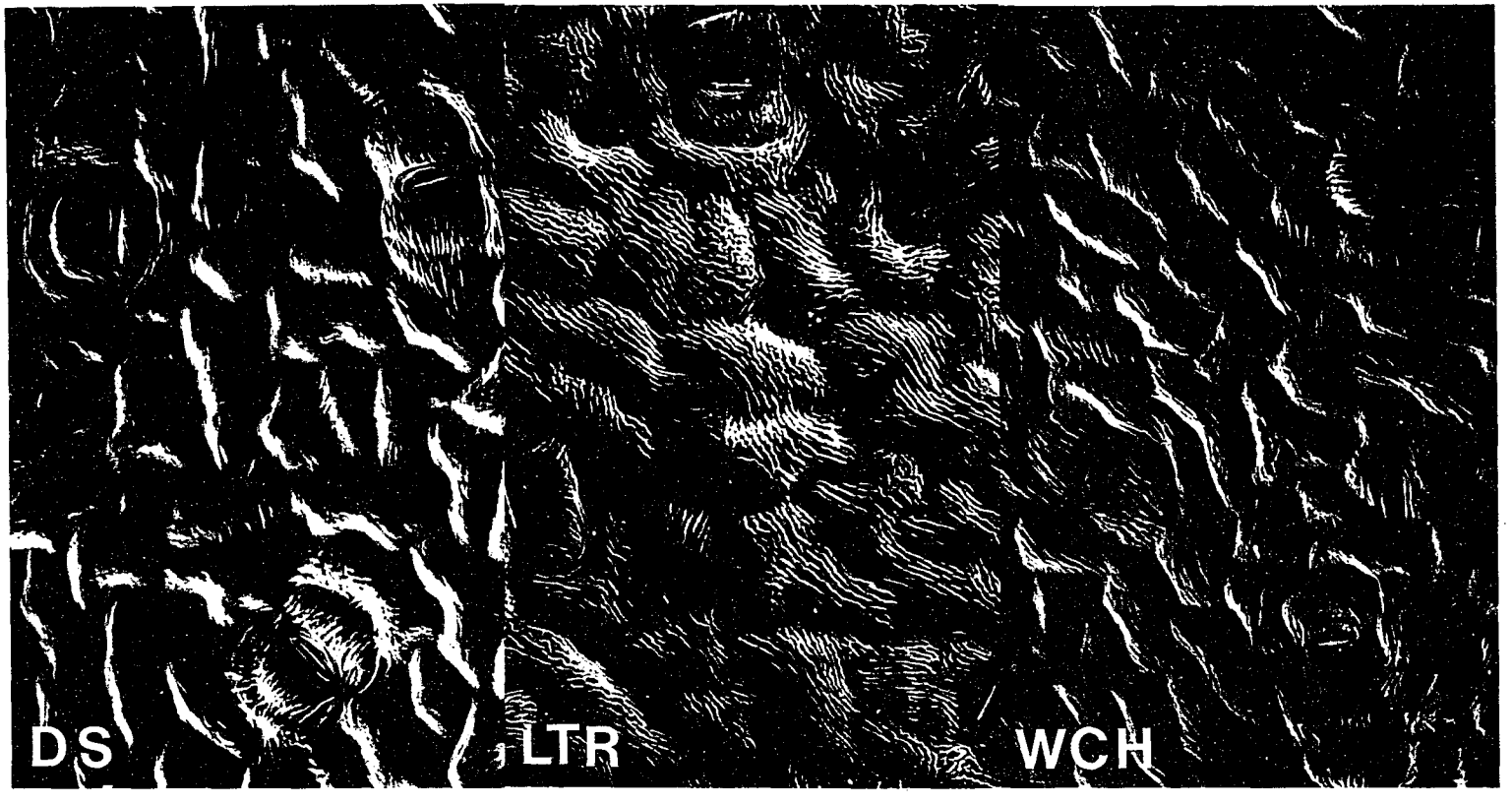

Fig. 11. Scanning electron micrographs showing the cuticular morphology (x500) of leaf adaxial surfaces of the three plant types.

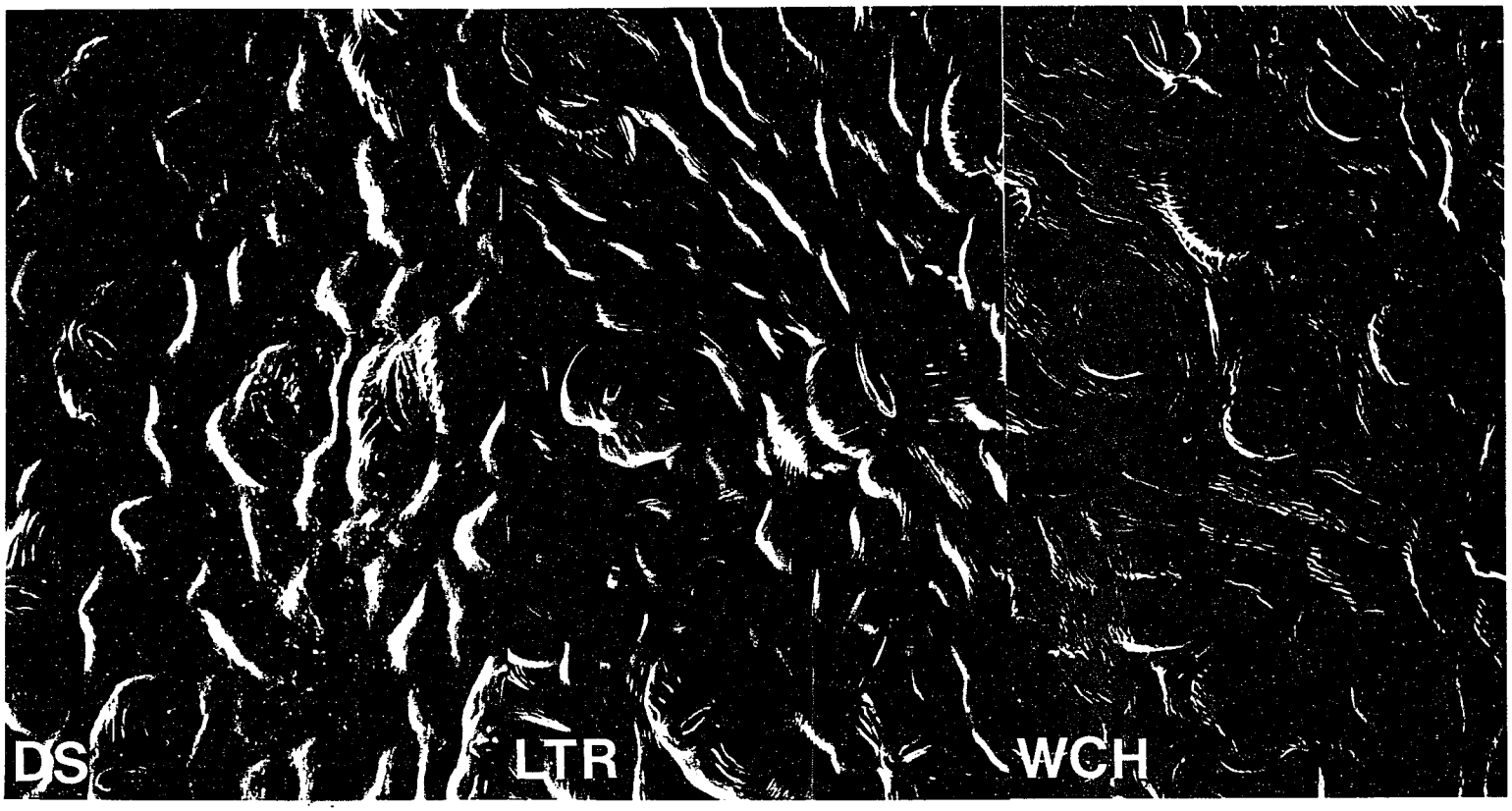

Fig. 12. Scanning electron micrographs showing the cuticular morphology (x500) of leaf abaxial surfaces of the three plant types.

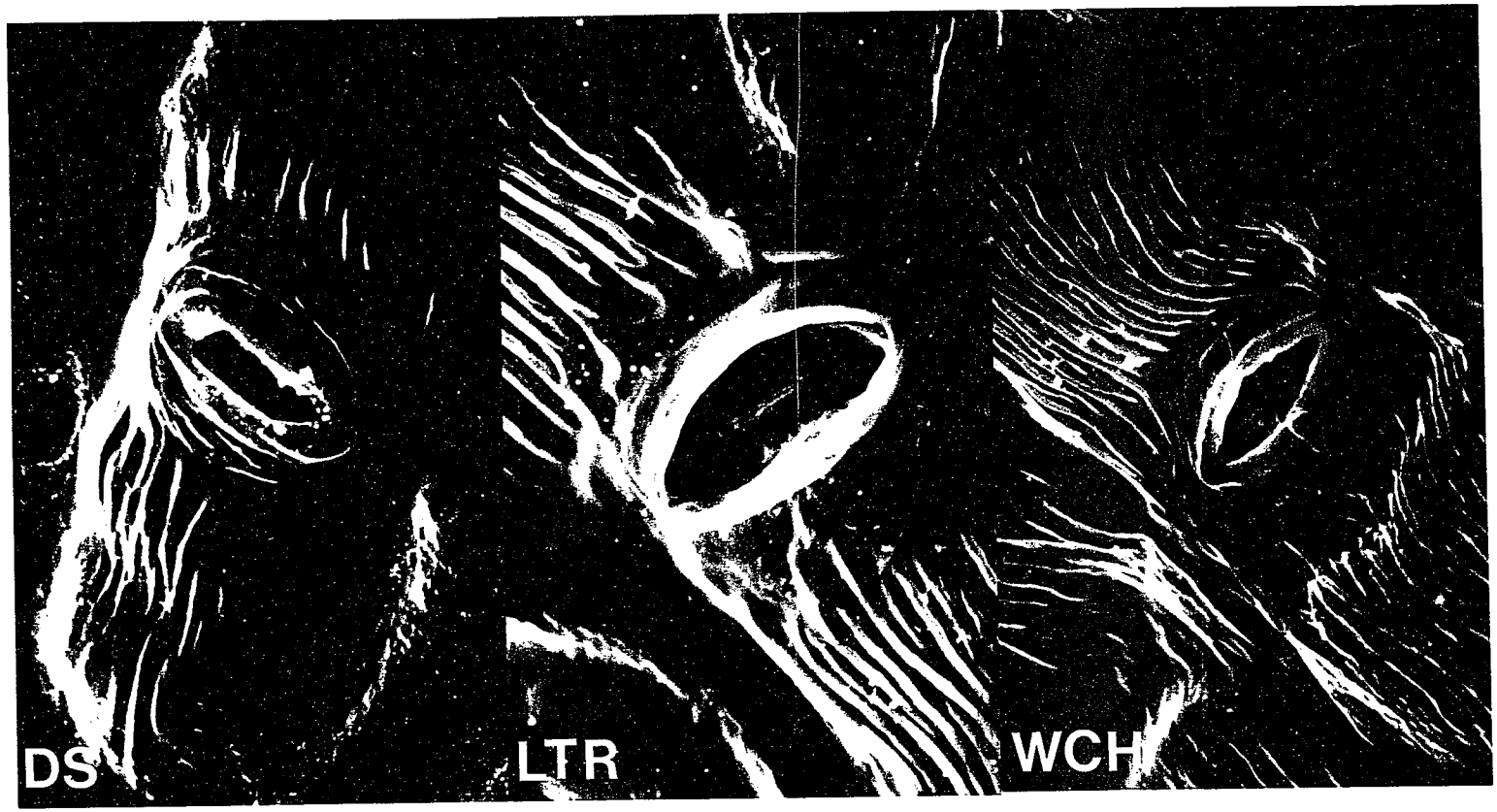

Fig. 13. Scanning electron micrographs of the stomates (x1000) of the three plant types.

Table 3. Leaf chlorophyll concentrations among the three plant types grown outside during summer. One-way ANOVA was done on each of the four variables listed as columns.

Ecosystem	N	Total ($\mu g\ cm^{-2}$)	Chl a ($\mu g\ cm^{-2}$)	Chl b ($\mu g\ cm^{-2}$)	a/b
DS	10	21.18 (±0.97)a	17.378 (±0.89)a	4.255 (±0.22)a	4.087 (±0.18)a
LTR	10	22.37 (±1.81)a	18.419 (±1.43)a	4.390 (±0.30)a	4.195 (±0.12)a
WCH	10	19.47 (±2.35)b	15.774 (±1.90)b	3.959 (±1.49)a	4.288 (±0.95)a
ANOVA					
F		6.56	8.24	0.62	0.32
P		0.005	0.002	0.548	0.727
R-square		0.33	0.38	0.04	0.02
PLSD		1.652	1.348	0.814	0.513

Means (±SD) followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using fisher PLSD)

concentration of WCH leaves was also significantly less when compared with DS and LTR leaves ($P<0.001$). Chlorophyll b concentration and Chlorophyll a/b ratio did not show any significant differences among the plants of the three ecosystems (Table 3).

Growth Characteristics

Plant Height

Plant heights were measured fortnightly between 12 and 24 weeks of age (Experiment 4). Average height of WCH plants was highly significantly lower ($P<0.001$) than DS and LTR plants at each measurement. During the 12th and 14th weeks LTR and DS plants showed similar heights. However, after the 16th week, LTR plants showed significantly higher plant height than DS plants (16th and 18th week $P<0.05$ and 20th, 22nd and 24th weeks $P<0.01$) (Fig. 14).

At the time of harvesting at 16 months, the height of WCH plants was significantly lower (91.4 cm, $P<0.001$) compared to the other plant types (DS, 127.1 cm and LTR, 125.7 cm) (Table 4). The plant heights between DS and LTR plants were not statistically different at the time of harvest.

Root length

The root system consists of a taproot and densely branched lateral roots. The average root lengths in pot grown plants was not significantly different among the plant types (50.3 cm, 46.9 cm and 41.9 cm in DS, LTR and WCH respectively).

Biomass production

At the time of uprooting (16 months) total plant weight, shoot weight and root weight did not show any significant differences among the three genotypes

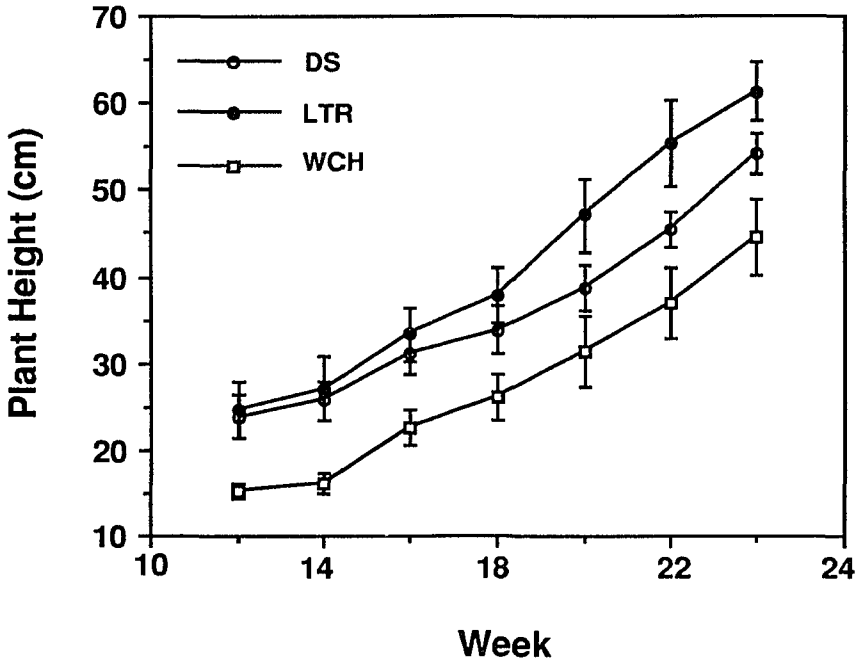

Fig. 14. Plant height of the three plant types in the common garden (mean±95% CI, N=10).

Table 4. Average plant height of the three plant types at the time of uprooting (F=37.8, P=0.0001, R-square=0.74).

Ecosystem	N	Plant Height (cm)
DS	10	127.1 (±9.2)a
LTR	10	125.7 (±11.3)a
WCH	10	91.4 (±10.6)b
PLSD	P<0.05	9.543

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

(Table 5)(Experiment 4). The plant weight:height ratio was significantly larger in WCH plants compared to DS plants ($P<0.05$) indicating a larger plant girth (Table 6).

Total leaf area was significantly larger in WCH plants compared to DS and LTR plants ($P<0.01$ in DS plants and $P<0.05$ with LTR plants)(Table 7). Number of leaves per plant did not show significant differences among the plant types (Table 8). However, the leaf area per leaf was significantly larger ($P<0.05$) in WCH plants compared to DS and LTR plants (Table 9).

Flowering

Differences in flowering were observed among the plants of the different ecotypes. Plants of LTR were the first to flower in the common garden. Six out of ten plants of LTR flowered at 6 months. Flower primodia initiation in WCH plants began during the 8th month. The plants of the DS did not flower up to the time of uprooting at 16 months.

The flower raceme is terminal. Therefore the rate of growth in height is reduced until an axillary bud is released. This was reflected in the plant height at the time of uprooting where DS and LTR plants were not significantly different (Table 4), compared to the juvenile stage when LTR plants were the tallest (Fig 14).

Physiological characteristics

Net Photosynthesis (P_{net})

Comparative net photosynthesis

Measurements done in Experiment 1 under glasshouse conditions during the period from September 1992 to June 1993 produced the results in Figure 15. As expected, a seasonal trend was observed in P_{net} of the three plant types.

Table 5. Comparative values of the plant dry mass (g) of the three plant types.

	Ecosystem			
	DS	**LTR**	**WCH**	**PLSD (P<0.05)**
Total Plant Weight	60.52 (±12.13)a	66.15 (±14.48)a	58.67 (±16.59)a	13.32
Leaf Weight	6.25 (±1.54)a	6.86 (±1.86)a	8.02 (±2.15)a	1.71
Shoot Weight	34.42 (±7.22)a	36.10 (±1.86)a	31.29 (±2.15)a	7.50
Root Weight	18.34 (±3.39)a	19.94 (±4.56)a	17.04 (±4.92)a	3.98

Means (±SD) followed by simillar letters denote statistical similarity between ecosystems (P<0.05, using Fisher PLSD)

Table 6. Weight/Height ratio of the three plant types (F=3.71, P=0.04, R-square=0.22).

Ecosystem	N	Weight/Height
DS	10	0.269a
LTR	10	0.285ab
WCH	10	0.340b
PLSD	P<0.05	0.056

Means followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

Table 7. Leaf area of the three plant types at 16 months (F=5.52, P=0.01, R-square=0.29).

Ecosystem	N	Leaf Area (cm^2)
DS	10	1157.5 (±256.7)a
LTR	10	1252.9 (±387.0)a
WCH	10	1670.9 (±435.1)b
PLSD	P<0.05	337.2

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

Table 8. Average number of leaves per plant of the three plant types (F=5.33, P=0.33, R-square=0.08).

Ecosystem	N	No. of leaves /plant
DS	10	7.0 (±1.15)a
LTR	10	6.8 (±0.63)a
WCH	10	7.5 (±1.27)a
PLSD	P<0.05	0.969

Means followed by simillar letters denote statistical similarity between ecosystems (P<0.05, using Fisher PLSD)

Table 9. Avarage area/leaf of the three plant types at 16 months (F=5.34, P=0.01, R-square=0.28)

Ecosystem	N	Area/leaf (cm^2)
DS	10	164.6 (±27.1)a
LTR	10	182.6 (±49.5)a
WCH	10	221.7 (±39.9)b
PLSD	P<0.05	36.63

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher,PLSD)

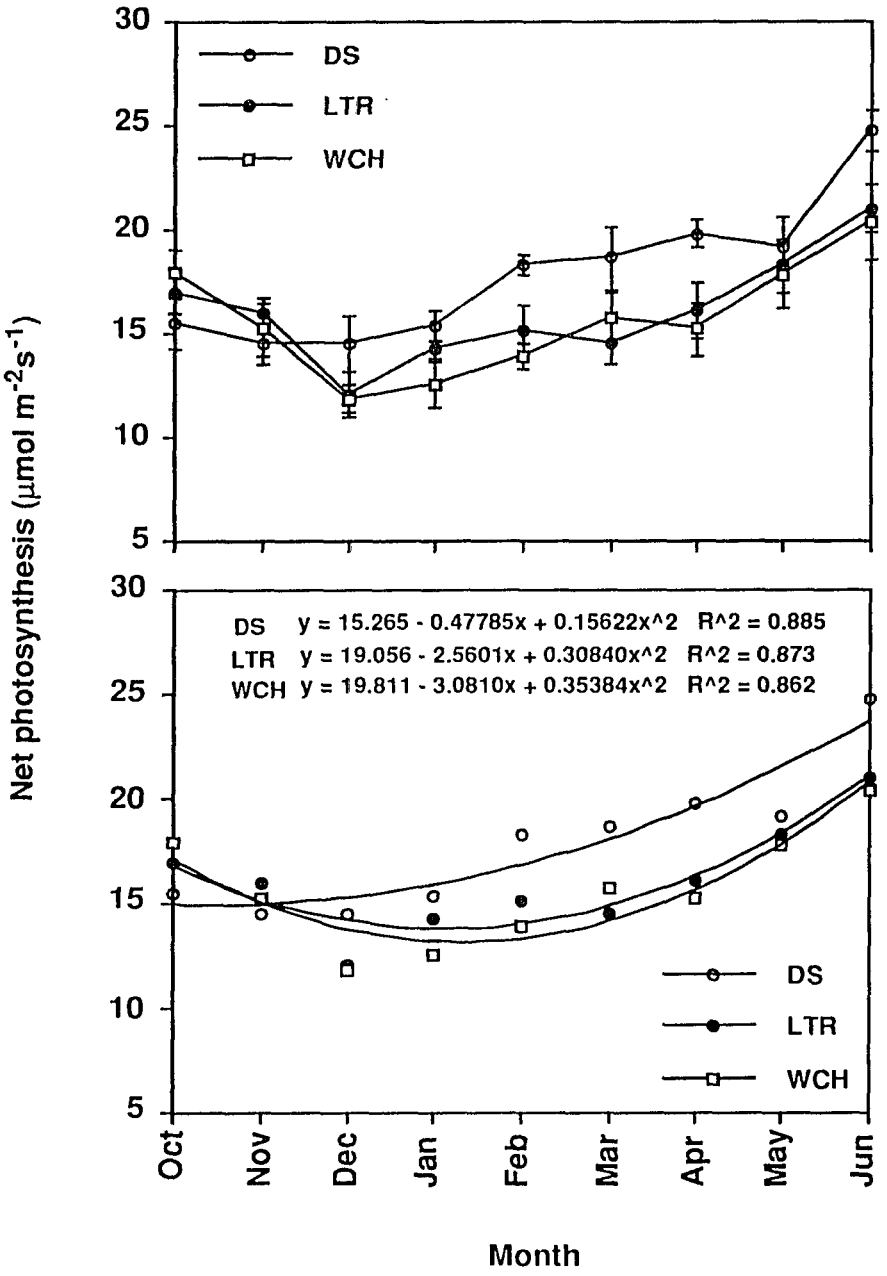

Fig. 15. Monthly average P*net* from bimonthly midday measurements. Upper graph-- Line graph of monthly means (±95% CI). Lower graph-- means fitted using 2nd degree polynomial regression curves.

For example, the average P_{net} was lower during winter months compared to spring months with brighter days.

DS plants had a different pattern of P_{net} compared to WCH and LTR plants, as seen in Figure 15. Dry shrubland plants had a steady seasonal increase in P_{net} while WCH and LTR plants had a parabolic trend. The parabolic trend in P_{net} for LTR and WCH plants follows the monthly light intensities that decline during winter months and increase during spring. In DS plants, P_{net} was significantly higher than in LTR and WCH plants ($P<0.05$, using Fisher pairwise LSD) in all the months except October and November. During the October measurements DS plants had significantly lower P_{net} compared with LTR and WCH plants ($P<0.05$, using Fisher pairwise LSD).

The grand mean of P_{net} across all measurements made during this period of 9 months gave significantly higher P_{net} for DS plants at 17.7 μmol $m^{-2}s^{-1}$ compared to LTR plants at 15.9 μmol $m^{-2}s^{-1}$ and WCH plants at 15.3 μmol $m^{-2}s^{-1}$ (Table 10). The P_{net} of LTR plants and WCH plants was not statistically significantly different (Note: During the months of October and November the plants were infested with mites which severely retarded the DS leaf growth and contributed to a lower P_{net}).

Net photosynthetic rates were also measured (Experiment 2) when the plants were 4 to 7 months old during Summer 1993. Five sets of measurements were done. During these measurements it was observed that the P_{net} of all three plant types was significanly different from each other ($P<0.05$, DS plants being the highest and LTR plants the lowest) except the measurement made on 15 September where P_{net} of DS and LTR plants were not different. In all five sets of measurements, P_{net} of DS plants was the highest (averaging 23.24 μmol/sq.m/s) and that of WCH plants was the lowest (17.72 μmol/sq.m/s) while LTR plants had a value in between (20.96 μmol/sq.m/s)(Table 11). These rates were significantly

Table 10. Monthly average net photosynthetic rates (μmol $m^{-2}s^{-1}$) of the three plant types.

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
October	20	15.487a	16.944b	17.903b	4.65	.0135	0.14	1.450
November	20	13.429a	14.934ab	12.510ac	3.08	.0533	0.10	2.123
December	20	14.511a	12.071b	11.872b	7.57	.0012	0.21	1.500
January	20	15.33a	14.260b	12.536c	11.92	.0001	0.29	1.042
February	20	18.254a	15.127b	13.874c	27.28	.0001	0.49	1.206
March	20	18.638a	14.523b	15.752b	10.68	.0001	0.27	1.735
April	20	19.804a	16.056b	15.196b	17.75	.0001	0.38	1.582
May	20	19.204a	18.263a	17.823a	0.926	.402	0.03	2.187
June	20	24.719a	21.003b	20.335b	11.15	.0001	0.28	2.004
Cumulative	180	17.708a	15.909b	15.311b	18.72	.0001	0.065	0.797

Means followed by different letters denote statistical dissimilarity between ecosystems (P<0.05, using Fisher PLSD)

Table 11. Average net photosynthetic rates (μmol $m^{-2}s^{-1}$) of the three plant types measured during summer 1993 in natural conditions (outside the greenhouse).

		Ecosystem						
Month	N	DS	LTR	WCH	F	P	R-sq	PLSD
25 July	20	24.251a	22.392a	19.184b	9.95	.0002	0.26	2.301
15 August	20	23.805a	20.101b	16.742c	25.42	.0001	0.47	1.985
21 August	20	21.013a	18.186b	15.340c	44.04	.0001	0.61	1.211
29 August	20	22.348a	19.999b	16.001c	69.53	.0001	0.71	1.090
15 Sept.	20	24.759a	24.102a	21.336b	13.15	.0001	0.32	1.419
Cumulative	100	23.235a	20.956b	17.720c	73.92	.0001	0.33	0.897

Means followed by different letters denote statistical dissimilarity between ecosystems (P<0.05, using Fisher PLSD)

different to each other (P<0.001 between DS and WCH plants, P<0.0.01 between LTR and WCH plants and between DS and LTR plants, using Fisher pairwise LSD).

Diurnal effects of net photosynthesis

Measurements were made during four discrete time intervals (8.30am,10am,11.30am,1pm, 2.30pm) to obtain diurnal curves. A discriminant function analysis of PAR, VPD, and air temperature logged at the time of P_{net} measurements in the common garden is seen in Fig.16, showing that the three multivariate means for these microclimatic variables are much less different as indicated by the size of F, than when compared to the field (Fig. 2)(Wilks' Lambda, F = 4.4; 6, 618 df, P < 0.0002).

Figure 17 (upper graph) shows the raw means of P_{net}. Measurements were made during four discrete time intervals. Net photosynthetic rates of WCH plants were significantly lower than that for DS and LTR plants (P<0.01) at all time intervals except at 2:30pm when WCH plants were not different from the other plant types. However, P_{net} of DS and LTR plants was significantly different at 2:30pm (P<0.05). Diurnal curves of the raw means were very similar to the curves obtained from the field data (Fig.3 and Fig.17).

Analysis of covariance (ANCOVA) was performed with data from each time period having PAR, Tair and VPD as multiple covariates to adjust for the minor microclimatic differences that occurred during measurements in the common garden (Fig. 17). The results obtained after adjustment were similar to those of the field data (Fig. 4). Net photosynthesis of WCH plants was significantly lower than that of DS and LTR plants during all other time intervals except 8:30 am and 10 am.

All P_{net} measurements were cross-classified by the 3 ecosystems and by 4 diurnal time intervals and analyzed by two-way ANCOVA with PAR, air

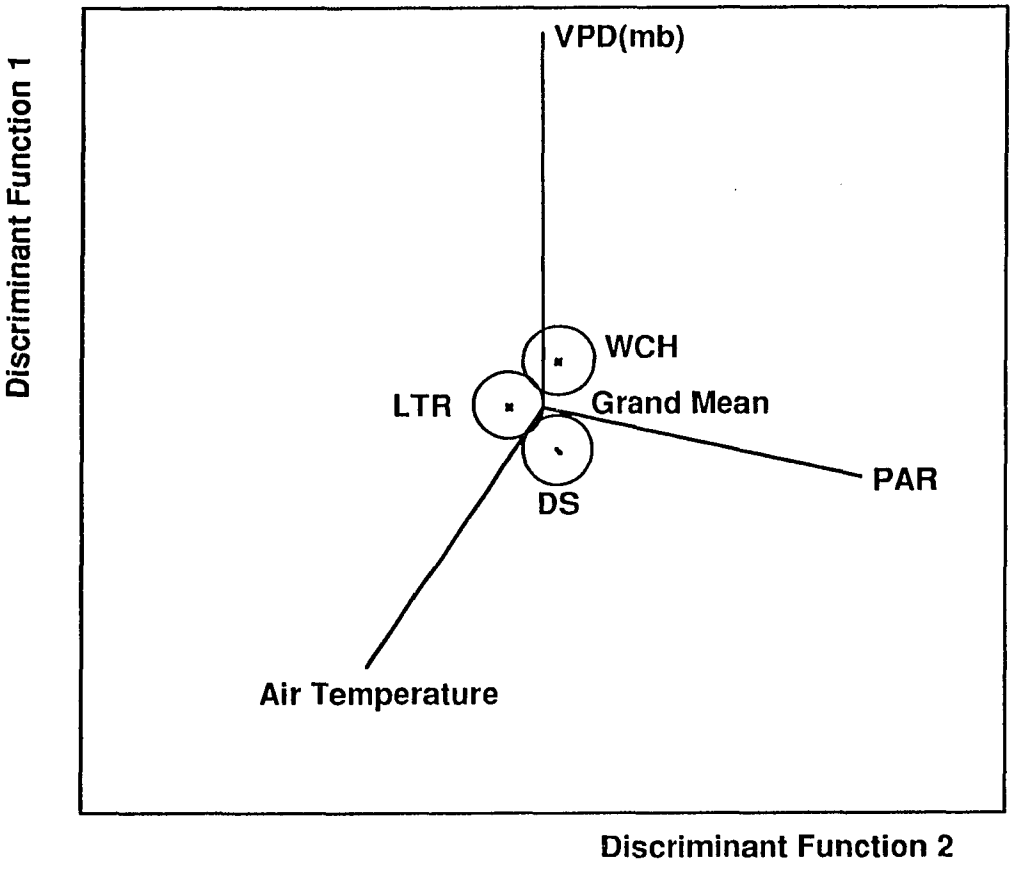

Fig. 16. A discriminant function analysis in the common garden converges the ecosystems in contast to the field databy their values on 3 microclimatic variables -- PAR, air temperature, and VPD. Centroids with 95% confidence regions are given for 3 sites on 2 discriminant functions. Rays show direction and contribution (ray length) of the original microclimatic variables in discriminant space.

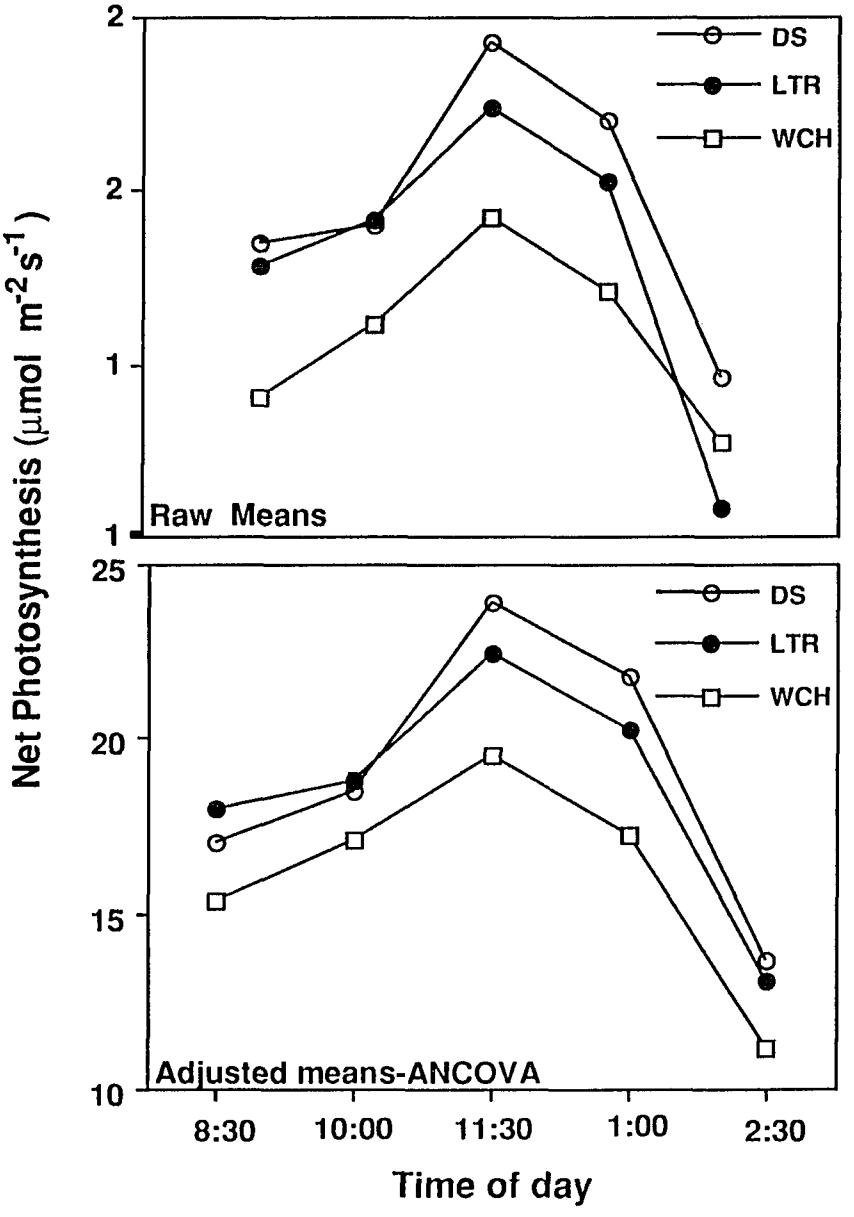

Fig. 17. Diurnal path of mean P*net* of each plant type in the common garden. Upper graph -- the raw means. Lower graph -- means adjusted in one way ANCOVA using PAR, air temperature, and VPD as covariates.

temperature, and VPD entered as multiple covariates. Figure 18 displays both the raw means and the means adjusted in ANCOVA and graphed against time-of-day. This model generated an explained sum of squares of 0.72 (R-square). Each effect in the model was significant except for the ecosystem-by-time interaction. The means over all diurnal time intervals, for P_{net} as adjusted in ANCOVA, were highly significantly different ($F = 36$; 2,313 df; $P < 0.00001$; R-square = 0.07) at 19.77, 19.49 and 16.25 $\mu mol\ m^{-2}s^{-1}$, for DS, LTR, and WCH plants, respectively. The average values of P_{net} of WCH plants were significantly different ($P<0.05$) from DS and LTR plants. This F-test for ecosystem type as a main effect on P_{net} had high statistical power (ca. 1.0).

Transpiration rate

In Experiment 1, during all measurements except during October and November, DS plants had significantly higher E compared to the plants of the other two ecotypes ($P<0.05$). When E across all months measured was averaged, DS plants had significantly higher E ($P<0.001$) compared to LTR and WCH plants (Table 12).

The measurements made in Experiment 2, outside the glasshouse during summer also indicated an overall trend toward higher transpiration rates by plants from DS compared to plants from LTR ($P<0.05$) and WCH (non significant, but supports a trend to be lower than DS plants). However, E of LTR plants and of WCH plants was not significantly different (Table 13).

Figure 19 shows the diurnal trend of E. During midday E was not significantly different among the plant types.

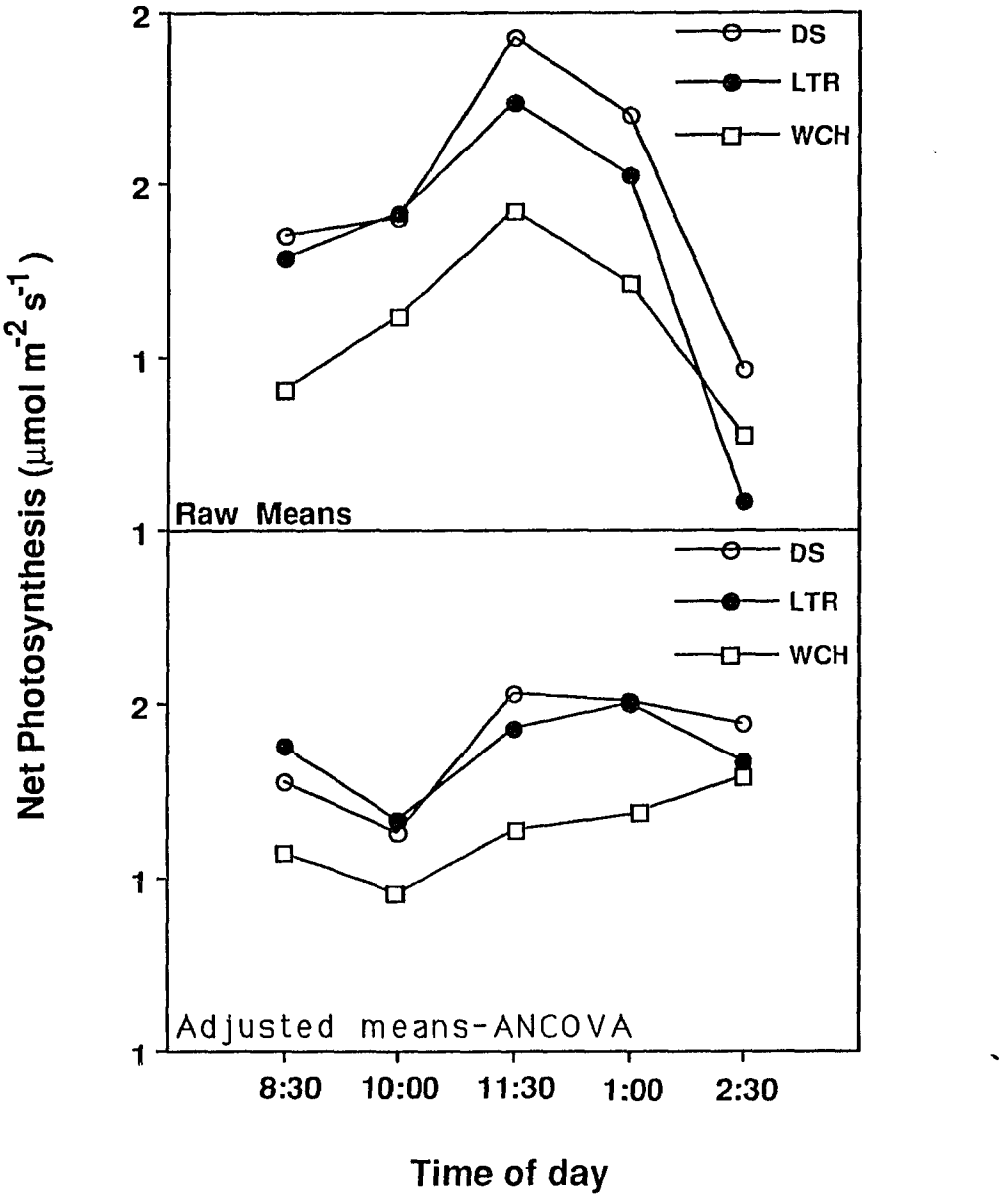

Fig. 18. Diurnal path of mean *Pnet* of each plant type in the common garden. Upper graph -- the raw means. Lower graph -- means adjusted in two-way ANCOVA using PAR, air temperature, and VPD as covariates.

Table 12. Monthly average transpiration (mol $m^{-2}s^{-1}$) of the three plant types.

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
October	20	0.00474a	0.00527b	0.00521b	2.37	.1027	0.07	0.00048
November	20	0.00500a	0.00523a	0.00408a	2.07	.1351	0.25	0.00126
December	20	0.00563a	0.00402b	0.00432b	7.65	.0011	0.21	0.00084
January	20	0.00616a	0.00565a	0.00527a	1.19	.3114	0.04	0.00105
February	20	0.00757a	0.00583b	0.00538b	13.43	.0001	0.32	0.00093
March	20	0.00946a	0.00677b	0.00768b	10.40	.0001	0.27	0.00118
April	20	0.00787a	0.00693ac	0.00639bc	11.07	.0001	0.04	0.00114
May	20	0.00746a	0.00630a	0.00686a	1.29	.2841	0.04	0.00139
June	20	0.01223a	0.00952b	0.01106a	5.63	.0059	0.16	0.00163
Cumulative	180	0.00735a	0.00620b	0.00622b	11.07	.0001	0.04	0.00053

Means followed by different letters denote statistical dissimilarity between ecosystems (P<0.05, using Fisher PLSD)

Table 13. Average transpiration rates (mol $m^{-2}s^{-1}$) of the three plant types measured during summer 1993 in natural conditions (outside the greenhouse).

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
25 July	20	0.02311a	0.01818a	0.02263a	3.67	.0316	0.10	.01203
15 August	20	0.01937a	0.01594b	0.01689b	7.69	.0011	0.22	.00181
August	20	0.01313a	0.01030b	0.01010b	25.75	.0001	0.50	.00095
August	20	0.0244a	0.02226b	0.02034c	14.54	.0001	0.34	.00151
Sept.	20	0.01342a	0.01299a	0.01359a	1.49	.2331	.052	.00071
Cumulative	100	0.01868a	0.01593b	0.01671ab	7.288	.0008	.046	.0026

Means followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using Fisher PLSD)

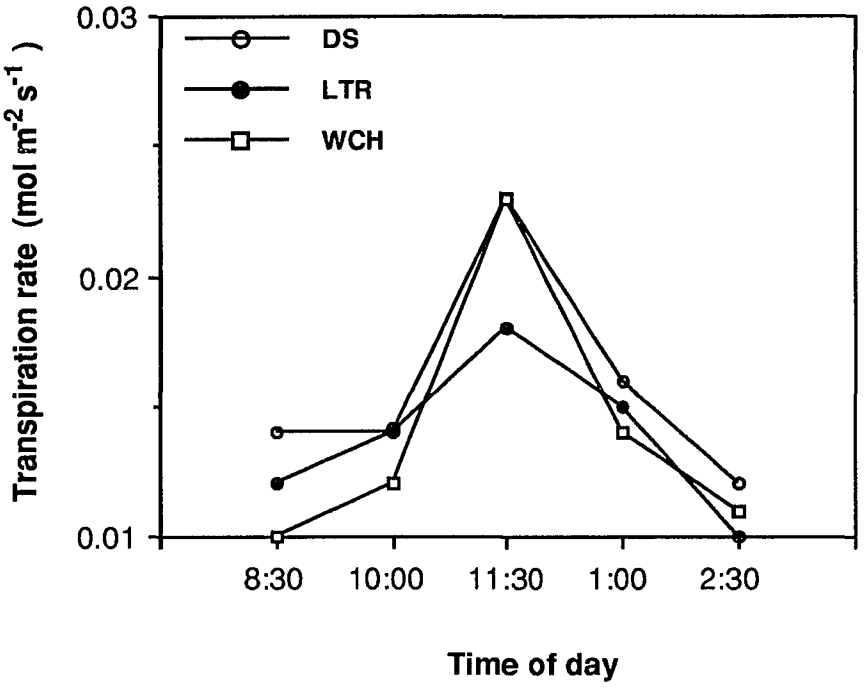

Fig. 19. Diurnal path of transpiration rates of each plant type in the common garden (N=20).

Stomatal conductance to water vapor (g_{wv})

Of the nine sets of measurements made during Experiment 1, six sets showed significantly higher g_{wv} in DS plants compared to LTR and WCH plants ($P<0.05$)(Table 14). The first two measurements made in October and November did not show differences in g_{wv} among the plant types. In the cumulative averages across all sets of measurements, g_{wv} of DS plants was higher as compared to WCH and LTR plants ($P<0.001$). The cumulative g_{wv} between LTR and WCH plants was not different.

For all 5 sets of measurements made during the summer (Experiment 2) outside the greenhouse, significantly higher g_{wv} was observed in DS plants ($P<0.05$), except the last measurement made during September which was different only between DS and LTR plants ($P<0.01$)(Table 15). The cumulative average of g_{wv} across all the summer measurements also was greater in plants from DS ($P<0.001$). No differences were observed between plants from LTR and plants from WCH. Experiment 2 supports the results of g_{wv} of Experiment 1.

The diurnal trend of g_{wv} for the three plant types is shown in Figure 20. During the measurements taken at 11:30am and 1pm, plants from DS had significantly higher g_{wv} compared to LTR and WCH plants. Midday stomatal closure was not observed in any of the three plant types.

Intercellular CO_2 (c_i)

Monthly averages of intercellular CO_2 (c_i) of measurements from October through June 1993 are given in Table 16. The grand average c_i of DS plants was significantly higher than that of LTR or WCH plants ($P<0.01$)(Table 16).

In Experiment 2, the c_i of DS plants was significantly greater than that of LTR plants in 4 of 5 measurements ($P<0.05$)(Table 17). Plants of WCH did not

Table 14. Monthly average stomatal conductance (mol $m^{-2}s^{-1}$) of three plant types.

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
October	20	0.373a	0.412a	0.364a	1.423	.2493	0.05	0.054
November	20	0.237a	0.219a	0.170a	2.355	.104	0.08	0.073
December	20	0.286a	0.184b	0.168b	11.7	.0001	0.41	0.047
January	20	0.313a	0.247ab	0.223b	1.57	.2179	0.05	0.070
February	20	0.256a	0.169b	0.182b	14.33	.0001	0.33	0.044
March	20	0.368a	0.232b	0.272b	18.46	.0001	0.39	0.044
April	20	0.333a	0.267b	0.236b	6.45	.0030	0.19	0.050
May	20	0.314a	0.239b	0.274ab	3.21	.0480	0.10	0.058
June	20	0.613a	0.400b	0.471b	13.88	.0001	0.33	0.082
Cumulative	180	0.344a	0.270b	0.265b	20.30	.0001	0.07	0.026

Means followed by different letters denote statistical dissimilarity between ecosystems (P<0.05, using Fisher PLSD)

Table 15. Average stomatal conductance (mol $m^{-2}s^{-1}$) of the three plant types measured during summer 1993 in natural conditions (outside the glasshouse).

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
25 July	20	0.954a	0.829b	0.779b	4.91	.0108	0.15	0.115
15 August	20	1.125a	0.758b	0.815b	11.94	.0001	0.30	0.162
21 August	20	0.792a	0.495b	0.476b	45.12	.0001	0.61	0.075
29 August	20	1.228a	0.947b	0.812c	33.71	.0001	0.54	0.103
15 Sept.	20	0.880a	0.785b	0.826ab	3.902	.0258	0.12	0.068
Cumulative	100	0.996a	0.763b	0.742b	39.03	.0001	0.21	0.063

Means followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using Fisher PLSD)

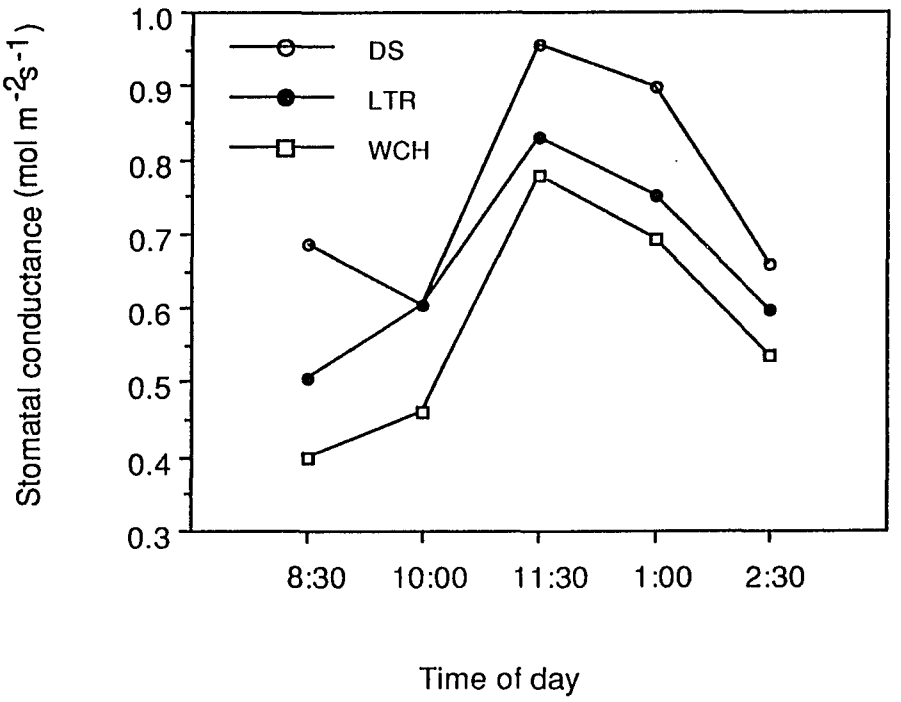

Fig. 20. Diurnal pattern of stomatal conductance for the three plant types in the common garden (N=20).

Table 16. Monthly average intercellular CO_2 (ppm) of the three plant types.

		Ecosystem						
Month	N	DS	LTR	WCH	F	P	R-sq	PLSD
October	20	326.24a	316.90a	319.24a	0.57	.569	0.02	20.18
November	20	242.04a	234.86a	215.00a	1.85	.1658	0.06	28.68
December	20	263.15a	239.52b	235.80b	4.47	.0157	0.14	19.36
January	20	247.26a	253.96a	245.29a	0.43	.6498	.015	18.64
February	20	245.37a	222.63b	229.95ab	5.67	.0057	0.17	16.97
March	20	267.76a	243.67b	238.98b	8.45	.0006	0.22	17.63
April	20	246.37a	245.45a	234.66a	1.36	.2657	0.05	16.73
May	20	217.96a	195.63b	207.93ab	3.70	.0309	0.12	16.19
June	20	246.36a	233.60b	248.57a	5.42	.0070	0.16	9.38
Cumulative	180	255.85a	242.91b	241.71b	6.60	.0015	0.02	9.04

Means followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using Fisher PLSD)

Table 17. Average intercellular CO_2 (ppm) of the three plant types measured during summer 1993 in natural conditions (outside the glasshouse).

		Ecosystem						
Month	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
25 July	20	263.1a	264.9a	269.8a	.906	.4101	0.03	10.6
15 August	20	296.0a	272.0b	271.7b	9.91	.0002	0.26	12.5
21 August	20	275.2a	263.6b	267.5ab	3.64	.0325	0.11	8.8
29 August	20	290.8a	276.9b	281.6ab	3.10	.0524	0.10	11.4
15 Sept.	20	286.9a	277.3b	291.3a	4.82	·0116	0.14	9.2
Cumulative	100	282.4a	270.9b	276.3c	9.40	.0001	0.06	5.2

Means followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using Fisher PLSD)

show a consistent pattern in relation to the other two plant types. However, the cumulative avarages indicate significant differences among all three genotypes ($P<0.001$ between LTR and DS plants, $P<0.05$ between WCH and DS plants, $P<0.05$ in LTR and WCH plants). The c_i in DS plants was the highest and in LTR plants it was the lowest (Table 17). Figure 21 shows the diurnal patterns of c_i..

Response to light

Figure 22 shows the P_{net} light response curves using Michaelis-Menton nonlinear regression (JMP ver. 3.1). All three plant types did not exhibit light saturation even at 2000 μmol $m^{-2}s^{-1}$.

One-way ANOVA was performed at each level of PAR averaging 196, 650, 1315, 1792 μmol $m^{-2}s^{-1}$ (Table 18). Net photosynthesis of DS plants was significantly higher at PAR above 650 μmol $m^{-2}s^{-1}$ compared to LTR and WCH plants ($P<0.01$). At PAR averaging 196 mol m^{-2} s^{-1} LTR and WCH plants also were significantly different ($P<0.001$).

Leaf Temperature

In Experiment 2 when the average midday air temperature was 34.3 (N=300), leaves of the DS plants maintained a lower average leaf temperature of 33.3 compared with LTR plants which averaged 33.9 ($P<0.05$). DS and WCH leaves (33.8) were not significantly different (Table 19). However, when the average daily midday air temperature was lower (28), during the course of Experiment 1, there were no significant differences in leaf temperature between plant types (Table 20), with means of 27.8 in DS plants, 28.3 in LTR plants and 28.1 in WCH plants (N=140).

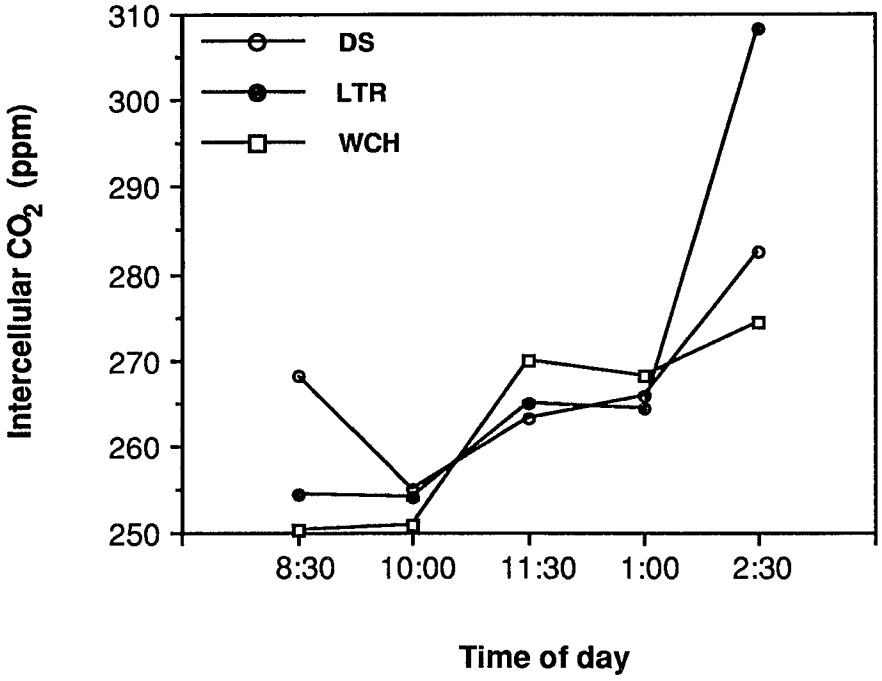

Fig. 21. Diurnal pattern of intercellular CO_2 for the three plant types in the common garden (N=20).

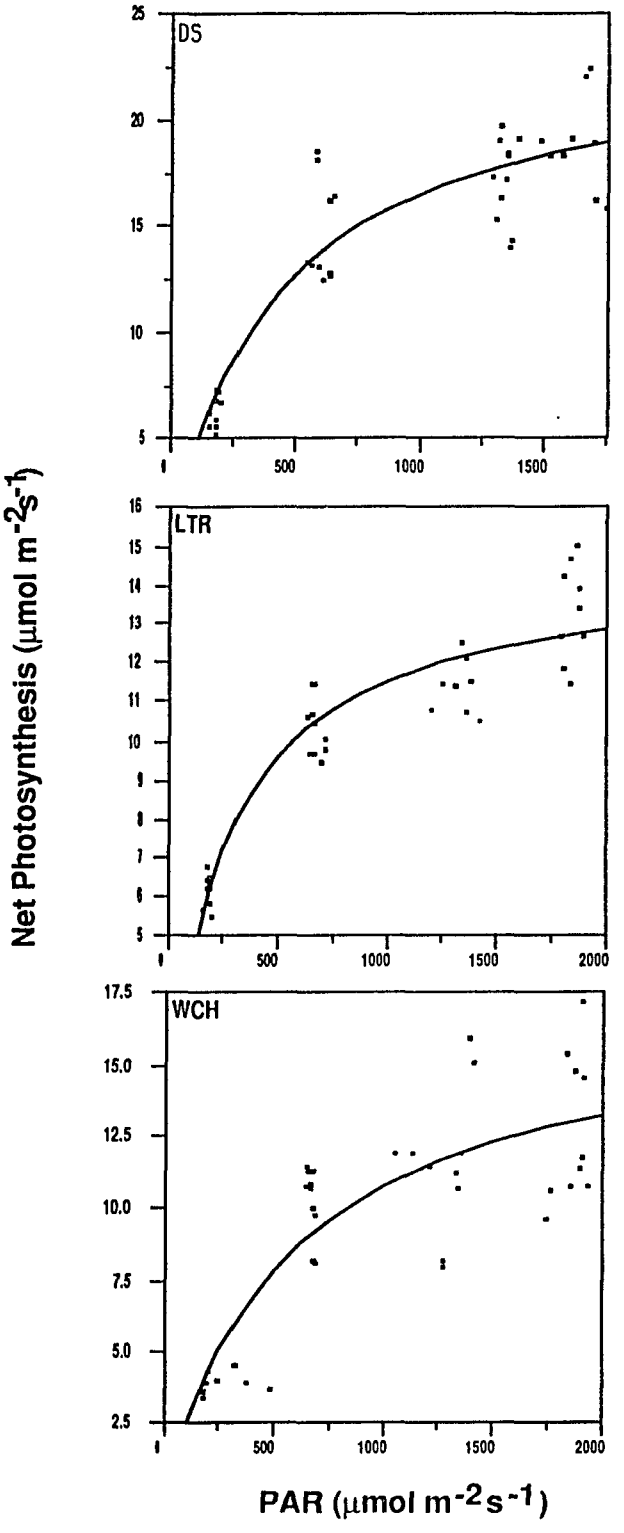

Fig. 22. Light response curves of the three plant types obtained using Michaelis-Menton regression model.

Table 18. Average net photosynthetic rates (µmol $m^{-2}s^{-1}$) of the three plant types with increasing PAR (µmol $m^{-2}s^{-1}$) levels.

		Ecosystem						
PAR	**N**	**DS**	**LTR**	**WCH**	**F**	**P**	**R-sq**	**PLSD**
196	10	6.27a	6.14a	3.92b	59.2	.0001	0.81	0.497
650	10	14.73a	10.35b	10.27b	25.5	.0001	0.65	1.466
1315	10	17.06a	11.38b	11.64b	25.9	.0001	0.67	1.909
1792	10	19.01a	13.34b	12.70b	29.1	.0001	0.68	1.867

Means followed by different letters denote statistical dissimilarity between ecosystems ($P<0.05$, using Fisher PLSD)

Table 19. Leaf temperature of the three plant types at average air temperatures of 34.3 °C (F=2.80, P=.06 R-square = 0.02).

Ecosystem	N	Leaf temperature °C
DS	100	33.3 (±1.9)c
LTR	100	33.9 (±1.9)ab
WCH	100	33.8 (±1.9)a
PLSD	P<0.05	0.537

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

Table 20. Leaf temperature of the three plant types at average air temperatures of 28.1 °C (F=1.64, P=0.19, R-square=0.01).

Ecosystem	N	Leaf temperature ^0C
DS	140	27.8 (±2.5)a
LTR	140	28.3 (±2.5)a
WCH	140	28.1 (±2.6)a
PLSD	P<0.05	0.593

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

The light intensities used in Experiment 2 were similar among the plant types, averaging 1681 mol m^{-2} s^{-1} in DS plants, 1689 in WCH plants and 1681 in LTR plants.

Leaf specific mass

Leaf specific mass of DS plants (20.64 μg/mm^2) and WCH plants (22.46) converged, and were not significantly different in the common garden (Table 21). Plants from LTR (26.77 μg/mm^2) maintained significantly higher LSM compared to DS and WCH plants ($P<0.05$). However, LSM of the three plant types in the common garden were much lower than values obtained for the same plant types in their natural environment (Table 1 and 21).

Leaf water potential

Pre-dawn leaf water potentials were similar among the three plant types with a grand mean of -0.25MPa (Table 22). Midday leaf water potential was not different among the plant types. The grand mean for the midday leaf water potential was -0.77MPa (Table 22).

Responses to drought stress

Net Photosynthesis

Net photosynthetic rates measured across the droughting period from the time the plants were fully saturated with water until they reached the temporary wilting point demonstrated many differences among the plant types. From the beginning of the droughting period to the 7th day, DS plants showed significantly higher P_{net} when compared with WCH plants (Fig. 23). After the 7th day WCH plants started showing higher P_{net} compared with DS plants, with differences

Table 21. Leaf specific mass ($\mu g/mm^2$) of the three plant types in the common garden (F=11.34, P=0.017 R-square=0.65).

Ecosystem	N	Leaf specific mass
DS	5	20.64 (±1.26)a
LTR	5	26.77 (±1.49)b
WCH	5	22.46 (±3.05)a
PLSD	P<0.05	2.88

Means (±SD) followed by different letters denote statistical dissimilarity (P<0.05, using Fisher, PLSD)

Table 22. Pre-dawn and midday leaf water potential of the three plant types in the common garden (F=0.81, P=0.46, R-square = 0.06 for pre-dawn and F=0.741, P=0.49, R-square = 0.03 for midday).

		Leaf water potential	
Ecosystem	**N**	**Pre-dawn MPa**	**Midday MPa**
DS	10	0.25 (±0.02)a	0.72 (±0.12)a
LTR	10	0.25 (±0.02)a	0.80 (±0.26)a
WCH	10	0.24 (±0.03)a	0.78 (±0.14)a
PLSD		P<0.05 0.14	0.24

Means (±SD) followed by similar letters denote statistical similarity (P<0.05, using Fisher PLSD)

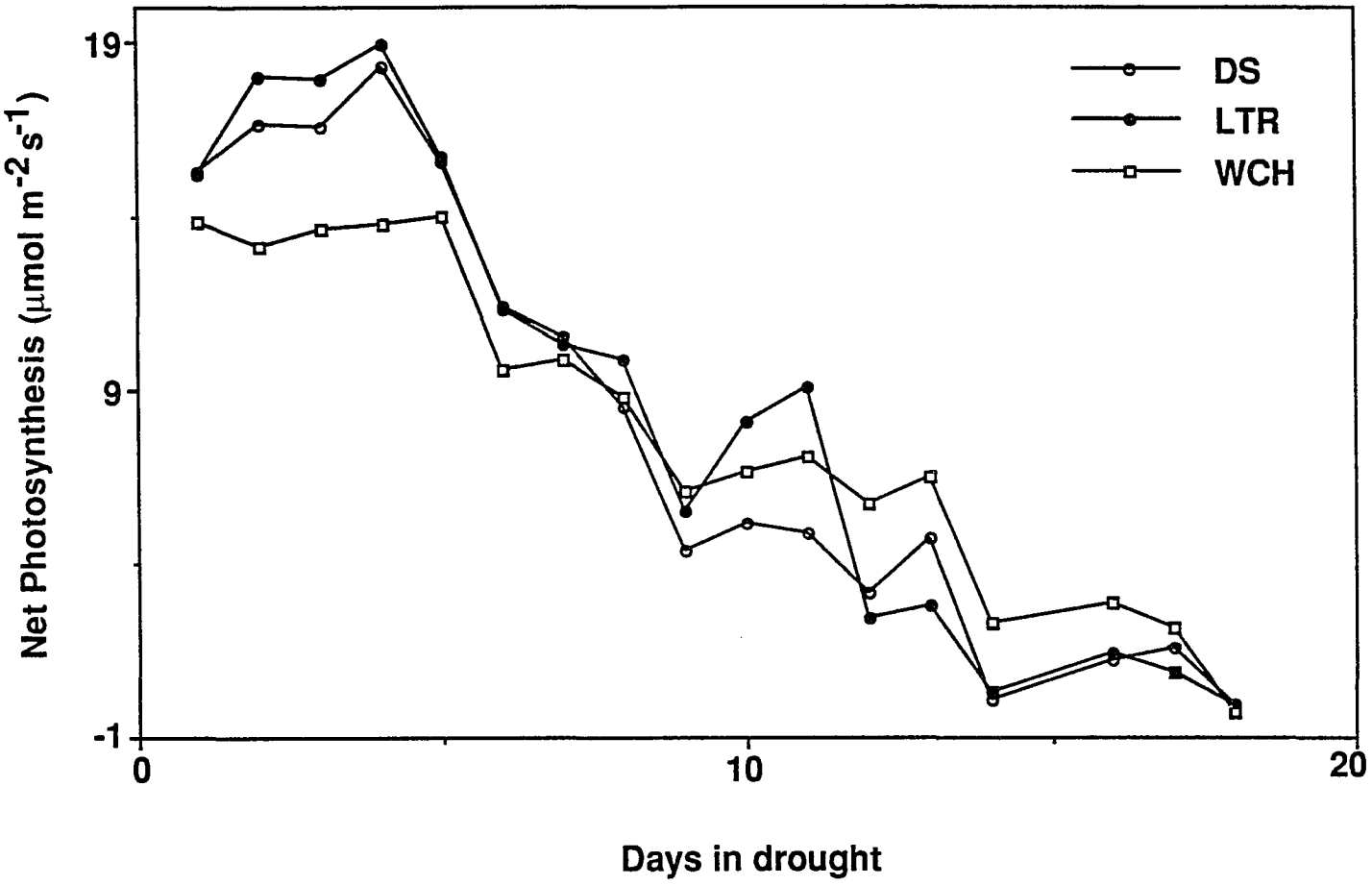

Fig. 23. Effect of droughting on net photosynthesis of the three plant types. Each value is an average of 10 values.

becoming significant from the 10th to the 17th day. By the 19th day all three plant types averaged zero P_{net} (some were showing negative P_{net} indicating that the respiratory CO_2 production is higher than the photosynthetic rate). Plants from LTR also maintained significantly higher P_{net} compared with WCH plants from the beginning of the period to the sixth day ($P<0.05$) and significantly lower values after the 12th day of droughting up to the 16th day ($P<0.05$).

During the droughting period it was also observed that as the drought progressed, plants with negative P_{net} on dry days switched to positive photosynthesis as the atmospheric humidity increased on rainy days. Towards the end of the cycle (the 13th, 16th and the 17th days) many days were cloudy and humid.

Stomatal conductance and transpiration

Transpiration and stomatal conductances followed similar patterns during the droughting cycle (Fig. 24 and Fig. 25). During the 12th, 13th, and 14th days WCH plants maintained higher transpiration rates and stomatal conductances compared with DS and LTR plants. All three plant types converged to show transpiration rates and stomatal conductances close to zero by the 18th day.

Leaf water potential

During the droughting cycle the midday leaf water potential was measured at the temporary wilting point. DS plants had significantly higher (less water stressed) leaf water potential (-0.93 MPa) compared to LTR plants (-1.08 MPa, $P<0.05$) and to WCH plants (-1.16 MPa, $P<0.01$) (Table 23). WCH and LTR plants showed similar midday leaf water potential.

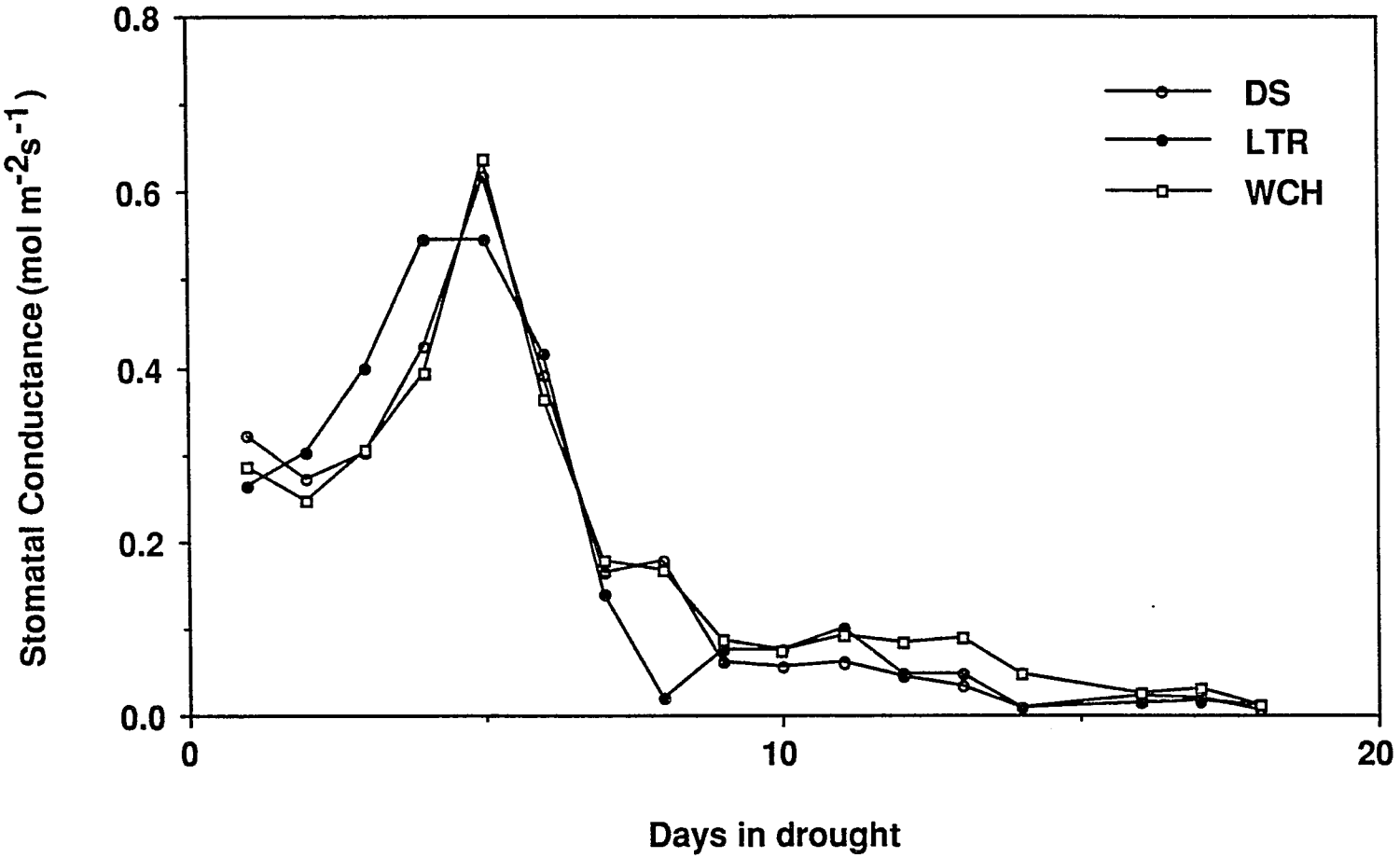

Fig. 24. Effect of droughting on stomatal conductance on the three plant types.

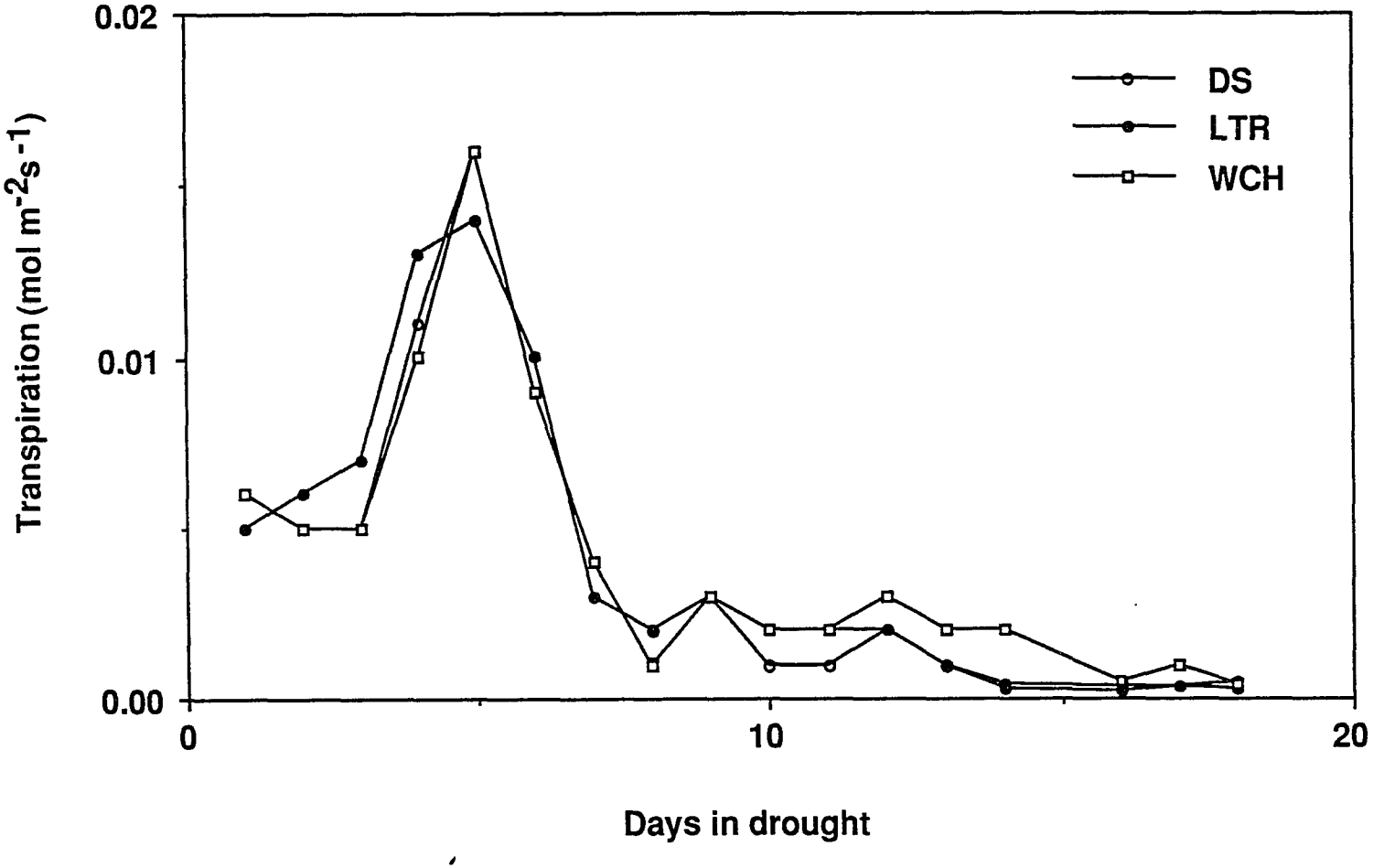

Fig. 25. Effect of droughting on transpiration rate on the three plant types.

Table 23. Midday leaf water potential at the temporary wilting point (F=7.28, P=0.003, R-square=0.35).

Ecosystem	N	Leaf Water Potential (-MPa)
DS	10	0.93 (±0.05)b
LTR	10	1.08 (±0.01)a
WCH	10	1.16 (±0.22)a
PLSD	P<0.05	0.13

Means followed by different letters denote statistical dissimilarity (P<0.05, using Fisher PLSD)

Discussion

The results from both field studies and glasshouse experiments suggest there are genetic differences in gas exchange characteristics in addition to genetically based morphological and phenological differences among wild castor originating in DS, LTR and WCH.

In the field, adjusted P_{net} of WCH plants (20.8μmol $m^{-2}s^{-1}$) plants was highly significantly lower than DS (25.3μmol $m^{-2}s^{-1}$) and LTR plants (25.8μmol $m^{-2}s^{-1}$). These results were obtained using a two-way ANCOVA model that generated an explained sum of squares of 0.46 (R-square). This is a very high proportion of total variability in P_{net} to be accounted for in a set of uncontrolled field measurements taken from 3 ecosystems with wide microclimatic differences (Fig. 2; Table 1).

Net photosynthesis could have been analyzed by ordinary two-way ANOVA without entering microclimatic variables as covariates but with very different results. For plants in general, the P_{net} of an individual leaf varies greatly with the microclimate, particularly with diurnal changes in PAR; therefore I used ANCOVA for the field data to adjust P_{net} by multiple linear regression in a statistical attempt to make the microclimate uniform among the ecosystems. The explained sum of squares for P_{net} decreases from R-square = 0.46 in ANCOVA, down to 0.33 in ordinary two-way ANOVA -- a distinct disadvantage. Moreover, the F-test for the contrast between P_{net} in the DS versus the LTR, instead of being nonsignificant (P = 0.06) in ANCOVA, becomes highly statistically significant (F = 18.6; P = 0.00002) in ANOVA, as easily visualized in the upper panel of Figure 3. However, this would be a misleading statistical result because at the time of measurement of P_{net}, PAR averaged 1820 mol $m^{-2}s^{-1}$ in the DS but only 1331 in the LTR, and it is not surprising to find a higher, raw value of P_{net} in the DS (26.6μmol $m^{-2}s^{-1}$) than in the LTR (23.5μmol $m^{-2}s^{-1}$). Multiple ANCOVA has a variety of assumptions and other drawbacks as applied to uncontrolled field

experiments. However, because ANCOVA, as opposed to ordinary ANOVA models, will make "use" of more of the variables gathered at the leaf by gas exchange instruments, there will be increases in the R-square value for the proportion of the total variability (total SS) being "explained" for the response variable (P_{net} in our case) -- a situation that can only bolster confidence in the reliability of the conclusions.

The measured rates of whole-leaf P_{net} in the field are very high for C3 plants. For instance, 36 μmol $m^{-2}s^{-1}$ was the 90th percentile of the 365 leaf measurements made from the three ecosystems. The values for P_{net} in the field for wild castor in Sri Lanka are within the range of those recorded by Dai et al. (1992) for a castor cultivar under glasshouse conditions. They found "The high capacity of photosynthesis (leaf area basis) in this C_3 species is apparently due to a high level of photosynthetic components: a higher Chl, RUBISCO protein, and total soluble protein per leaf area compared with the C_3 species tobacco and the C_4 species maize" (Dai et al. 1992).

In the common garden, midday P_{net} of DS and WCH plants was significantly different in almost all instances (Tables 10,11 and Fig.17,18). However, the P_{net} values of LTR plants formed no consistent pattern. The average midday P_{net} of LTR and WCH plants was not different in Experiment 1 performed in the glasshouse (Table 10). The average P_{net} across all the measurements made outside the glasshouse was significantly different among all three plant types and the P_{net} of LTR plants was between the DS and WCH plant means (Table 11). These results indicate that the photosynthetic capacity of wild castor in the LTR, the mesic habitat, is more variable than that of wild castor in the DS and WCH. This supports the suggestion made by Kubiske and Abrams (1992) that mesic habitats hold a greater array of genotypes. They observed that *Quercus rubra* seedlings obtained from

mesic habitats had greater variance in P_{net} during experimental drought than in the seedlings obtained from xeric habitats.

In the common garden experiments performed both inside and outside the glasshouse (Table 10 and 11), the midday P_{net} of DS plants was significantly higher than that of WCH and LTR plants. In xeric plants, high photosynthetic rates are characteristic when water is readily available (Kubiske and Abrams 1992; Mooney et al., 1976; Ehleringer 1983). In contrast, WCH plants in the outdoor experiment (Table 11) and in the diurnal experiment (Fig. 17 and 18) had significantly lower P_{net} during midday when compared to DS and LTR plants (24% and 15% less than DS and LTR plants respectively in the outdoor experiment; 18% and 16% less in the diurnal experiment). This could be due to the significantly lower leaf chlorophyll concentration in WCH plants. The leaf cholorophyll concentration of WCH plants was 8% lower than that of DS plants and 13% lower than that of LTR plants (Table 3). In most instances (in the field and in the common garden) DS plants had significantly higher P_{net} when compared with WCH plants ($P<0.05$). The average across all the experiments performed showed a 24% higher P_{net} in DS plants than in WCH plants (26% higher in the field study, 16% higher in the glasshouse and 31% higher outside the glasshouse, Tables 1, 10 and 11).

In the common garden, the light conditions of the immediate past affected P_{net}, although light supplied artificially at gas-exchange measurement also plays a significant role in the overall photosynthetic component. This can be explained as acclimation; a plastic temporary change in a character (in this case P_{net}) caused by an environment to which the plant has been recently exposed (Barbour et al., 1987). This phenomenon probably explains the seasonal variation in P_{net} which was observed during these measurements as well. Compared to spring, P_{net} during winter months was low, corresponding to lower average daily light

intensity (Fig. 13). Brooks et.al. (1994) studied acclimation of sun foliage to shading in the conifer *Abies amabilis*. They observed that a long term shading treatment of sun leaves reduced maximum photosynthesis by 50%.

Transpiration rates of the three plant types in the common garden did not show consistent differences. Although the cumulative averages were significantly higher for DS plants compared to WCH plants, five out of 14 datasets exhibited the same transpiration rates (Table 12 and 13). Midday transpiration rates during diurnal measurements were not statistically significantly different among the plant types (Fig.19). The results do not provide clear evidence on genetic differentiation in transpiration rates among the plants from these habitats.

When the plants were well watered in the common garden (both inside and outside the glasshouse), higher midday stomatal conductance (g_{wv}) in DS plants indicates that stomatal factors may be contributing to the higher P_{net}. Plants of LTR and WCH had lower conductances than did DS in the common garden (Tables 14 and 15 and Fig. 20). These results indicate genetic divergence in g_{wv} for castor from the DS as compared to castor from the other two sites.

In the field study the range of VPD was 5-27 mbars. When P_{net} was regressed against VPD, it was observed that LTR plants showed a negative trend with a significant slope ($P<0.0002$) with an r^2 of 0.17. Conversely, plants from WCH exhibited a positive trend ($r^2=0.15$) with a significant slope ($P<0.0001$). DS plants did not show a significant relationship (Fig. 8). There was no statistically significant relationship between P_{net} and increasing VPD when all leaves were merged from the three ecosystems (Fig. 7). Since these data were obtained in the field, one cannot deduce a proper conclusive relationship between P_{net} and VPD, as most factors which may affect this relationship are not controlled in a field situation. Dai *et al.* (1992) showed a significant relationship between declining P_{net} and increasing VPD under glasshouse conditions in castor cultivars. These

different trends in the response of P_{net} to changing VPD may reflect a physiological difference between wild castor and castor cultivars. The positive trend observed between P_{net} and VPD by WCH plants may deserve further investigation under controlled conditions to characterize any differences in this relationship among genotypes. Such investigations may further support the hypothesis of genetic differentiation among the plants of the three ecosystems.

Dry shrubland plants curtail water loss through stomatal control during severe drought more than do WCH plants. This is shown by the lower stomatal conductance of the DS plants compared to WCH plants during 9 to 17 days of severe experimental drought (Fig. 24). This is also reflected by lower transpiration rates of DS plants (Fig. 25) compared to WCH plants during experimental drought. It is difficult to consider the maintenance of higher P_{net}, higher stomatal conductances and higher transpiration rates in WCH plants during severe drought (Fig. 23, 24 and 25) to be an efficient drought survival strategy. However, in the native environment of WCH plants, although the plants must be under some physiological drought due to high salinity, they grow in a humid, cloudy, and therefore low light environment during much of the year, thus perhaps providing a less stressful micro-environment than that of the DS.

Midday leaf xylem water potential of the three plant types at the temporary wilting point (Table 13) averaged -0.93 MPa, -1.1 MPa and -1.2 MPa for DS, LTR, WCH plants respectively. These reflect innate differences in the control of the water balance of the three plant types under experimentally droughted conditions. Dry shrubland plants wilted at statistically significantly higher levels (less stressful) of xylem water potential. This is characteristic of a drought deciduous plant. In a subsequent droughting experiment DS plants exhibited significantly higher (9% abcission of the total) leaf abscission compared to LTR (1% abcission) and WCH plants (no abscission) during a drought cycle (data not

reported). Drought deciduousness is usually regarded as a drought avoidance mechanism (Kolb and Davis 1994; Abrams1990). Lowland tropical rain forest and WCH plants wilted at lower (more negative) xylem water potentials exhibiting less efficient drought avoidance. There was no difference in the leaf water potential at wilting point between LTR and WCH plants. At field capacity, pre-dawn water potential of the three plant types was similar (grand mean = 0.27MPa). This indicates that this character is conserved. The differences in leaf water potential at temporary wilting point in the common garden between DS plants versus the other two plant types could be due to genetic differences in stomatal behavior, among other factors involved with leaf water balance.

The experiment done to test the leaf reflective abilities of the three plant types (Table 2) showed that the DS plants have the largest difference between the abaxial and adaxial P_{net} rates when exposed to full sunlight. A large difference indicates that the abaxial surface reflects more light (ie. absorbs less light for photosynthetic purposes) compared to the plant showing a lower difference. The observation that leaves of DS had a silvery white waxy abaxial surface absent in leaves from plants of WCH and LTR also supports this finding. Having an efficient reflective surface is a well documented adaptation of plants inhabiting dry, desert ecosystems (Ehleringer 1981,1983; Ehleringer and Björkman 1978a,1978b; Mooney 1980). This can have a dramatic effect on the leaf energy budget and thereby on the physiology of the plant (Gates 1980,1965). The silvery white waxy coating observed on the abaxial surface of the DS plants can be an effective way of reflecting part of the radiation incident on the lower surface of the leaf (Gates 1980,1965). Soils in the dry shrublands are generally sandy and reflect more radiation compared to a loamy mesic soil. This adaptation by DS plants is a fine example of a morphological adaptation resulting in a physiological function (Ehleringer 1981; Ehleringer and Björkman 1978a and 1978b; Mooney et al.,1977).

In fact, wild castor plants obtained from seeds collected from dry habitats in Greece (west outside the city of Hania on the Island of Crete) demonstrated similar leaf reflective surfaces (personal observations). The above mentioned leaf morphological characteristics in wild castor were maintained in the field and in the common garden indicating that they are genetically fixed.

Stomatal density is apparently conserved across different ecosystems in wild castor as no significant differences were observed in mean stomatal density among plants growing in the three field sites (Table 1). Kubiske and Abrams (1992) in a study of *Quercus rubra* seedlings grown under glasshouse conditions, found no difference in mean stomatal density between xeric and mesic ecotypes. The castor leaf is amphisomatous (Fig.11 and 12). This is often observed in plants which populate drier habitats and this feature may help regulate leaf temperature because transpirational cooling can occur at both leaf surfaces. In DS plants, it was observed that the stomates are located below an ante-chamber formed by the cuticle. In scanning electron microscopy, the guard cells in DS plants cannot be observed through the cuticular pore as they are located deeper within (Fig. 12, 13 and 14). In plants from LTR and WCH the guard cells are clearly observed to lie just beneath the cuticular pore and nearly level with the epidermal plane. Sunken stomates reduce water loss during drought (Duddington1974). The water vapor collects in the ante-chamber above the stomata and reduces the steepness of the diffusion gradient between the leaf and the atmosphere.

During the outdoor common garden experiments it was observed that at an average air temperature of 34C, the leaf temperature of DS plants in the gas exchange cuvette was maintained at a lower level than that of LTR ($P<0.05$) and WCH plants ($P<0.08$). Cuvette leaf temperatures of all three plant types were not different when the average air temperature was at 28C. At temperatures higher than 34C this difference may be more prominent and physiologically

advantageous to DS plants. This characteristic of DS leaves may be useful in reducing the heat load and drought stress and thereby optimizing photosynthesis (Ehleringer and Björkman 1978a and 1978b). Compared to most xeric plants, castor possesses very large leaves. Despite the biophysical and negative thermal effects of a large leaf, to survive in a xeric habitat it is important that these castor plants maintain optimal leaf temperatures, moderate transpiration rates and positive photosynthetic gain (Ehleringer 1981).

Higher leaf carbon gain (P_{net}) did not translate into higher plant growth rates for castor from the DS when compared to castor from the WCH (Table 5). *Amaranthus palmeri* under similar experimental conditions was found to have a higher carbon gain which inferred higher growth rates (Ehleringer 1983). Plants from WCH exhibited significantly lower P_{net} under most conditions. Lower P_{net} could be partially explained by the lower chlorophyll concentrations observed in WCH compared to the other plant types. However, the leaf area of WCH plants was significantly larger (Table 7) which may compensate for the effects of low P_{net}. Lower chlorophyll concentration spread over a larger leaf area may be a strategy for efficient light harvesting even at low PAR.

At the time of uprooting the adult plants in the common garden, WCH plants were significantly shorter compared to DS and LTR plants (Table 4). There was no significant difference between DS and LTR adult plants. However, height was different in the juvenile stage when significant differences were observed between DS (shorter) and LTR plants (taller)(Fig.14). Plants from WCH exhibited the largest girth (Table 6). Production of a shorter, wider phenotype in WCH plants is a character which is genetically fixed. Interestingly, the three plant types converged in total biomass production on a per plant basis in the common garden (Table 5).

During vegetative growth, LTR plants were tallest followed by DS and WCH plants. The switch in the plant heights of DS and LTR plants, from LTR plants being taller than DS plants during juvenile stage (Fig. 14), to being shorter at the time of harvest may be due to the fact that only LTR and WCH plants flowered during the experimental period. Flower primodia are initiated at the terminal end of the castor shoot. Therefore flowering retards growth in height until a new branch is produced. None of the plants from the DS flowered in the common garden. It is possible that the environmental cues to trigger flowering in DS plants were not provided under my experimental conditions. These environmental cues include photoperiod, moisture, temperature (Rathcke and Lacey 1985; Bowers and Dimmitt 1994) and/or severe stress (Fox 1990) or a combination of these factors. Bowers and Dimmitt (1994) explain that "repeat bloomers (plants that flower during more than one season) flower in response to rain triggers within a certain range of temperatures." It is important for individual plants to have a critical phenological pattern for survival through cyclic environmental changes (e.g., drought cycles) with successful reproduction (Rathcke and Lacey 1985). The difference in the flowering phenology of DS plants is another contrasting genetic difference, compared with LTR and WCH plants. It is documented that there is genetic differentiation among natural populations with regard to flowering phenology (Best and McIntyre 1972). Genetic variations in flowering time have also been observed within natural populations (Akeroyd and Briggs 1983).

It is known that plant adaptations to drought could be achieved via deeper roots or by low conductances in the dry season (Wright et.al., 1992). Castor is found to develop deeper roots during dry seasons and to obtain water from deeper layers of soil (Moskin 1986). There were no differences observed in root length in the potted plants of the common garden among the three plant types. Root/shoot ratio was not different among the plant types in the common garden

growth experiment. In general, xeromorphic plants possess a higher root/shoot ratio (Barbour *et al.*, 1987).

On average, in the field, castor leaves had about 80% greater leaf specific mass in the DS than they do in the WCH (Fig 4) and leaves from WCH maintained lower rates of P_{net} across the day (Fig. 3). Decreases in habitat water availability are often associated with increases in LSM (Witkowski and Lamont 1991). Increasing LSM across the ecosystems was found to be related to increasing P_{net} (Fig. 6), a well-documented relationship for many plants (Kleoppel et al.,1993). The common garden experiment addressed the question whether this response is environmentally induced (Geeske et al., 1994) or genetically fixed (Kubiske and Abrams 1992). In the common garden, LSM of DS and WCH plants converged, thus exemplifying phenotypic plasticity. Phenotypic plasticity of LSM may have been selected in castor enabling it to survive in habitats with widely varying temperature, wind, light and humidity conditions.

In the experiment conducted to study the effect of light intensities on P_{net}, all three plant types did not exhibit light saturation even at 2000 μmol $m^{-2}s^{-1}$ PAR (Fig. 22). However, it was observed that at PAR above 650 μmol $m^{-2}s^{-1}$ DS plants maintained significantly higher P_{net} than did the other two plant types. These results provide further evidence to support my hypothesis that DS plants have an intrinsic capacity for maintaining a higher P_{net} at light intensities above 650 μmol $m^{-2}s^{-1}$ than do the other two plant types.

Diurnal P_{net} measurements obtained from field and glasshouse experiments showed no midday stomatal closure. Midday stomatal closure for a large leaved plant like castor could be physiologically disadvantageous. This could over-heat the leaf as large leaves are not good convective coolers and rely on transpirational cooling to maintain leaf temperature within physiological range (Gates 1968, Kincaid et.al.,1984).

Under well-watered conditions in the common garden all three plant types demonstrate their peak P_{net} during midday showing significant differences amongst themselves (Fig.15).

In the field and in the common garden two way ANCOVA on the P_{net} data using PAR, air temperature and VPD as covariates demonstrated no significant interaction between ecosystem and time. This indicates that the diurnal P_{net} patterns of the three plant types are similar. Plotting the adjusted means against time-of-day of the field data (Fig. 3 and 4) shows a lower photosynthetic performance of plants from the WCH throughout the day. Diurnal P_{net} in the common garden also generated closely similar results (Fig. 17 and 18). The lower photosynthetic performance of plants from the WCH throughout the day in the common garden can be interpreted as evidence of a possible genetic difference between plants of the WCH and plants from the other two ecosystems. Comparatively low P_{net} and g_{wv} are indicative of adaptation to stressful, resource limited environments (Kloeppel *et.al*, 1993; Chapin *et.al.*, 1987). The overall results indicate that wild plants of *R. communis* are not "general purpose genotypes" which show plasticity as they occur across drastically different ecosystems. In further support of these results, I did not see convergence in mean P_{net} in the common garden as the effects of PAR, air temperature, and VPD were experimentally leveled and further removed statistically in ANCOVA.

Increases in intercellular CO_2 could be attributed to a combination of several factors which include P_{net}, stomatal resistance, and respiratory rate. The diurnal curves obtained from the common garden show the highest c_i at 2:30pm (Fig. 21). This may have resulted from the dominance of respiratory rates along with high stomatal resistance and lower P_{net} rates during this time. Similarly, the lowest c_i was at 10am; this could be explained by comparatively lower metabolic activity with higher P_{net} combined with lower stomatal resistance. Diurnal

transpiration rates and stomatal conductances reached their peak during midday as expected. DS plants had significantly higher ($P<0.05$) g_{wv} than LTR and WCH plants during midday. However there was no significant difference in E between the plant types (Fig.19 and 20).

In its successful colonization of a wide range of habitats, wild castor seems to have evolved an assortment of physiological, morphological and phenological changes. The changes may reflect adaptation to mesophytic, xerophytic and halophytic environments via independent suites of genetic differentiation and phenotypic plasticity. In reference to natural selection, dry shrubland favors phenotypes with higher photosynthetic capacity, higher chlorophyll concentration, higher stomatal conductances, greater height, smaller leaf area and leaves with higher reflective capacities while wet coastal halophytic zone favors phenotypes evincing the reverse of all these traits. These results thus provide substantial evidence to classify wild, self perpetuating castor growing in the dry shrubland, lowland tropical rainforest and the wet coastal halophytic zone of Sri Lanka as distinct ecotypes.

Conclusions

Wild castor like any other plant, adjusts to its environment through a combination of genotypic differentiation and phenotypic plasticity. Gas exchange characters such as net photosynthesis, stomatal conductance, leaf chlorophyll concentrations and morphological characteristics such as plant height, leaf area, leaf size, surface morphology and flowering phenology of these three plant types have been shown be different in the common garden, thus probably reflecting adaptation to their local environment via genetic differentiation. Leaf specific mass exhibits phenotypic plasticity, while stomatal density is conserved among the plant types.

In adapting to the xeric environment of the dry shrubland, wild castor growing therein has developed morphological, physiological and phenological adjustments. Modifications of DS plants in leaf surface morphology are important genetic differentiations relative to the local environment. These plants maintain higher net photosynthetic rates, higher stomatal conductances and higher transpiration rates at full sunlight in well watered conditions. In droughted conditions, DS plants maintain lower rates of the above variables compared to plants from the wet coastal halophytic zone. Plants from DS have a greater capacity to conserve moisture during drought by somatal control compared to the other plant types. They wilt at a higher water potential probably in order to conserve water which may aid survival in prolonged drought. These plants maintained lower leaf cuvette temperature when the atmospheric temperature was high. They did not flower under any common garden experimental conditions, demonstrating innate differences in flowering phenology.

In contrast, WCH plants in the common garden maintain significantly lower midday P_{net} when compared to DS and LTR plants under wet conditions. Plotting the adjusted means against time of day indicates a lower photosynthetic

performance of WCH plants throughout the day in the field and in the common garden. The leaf chlorophyll concentration of WCH plants is the lowest among the three plant types, a fact that partly explains the lower P_{net}. Compared to the other two plant types, WCH plants maintain larger leaves and have the largest total leaf area. This compensates for the lower chlorophyll concentration; and WCH plants accumulate biomass equivalent to the other two plant types. During severe drought, plants from the WCH seem to maintain higher stomatal conductances compared to the other plant types indicating lesser stomatal control over water loss during drought. The above characteristics could be interpreted as evidence of genetic divergences between WCH plants and castor from the other two ecosystems.

The plants of the LTR photosynthesize at a moderate rate and maintain values between DS and WCH plants. Apparently, the variability of this population's genotype is such that the ranges of P_{net} overlap the ranges of both DS and WCH plants. This may involve the accommodation of a wider genetic variability by plants growing in mesophytic habitats as opposed to more resource limited xerophytic or halophytic habitats. Conversely, plants colonizing xerophytic and halophytic habitats may be selected for a narrower and more specific genotype. This is exemplified by the consistant differences in P_{net} of the plants from DS versus the WCH.

Plants from DS and WCH exhibit phenotypic plasticity in leaf specific mass. This was exhibited by convergence in the common garden while field data showed significant differences among the plants from these two ecosystems. However, LSM of LTR plants in the common garden was significantly higher than DS and WCH plants. Leaf specific mass of all three plant types was lower in the common garden than in the field, further confirming its plastic nature.

Among the three plant types, I found that some aspects of their morphology, physiology and phenology were phenotypically plastic and some were genetically fixed. The evidence for genetic variability of these plant types allows them to be characterized as ecotypes. Furthermore, it can be concluded that DS and WCH plants in the process of adaptation to their local environmental conditions have utilized widely different strategies, which reflect the extremes of their environments. Genotypes of wild castor in DS and WCH exhibit contrasting characteristics. My results indicate that in the DS, selection may favor high P_{net}, high stomatal conductances, smaller leaf, lower total leaf area, higher chlorophyll concentration and a taller plant, while in the WCH it may favor lower P_{net} lower stomatal conductances, larger leaf, larger total leaf area, lower chlorophyll concentration and a shorter plant. These ecotype-specific characteristics in DS and WCH plants probably depict early stages of natural selection operating within these wild populations.

Drought tolerant characteristics along with high P_{net} of DS plants could be utilized in a program to improve drought tolerance in cultivars. Future research in experimental testing of phenotypic and genetic components of variation could also be a useful tool in plant selection. A significant insight into adaptations and acclimations of WCH plants to physiological drought in its local saline environment relative to the performance of the other two ecotypes can be tested by using salinity as a treatment in the common garden; an area open for future research.

In most xeric habitats salinity is also a potential problem due to salt accumulation in surface soils due to capillary pull of the deep ground water. It will not be surprising if plants from the DS exhibit salt tolerance as well, along with its xeromorphic characteristics. If this is true, wild castor from the DS will be a potential candidate for a breeding program which selects cultivars with both

drought and salt tolerance. Thus, these plants may have agricultural potential in xeric, irrigated agricultural land where salt accumulation is often a problem.

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