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ENVIRONMENTAL CONSTRAINTS ON PRODUCTIVITY OF THE MEDITERRANEAN SCLEROPHYLL SHRUB QUERCUS COCCIFERA

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ABSTRACT

Primary production of plants depends on their ability to fix carbon from the atmosphere. This in turn is limited by the ability to supply water and nutrients to the fixation sites. Indirect evidence suggests that the plant species which have evolved at particular locations are adapted to utilizing available resources in the habitat in an efficient manner. The development of efficient resource use in a plant species involves modification of physiological function and plant structure, the latter being related to carbon reallocation. More specifically, differences in potential net photosynthesis rates, canopy structure, leaf area index, or amount of energy and material invested in stems and roots to acquire resources explain differences in primary productivity. Greater investment to acquire resources is directly responsible for greater respiration costs involved in maintaining the supply organs. These principles are illustrated with examples based on our present understanding of the production process of the Mediterranean sclerophyll shrub *Quercus coccifera*.

RESUMEN

La producción primaria de las plantas depende de su capacidad para fijar carbono de la atmósfera. La que a su vez, se ve limitada por la capacidad de suministrar agua y nutrientes a los lugares de fijación. Indirectamente, la evidencia sugiere que las especies de plantas que han evolucionado en emplazamientos determinados están adaptadas para utilizar los recursos disponibles en ese hábitat de forma eficaz. El desarrollo del uso eficaz de recursos en una especie implica la modificación de la función fisiológica y de la estructura de la planta, estando esta última relacionada a la redistribución del carbono. Más en detalle, las diferencias en niveles potenciales netos de fotosíntesis, estructura de la bóveda forestal, índice foliar, o cantidad de energía y material invertido en tallos y raíces para adquirir recursos, explica las diferencias en productividad primaria. Una mayor inversión para la adquisición de los recursos es directamente responsable de los costos más elevados de respiración implicados en el mantenimiento de los órganos de suministro. Estos principios están ilustrados con ejemplos basados en nuestro conocimiento actual del proceso de producción del arbusto esclerófilo mediterráneo, *Quercus coccifera*.

INTRODUCTION

Primary productivity within a biological system is determined by the efficiency with which the system is able to trap solar energy. This depends on the state and the distribution in time and space of chloroplast-containing tissues. These tissues must be sufficiently hydrated, be supplied with inorganic raw materials, and must efficiently intercept solar radiation. Indirect evidence indicates that natural primary productivity of a given habitat is determined by the resources available at the site (Mooney and Gulmon, 1983). This has lead to convergent evolution of structural and physiological characteristics of plants which ensure efficient supply of resources to productive tissues. The supply process becomes evermore energy costly with diminishing availability of resources. The tissues involved in supply functions consume an increasingly larger proportion of the plant's energy and materials, thus imposing a limitation on the level of productivity that can be achieved. While production in a particular habitat can change as major alterations in plant form occur during the process of sucession (Whittaker, 1975), production of mature vegetation in similar climatic regions of the world is quite comparable (Whittaker and Woodwell, 1971; Mooney, 1977; Ehleringer and Mooney, 1983; Saugier, 1983; see also Mooney and Gulmon, 1983).

We may attempt to deduce the order of magnitude of the upper limit on productivity by measuring productivity rates of systems which are particularly favorably supplied with resources. One extremely well supplied natural system is that of phytoplankton populations in coastal waters, where nutrients are supplied by terrestrial run-off, upwelling, and coastal turbulence. During favorable periods, productivity rates of 50 to 60 kg C ha^{-1} day^{-1} are attained (Boynton *et al.*, 1983). Correctly manipulated terrestrial agricultural crop systems realize yet higher productivity rates. The sugar cane field, for example, is extremely effective in energy trapping. Since this is a C_4 species, CO_2 saturation of the enzymatic capacity for CO_2 fixation is achieved with normal air, and only light distribution within the plant canopy limits growth and production. Van Keulen (personal communication) estimated net production rates of 325 to 375 kg C ha^{-1} day^{-1} for stands subsidized heavily in terms of irrigation water and high levels of fertilization. Similar estimates were made by Loomis (1983), who also suggests approximate upper limits on productivity that are possible for other agricultural crop species according to their genetic and physiological traits and given the environments in which they are normally grown.

If we consider environments and habitats in which resources are limited, we find that naturally occurring species have traits that allow them to effectively function for long periods under stress. Low production may only be an adjustment to these environmental constraints (Noy-Meir 1973, 1974; Evenari *et al.,* 1982). Van Keulen (1975), for example, demonstrated that fertilization of native desert annuals in the Negev resulted in production rates equal to those obtained for wheat grown with fertilization in the same area. In other species, ability to take up nutrients from fertilizers or ability to utilize added nutrients in a manner that enhances growth may have been lost during generations of growth under nutrient poor conditions (Chapin 1980).

The basic differences in productivity characteristics of plants occupying disturbed habitats (or habitats relatively rich in nutrient resources) and those occupying late successional habitats have been put forward by Mooney and Gulmon (1983). In the agricultural plant, photosynthetic rates are high, allocation to production and maintenance of shoot material is high, and their short term productivity is also high; but resources are rapidly depleted and long term productivity in the absence of further resource supplementation is low. Such systems can be sustained only with continual energy and resource input. In contrast, the natural vegetation relies solely on resources naturally present and ensures the cycling of these resources in an efficient long term manner. In Mediterranean sclerophyll shrub communities, which we examine in more detail below, we find low photosynthetic rates, high allocation to stems and to roots, low short term productivity, but long term establishment which results in high long term productivity (see Figs. 4 and 5 of Mooney and Gulmon 1983).

FACTORS AFFECTING PRODUCTION

In recent studies, we have investigated the ecophysiology of the sclerophyll shrub, *Quercus coccifera,* growing in a natural macchia formation near Lisbon, Portugal (see Tenhunen *et al.,* 1981). The intent of these studies is to better understand factors affecting primary production of sclerophyllous species throughout annual cycles, and especially during periods of stress when rates of productivity decrease sharply and adaptive function allowing survival is most likely to become apparent. The ecology of sclerophyll shrubs has been studied rather intensively during the past two decades (see Di Castri and Mooney, 1973; Mooney, 1977; Miller, 1981; Kruger *et al.*, 1983) but it is still fair to say that detailed knowledge and understanding of the factors influencing productivity and growth are much more incomplete for these plants than for agricultural crop species. We will describe in this paper, our approach to examining the factors which affect primary production in *Quercus coccifera* stands and will relate our field measurements to a general scheme describing constraints on production.

The physiological basis of growth and production has been discussed by many authors; we refer here only to a small number of recent papers belonging to this vast literature (Mooney and Gulmon 1979, 1983; Schulze 1982; Jarvis and Leverenz, 1983; Ledig, 1969; Reynolds *et al.*, 1980; Penning de Vries, 1983; Jones *et al.*, 1983; Loomis, 1983). Factors affecting production of sclerophyll shrubs have been discussed in detail by contributors to the volume edited by Miller (1981). For the scope of the present paper, we suggest that the important considerations may be summarized in a form similar to that shown in Table 1. We illustrate that net carbon gain on a whole plant basis supplies (arrow into pool)

Table 1. Schematic representation of factors determining short-term net carbon fixation and contibuting to production.

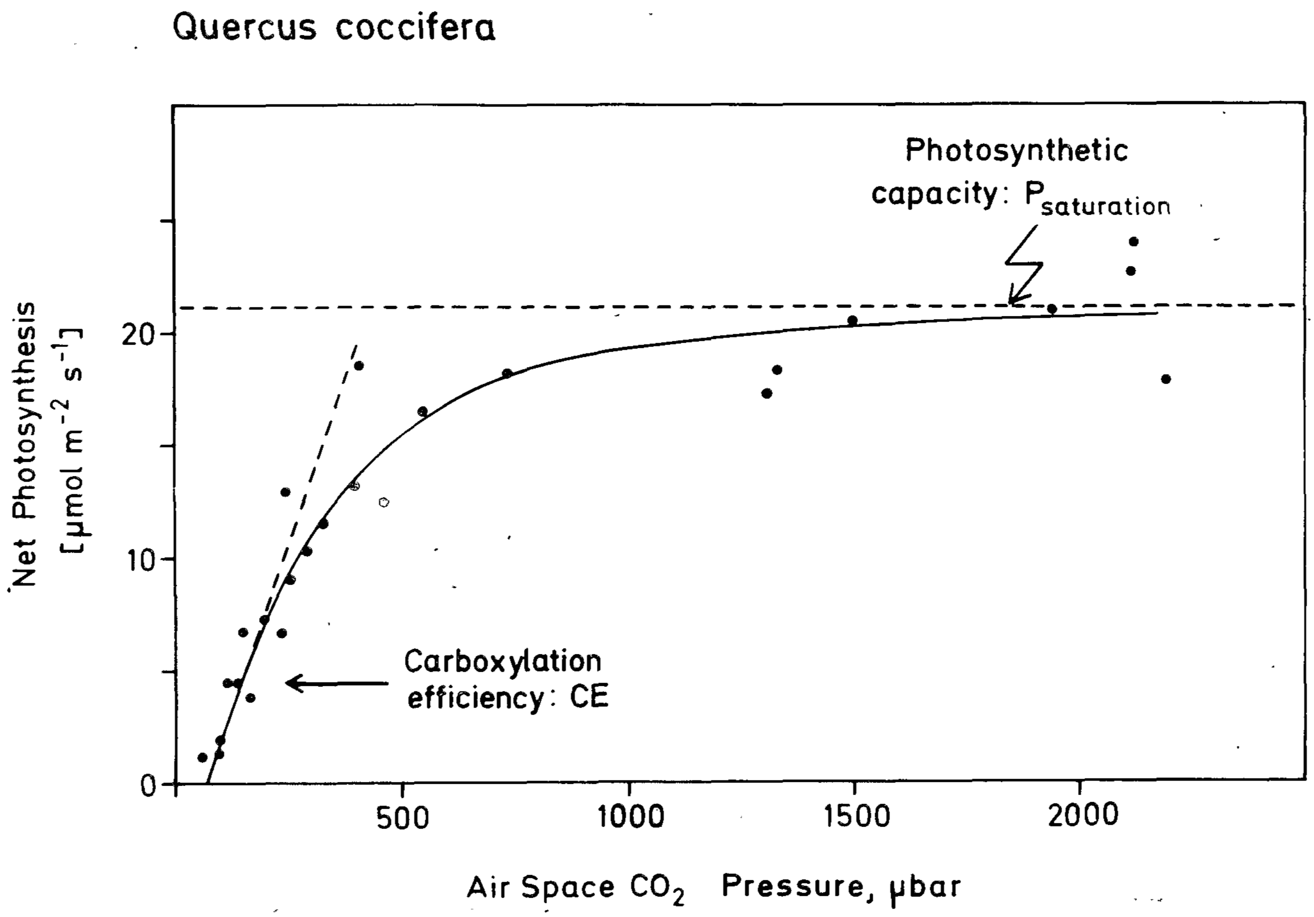
Multiplicative factors selected for discussion

POOL	NP_{pot} dt	× CAN	× LAI	× (1-SUP)
Units	NP_{pot} in $\mu mol\ m^{-2}\ s^{-1}$	proportion between 0 and 1	m^2 leaf per m^2 soil	proportion between 0 and 1
Factor definition	genetically determined potential photosynthesis characterized by one of several parameters described in text and evaluated: 1) with no water stress and 2) for average available nutrient level	canopy effectiveness factor which depends on idealized average leaf NP determined in response to: 1) sun and shade light 2) temperature 3) conductance and leaf internal CO_2	leaf area index	total cost factor which assesses the respiration involved in maintaining present structures involved in: 1) light supply 2) water supply 3) nutrient supply including growth respiration due to turnover (carbon for incrementing stem and root biomass would be removed from the POOL)
Modifiers	modified over the long-term by seasonal shift in: 1) water availability 2) nutrient availability and by developmental effects due to: 1) environmental history 2) canopy position 3) leaf age	influenced by: 1) leaf size 2) leaf angle 3) leaf spatial distribution 4) light intensity and angle of incident beam on canopy 5) air temperature 6) turbulence 7) leaf conductance 8) momentary leaf water status	affected by canopy development, new leaf growth, and leaf fall	modified by growth in reponse to demand for resources, by seasonal temperature, and in some cases with development of specialized structures (Lamont, 1983)

an excess carbohydrate pool which is then used to increment standing biomass (arrow out of pool). The gain of carbohydrate to the pool during any short time period is determined by the extent to which canopy carbon fixation processes outweigh direct and indirect respiration costs involved in maintaining resource supply, i.e. maintenance respiration of roots, stems, and leaves, as well as growth respiration involved in turnover of these organs. Carbon fixation is simultaneously affected by several factors: NP_{pot} is the genetically determined photosynthetic potential of the leaves as modified by their age and previous environmental history; CAN is a canopy effectiveness factor which accounts for actual differences in microenvironment of the leaves in the canopy, momentary tissue water status, and stomatal conductance of these leaves, and LAI is the leaf area index. Actual photosynthetic rates (NP) of individual leaves are determined during any time period considered, by their photosynthetic potentials and by their particular microenvironmental situation, that is, by properties and processes included in the estimation of CAN. These actual NP rates as well as the proportion of total leaf area index experiencing a particular microclimate must be evaluated simultaneously, and similarly they contribute to a final determination of CAN. Only to illustrate how particular types of data from our measurements relate to overall production have we defined the factors as shown in Table 1.

Necessary energy expenditure to supply light, water, and nutrients to the leaf mesophyll by stems and roots, is also formulated here in a very simple fashion. The quantity, (1-SUP), is the proportion of fixed carbon respired during any time period to accomplish resource supply to the canopy. This respiration component depends first on the amount of standing biomass involved in resource supply and secondly on the turnover of this standing biomass required to maintain the status quo of the system. The factor SUP is estimated to have a value between 0 and 1, excluding the possibility for now that respiration costs alone can exceed carbon fixation. In order to estimate the extent to which increments in biomass are limited by the carbon pool, all factors indicated and described must be consider-

Figure 1. *Net photosynthesis rate as a function of internal CO_2 pressure for leaves of a non-water-stressed* Quercus coccifera *plant in the natural habitat in Sobreda, Portugal. T_L = 20 °C, ΔW = 17 mbar bar^{-1}, and PAR = 1500 μ mol^{-2} s^{-1}. The initial slope (CE) and CO_2 saturated rate ($P_{saturation}$) are important parameters defining the response curve.*



ed in an integrative fashion. The rate of removal of materials from the pool to synthesize new biomass and changes in pool size over time are not considered further in our discussion (see in this regard Shaver, 1981, and Mooney and Chu, 1974). To describe growth processes per se much more complex formulations are obviously required. The equation in Table 1 is meant to provide perspective and is not for use in calculations.

Net photosynthetic potential NP_{pot}

For leaves of a well watered plant in a habitat with a particular level of available nutrients, the genetically determined potential photosynthesis may be described as a function of light intensity, leaf temperature (T_L), and leaf air space CO_2 partial pressure (P_i). Such a mathematical model of net photosynthesis may be used to calculate daily time courses of net photosynthesis of individual leaves (Tenhunen *et al.*, 1980a, b), when the equations are solved using actual values of light intensity, temperature, and P_i to which the leaves are exposed. The potential photosynthetic function of any particular leaf is understood well, if the relationship of net photosynthesis rate to P_i for all relevant combinations of constant light intensity and constant leaf temperature is clearly expressed. A carbon dioxide response curve of net photosynthesis obtained in the natural habitat with leaves of a *Quercus coccifera* plant which was not experiencing water stress is shown in Fig. 1. Leaf temperature was 20 °C, water vapor mole fraction difference between leaf and air, ΔW, was approximately 17 mbar bar^{-1}, and light intensity was saturating (1500 μmol^{-2} s^{-1} photosynthetically active radiation, PAR - for methods see Tenhunen *et al.*, 1984). The important characteristics of the CO_2 response curve are indicated in the figure. The CO_2 saturated of net photosynthesis, most commonly interpreted as a limitation set by the rate of regeneration of CO_2 acceptor, is indicated as the photosynthetic capacity ($P_{saturation}$).

Figure 2. Potential photosynthesis of leaves of a non-water- stressed Quercus coccifera *plant expressed in terms of carboxylation efficiency (CE) and photosynthetic capacity ($P_{saturation}$). Symbols indicate determinations at saturating light and between 5 and 28 °C. Measurements were conducted in the natural habitat in Sobreda, Portugal.*

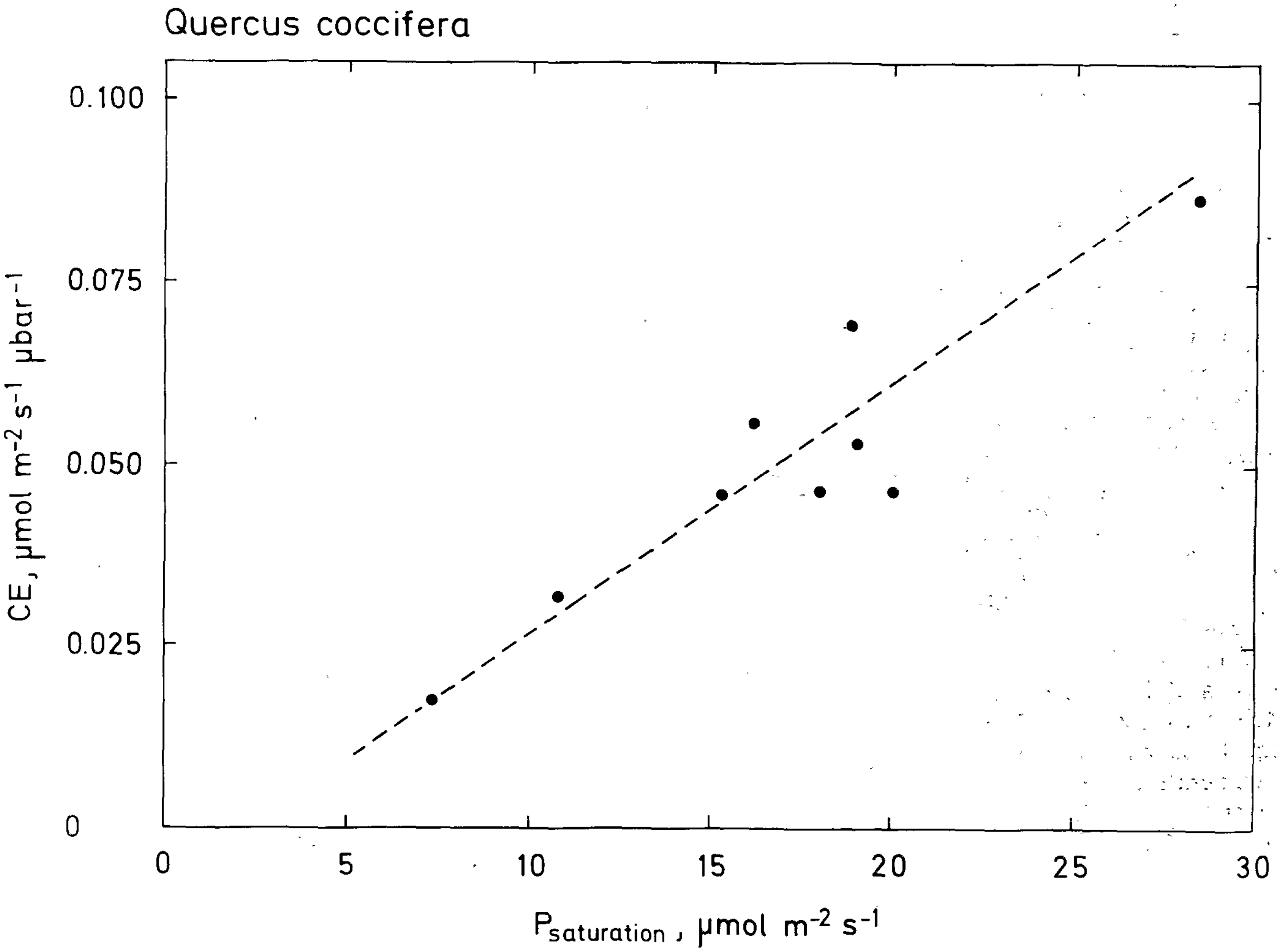
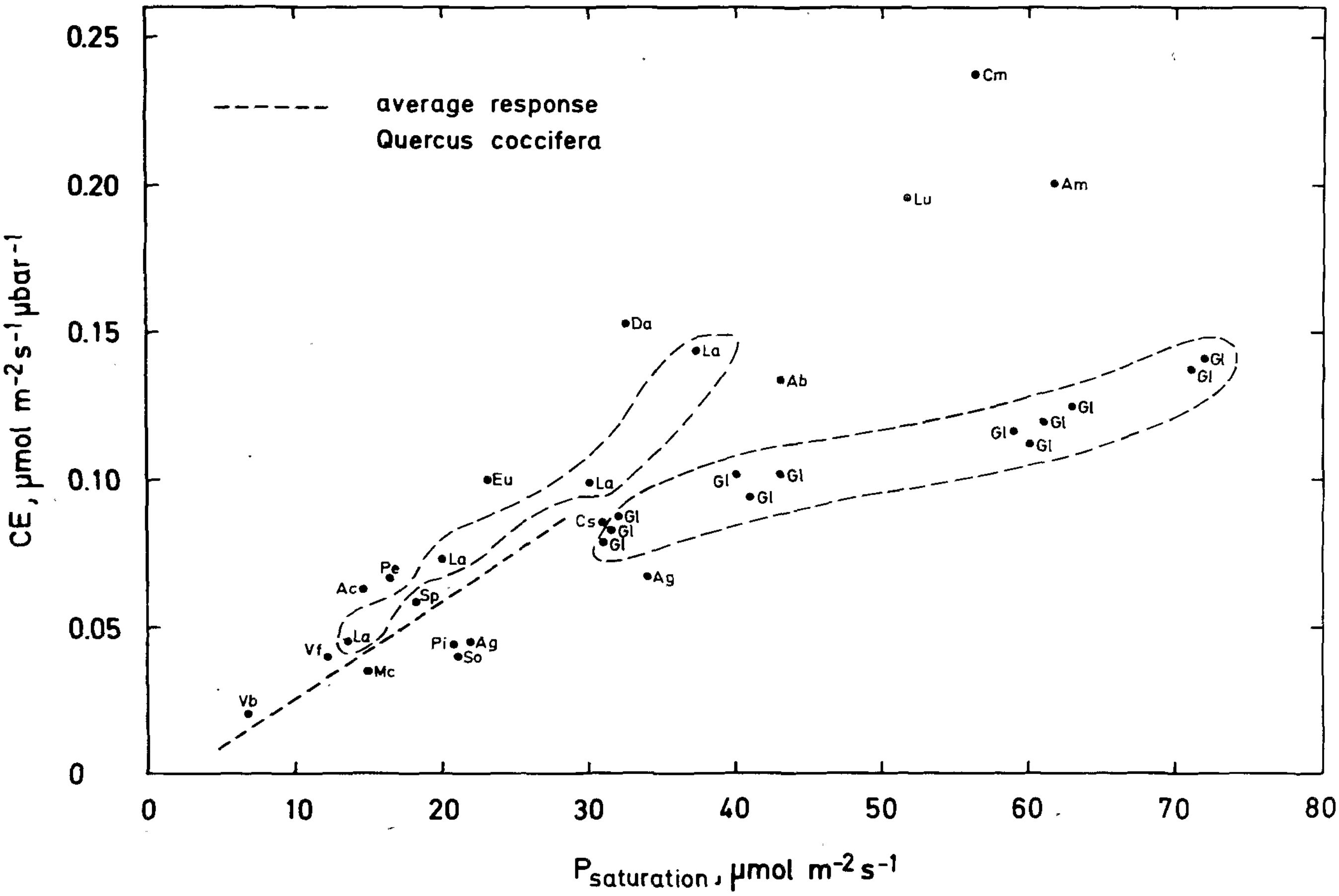


Figure 3. Potential photosynthesis of a variety of C_3 species as evaluated from their CO_2 response curves (see Fig. 2). Species names for letter abbreviations and the literature sources are given in Table 2. Dashed line is for Quercus coccifera *as shown in Fig. 2. Symbols for* Quercus coccifera as shown in Fig. 2. Symbols for Glycine max *(Gl) indicate measurements at different temperatures (Harley* et al., *1984) and symbols for* Larrea divaricata *(La) measurements at different stages of water stress (Mooney* et al., *1977) as described in the text.*



The initial slope of the response curve at light saturation, carboxylation efficiency (CE), is determined primarily by kinetic characteristics of RuBP-carboxylase, but also by a wall and liquid phase diffusion conductance (Raven and Glidewell, 1981; Evans, 1983) which has been little studied to date.

For *Quercus coccifera,* the potential photosynthetic function NP_{pot}, is given in terms of photosynthetic capacity and carboxylation efficiency in Fig. 2 (symbols indicate measurements at temperatures between 5 °C and 28 °C with saturating light and water potential near zero). As was indicated in Table 1, potential photosynthesis is modified due to short-term as well as seasonal changes in light intensity and temperature and long-term changes in water and nutrient availability. For non-water-stressed plants, seasonal modification NP_{pot}, in response to temperature below 28 °C may be visualized as a shift along the dashed line shown in the figure, lower temperature decreasing $P_{saturation}$ and CE. At temperatures above 28 °C, change in temperature may again shift $P_{saturation}$ and CE along the dashed line shown but such that increasing temperature decreases $P_{saturation}$ and CE. The optimum temperature for photosynthesis is then exceeded and midday depression of gas exchange occurs (see below). Data indicate that response to water stress also involves a shift along the same line. In this case the magnitude of $P_{saturation}$ and CE achieved at any particular temperature decreases with increasing water stress.

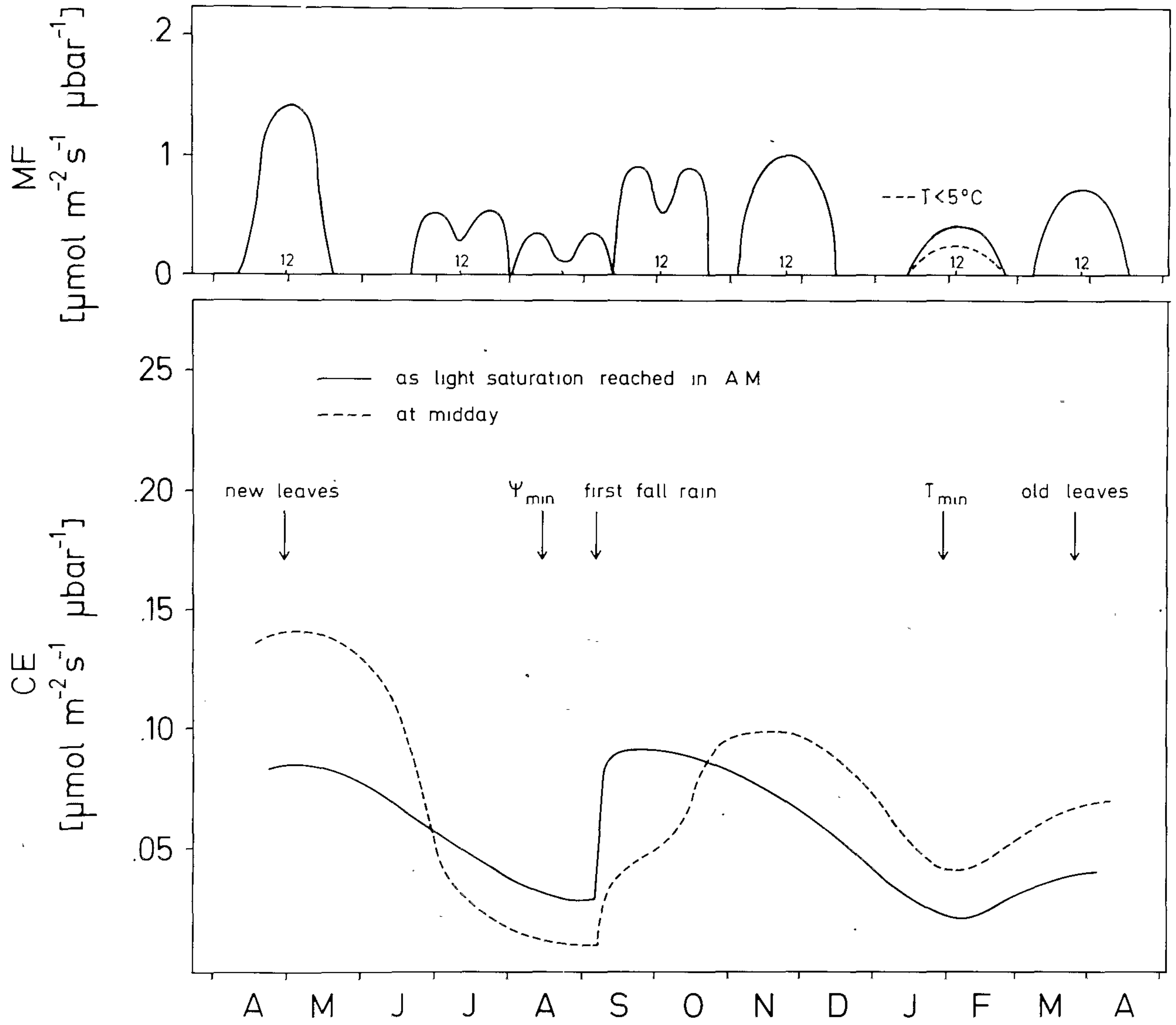
The carbon fixing potential of several C_3 species, including *Quercus coccifera,* is compared in Fig. 3. The dashed line shown for *Quercus coccifera* is the same as that indicated in Fig. 2 and illustrates the range of performance exhibited by leaves of well watered plants. Data shown as solid circles in the figure were obtained from CO_2 response curves either published in the literature or from unpublished curves of our own.

Table 2. Abbreviations used for plant species names in Fig. 3 and literature source.

Symbol	**Species**	**Literature source**
Ab	*Abronia maritima*	De Jong 1978a
Am	*Ambrosia chamissonis*	De Jong 1978a
Ac	*Atriplex californica*	De Jong 1978b
Ag	*Atriplex glabriuscula*	Björkman *et al.*, 1975
Cm	*Cakile maritima*	De Jong 1978a
Cs	*Cistus salvifolius*	Tenhunen, unpublished
Da	*Datura meteloides*	Armond and Mooney 1978
Eu	*Eucalyptus globulus*	Tenhunen, unpublished
Gl	*Glycine max*	Harley 1984
La	*Larrea divaricata*	Mooney *et al.*, 1977
Lu	*Lupinus sparsiflorus*	Armond and Mooney 1978
Mc	*Myrtus communis*	Tenhunen, unpublished
Pe	*Perityle emoryi*	Armond and Mooney 1978
Pi	*Picea sitchensis*	Ludlow and Jarvis 1971
So	*Solanum tuberosum*	Ku *et al.*, 1977
Sp	*Spinacia oleracea*	Beyschlag, unpublished
Vb	*Viola blanda*	Curtis 1979
Vf	*Viola fimbriatula*	Curtis 1979

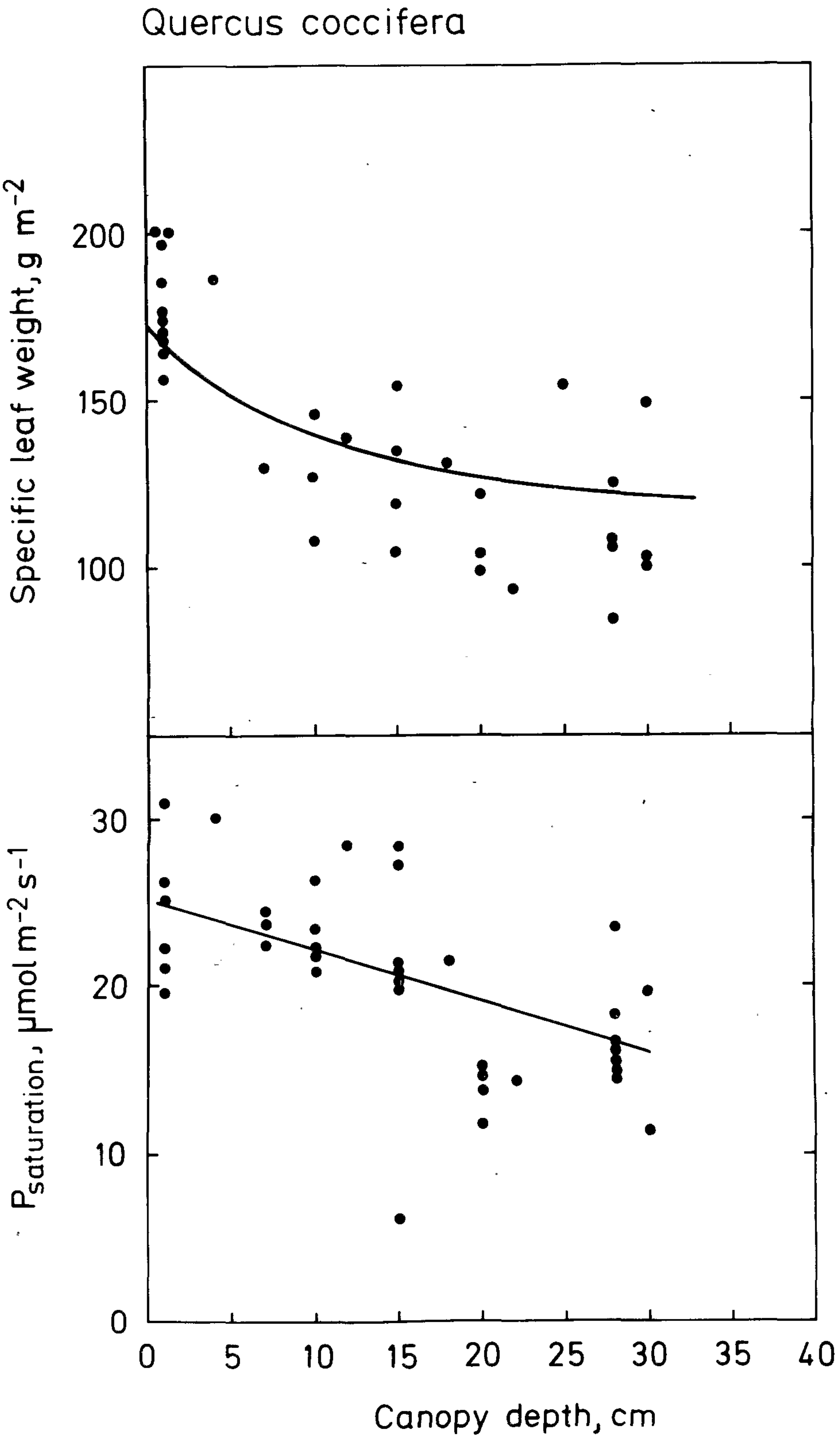
The selected responses were based on internal CO_2 and measured to CO_2 saturation at saturating light intensity. Names of species indicated by letter abbreviations in Fig. 3 and the literature sources are given in Table 2. Crop species such as *Glycine max* (symbol Gl) exhibit both high $P_{saturation}$ values and high CE values. Sclerophyll shrub species, such as *Quercus spp.*, *Myrtus communis* (symbol Mc), and *Pistacia lentiscus* (symbol Pi) exhibit relatively low values of $P_{saturation}$ and CE (see also Mooney, 1983; Ehleringer and Mooney, 1983). As in the case of *Quercus coccifera*, the linear relationship between $P_{saturation}$ and CE is apparent in Fig. 3 for *Glycine max* (symbol Gl) where temperature of leaves of well watered plants was changed (Harley *et al.*, 1984) and for *Larrea divaricata* (symbol La) where degree of water stress changed (Mooney *et al.*, 1977). The increase in spread of data points with increase in $P_{saturation}$, while possibly due to measurement errors and differences in methods used by various investigators, may also indicate differences in photosynthetic metabolism between species. If such differences exist, it suggests possibly that different species may invest relatively more or less nitrogen and protein in carboxylase for CO_2 fixation or in capacity for RuBP regeneration. This possibility and reasons for it must be investigated further. To further illustrative variation in NP_{pot}, a hypothetical scheme for change in CE of leaves of a sclerophyll shrub during an annual cycle is proposed in Fig. 4. The figure is based on data obtained with leaves of *Quercus coccifera* and *Quercus suber* and we include an approximate quantitative scale. Since at light saturation internal CO_2 pressure of leaves is rather constant (Wong *et al.*, 1979; Evans, 1983, approximately 225 μ bar for *Quercus suber* with 350 μ bar in the external air - Tenhunen *et al.*, 1984), a description of seasonal change in CE allows estimation of the annual pattern of change in net photosynthesis rates. Such an estimate does not, however, include shift in the leaf CO_2 compensation point. Shown in Fig. 4 are values for CE which might be obtained during the morning on clear days when ligt saturation is first reached (solid line) and under the warmest and driest conditions at midday (dashed line). Since CE is assessed only at saturating light intensities, we have defined a CO_2 response curve parameter called marginal CO_2 fixation, MF, valid during both periods of light limitation and light saturation. With marginal CO_2 fixation we refer to the slope of the NP versus P_i response curve (see Fig. 1) estimated from determinations of NP as P_i varies between 150 and 300 μbar CO_2, i. e. in the region relevant to leaf function in normal air, and with any constant light intensity and temperature. Shown in the upper part of Fig. 4 are typical time courses for MF during different seasons and under clear weather conditions. The midday point of each time course, indicated as 12 o'clock, is positioned at that point in the season when the daily time course is expected.

Figure 4. Hypothetical scheme illustrating change in carboxylation efficiency (CE) during an annual cycle and in marginal CO_2 fixation (MF) on typical clear days during different seasons for leaves of a sclerophyll shrub growing under Mediterranean climate conditions. Solid line for CE is the value as light saturation is first reached in the morning; dashed line for CE is the value at midday. Daily courses for MF have been inserted so that the middle of the day (indicated as 12 o'clock) is positioned at that point in the season when the daily time course is expected. The dashed line time course during February indicates response to low temperature.



Carboxylation efficiency of leaves is highest in the spring, but CE decreases as leaves mature and as water stress increases during June, July and August. In the species under consideration, the value of CE is depressed at midday when midday temperatures exceed 28 °C and the daily pattern in MF has two optima (Tenhunen *et al.*, 1984). Fall rains allow recovery of water potentials and increase in CE. When midday temperatures remain below 28 °C, the daily pattern in MF is again characterized by a single peak. The value of CE is maximal at midday when temperatures are highest. Levels for CE equal to those found in early spring are no longer achieved. Decreases in temperature during the winter months reduce CE and cold stress effects can cause severe reduction over short periods. Gradual increase in CE occurs during March and April, after which a new flush of growth occurs and the leaves are replaced.

Figure 5. *Specific leaf weight and CO_2 saturated photosynthesis rate ($P_{saturation}$ assessed at 24 °C and light saturation) of leaves located at different positions with respect to canopy depth. The top of the canopy is indicated as 0 cm depth. Measurements were conducted in January 1983 at Quinta São Pedro, Sobreda, Portugal.*



The photosynthetic potential of leaves is also influenced by developmental effects due to leaf age and due to position in the canopy. Potential photosynthesis rates of leaves of *Quercus coccifera* appear to decrease due to aging as leaves mature in the late spring. After recovery of water potentials in the fall, however, change in *Quercus coccifera* potential photosynthesis rates observed between September and the following April could be accounted for by change in temperature. The work of Field (1981) demonstrated that age effects may be much stronger in other mediterranean shrub species, especially in species with shorter leaf duration. Change in NP_{pot} of leaves of *Quercus coccifera* due to degree of shading during growth is substantial. As shown in Fig. 5, specific leaf weight decreases with depth in the canopy from approximately 170 g m^{-2} to 120 g m^{-2} at 30 cm depth where the innermost leaves occur. The decrease is paralleled by a proportional decrease in leaf photosynthetic capacity measured at optimal temperature, light saturation and CO_2 saturation.

EFFECTIVENESS FACTOR FOR CANOPY PHOTOSYNTHESIS (CAN)

The actual rate of carbon fixation by a plant canopy equals the sum of the CO_2 fixation rates of all individual leaves. As discussed above, individual NP depends on the leaf capacity $P_{saturation}$, the associated MF value for prevailing light intensity and temperature at a particular canopy position. It depends further on stomatal response which determines leaf internal CO_2 partial pressure interactively with photosynthesis, and thus the operating point on the CO_2 response curve. An estimate of total canopy CO_2 fixation may be calculated with the aid of 1) a model of leaf photosynthesis rate as a function of light intensity, leaf temperature, and internal CO_2 pressure for leaves at all canopy depths, 2) a model canopy light interception and microclimate, which describes light and temperature conditions to which leaves are exposed, and 3) a model for leaf conductance as a function of prevailing light intensity, leaf temperature, air humidity, and leaf water potential for leaves at all canopy depths. The models must account for seasonal changes in plant response as, for example, has been discussed with respect to NP_{pot}, in addition to changes in LAI. We have begun to develop such models for *Quercus coccifera* and describe here the types of input information required.

The *Quercus coccifera* canopy that we have considered is approximately 2.7 meters in height with the leaves densely packed in the uppermost 30 cm (Research Station Quinta São Pedro, Sobreda, Portugal). The leaves of *Quercus coccifera* are quite variable; however, the size of most leaves in the particular canopy studied are between 4 and 7 cm^2. Extreme sun leaves are smaller and a few exceptionally large leaves occur at the most shaded canopy level. Leaf area index is maintained around 4. The distribution of leaf area with respect to canopy depth is shown in Fig. 6. Due to the dense packing of leaves, considerable light attenuation and shading occurs between 6 and 12 cm depth (approximately 50 % of leaves are shaded between 6 and 9 cm and 80 % between 9 and 12 cm at noon on a sunny winter day). Also shown in Fig. 6 is the average leaf angle in five canopy layers. Outermost leaves are more vertical (60 degrees from the horizontal) and leaves at the lowest level are oriented more horizontally (28 degrees from horizontal). Similar leaf orientation was reported for sclerophyll shrubs of California and Chile by Kummerow *et al.* (1981). With respect to leaf angle and leaf area index, canopy design of *Quercus coccifera* is similar to that found for a variety of agricultural crop species (Loomis 1983).

This information on canopy characteristics has been used to calculate interception and attenuation of radiation, and the average light intensity on sunlit and shaded leaves in different canopy layers, according to equations derived by Duncan *et al.* (1967, our application of the Duncan-equations provides a model similar to that discussed as case 2 by Norman, 1980). Canopy photosynthesis is estimated by determining the beam and diffuse light flux densities in layers distributed throughout the depth of the canopy, by calculating the light incident on sunlit and shaded leaves separately, assuming a random azimuth angle distribution for the leaves in each layer, and then evaluating photosynthesis in each layer as the sum of sunlit and shaded photosynthesis rates weighted by their respective areas.

In Fig. 7 the light climate of leaves in the canopy is shown as simulated for a sunny winter day. The leaf area (as LAI) exposed to different intensities of photosynthetically active radiation (PAR) at two times of day is indicated. The two leaf classes included in this model, i. e. those which intercept direct beam radiation and those exposed to average shade light (penumbral effects have not yet been considered) are readily recognized from the clustering of bars at high and low light intensities. The simulation at 9 o'clock illustrates the situation found early and late in the day, while simulation at 11 o'clock repre-

Figure 6. Leaf area index and average leaf angle from the horizontal plane in a stand of Quercus coccifera *at Quinta São Pedro, Sobreda, Portugal. Data shown for five canopy layers, 6 cm thick. The top of the canopy is indicated as 0 cm depth. Measurements were conducted in September 1981.*

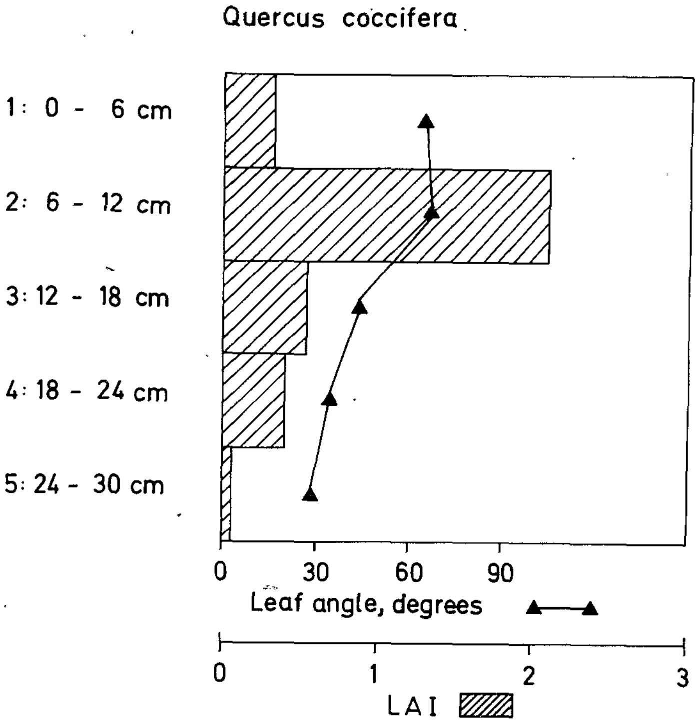


Figure 7. Simulated light climate of leaves in the Quercus coccifera canopy discussed in the text. Leaf area index (LAI) according to the simulation which is exposed to different light intensities during the morning and at midday is shown.

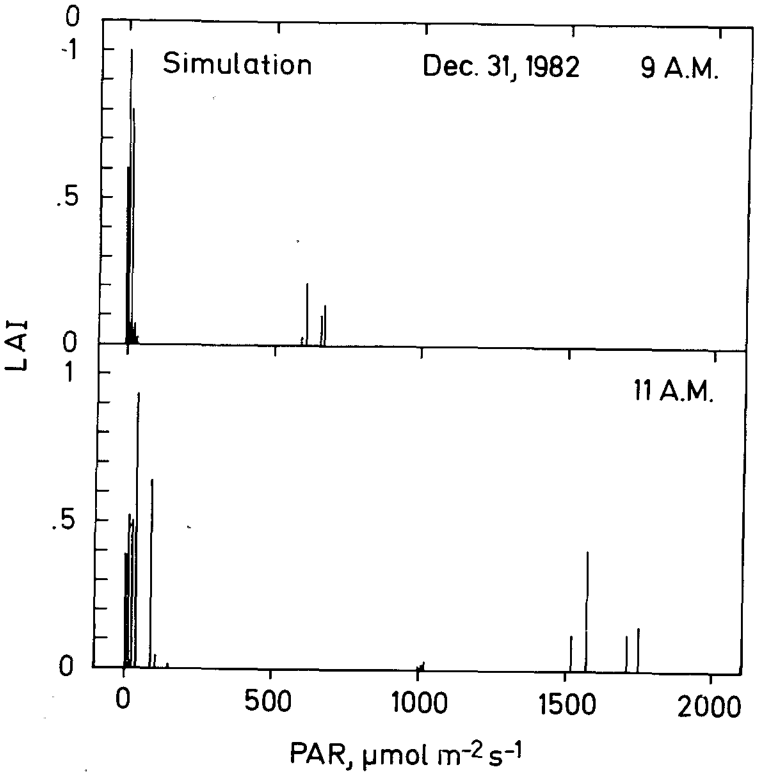


Figure 8. Daily time courses of transpiration rate (Tr), net photosynthesis rate (NP), and leaf conductance (G) measured for leaves of Quercus coccifera *at 0, 10 and 20 cm canopy depth on a clear winter day. Top of the canopy is indicated as 0 cm depth. Information on leaf microclimate is given in Table 3. Measurements were conducted at Quinta São Pedro, Sobreda, Portugal.*

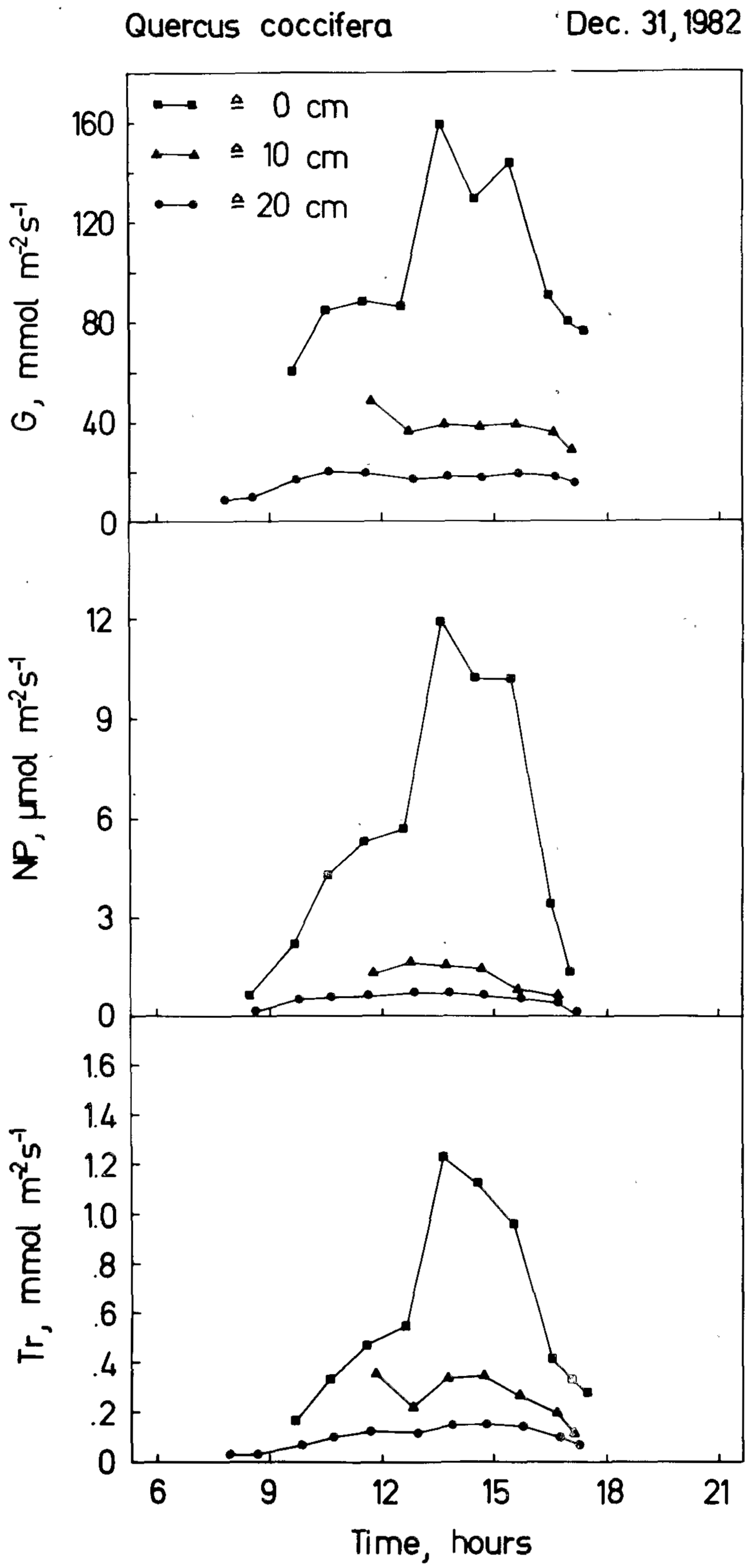
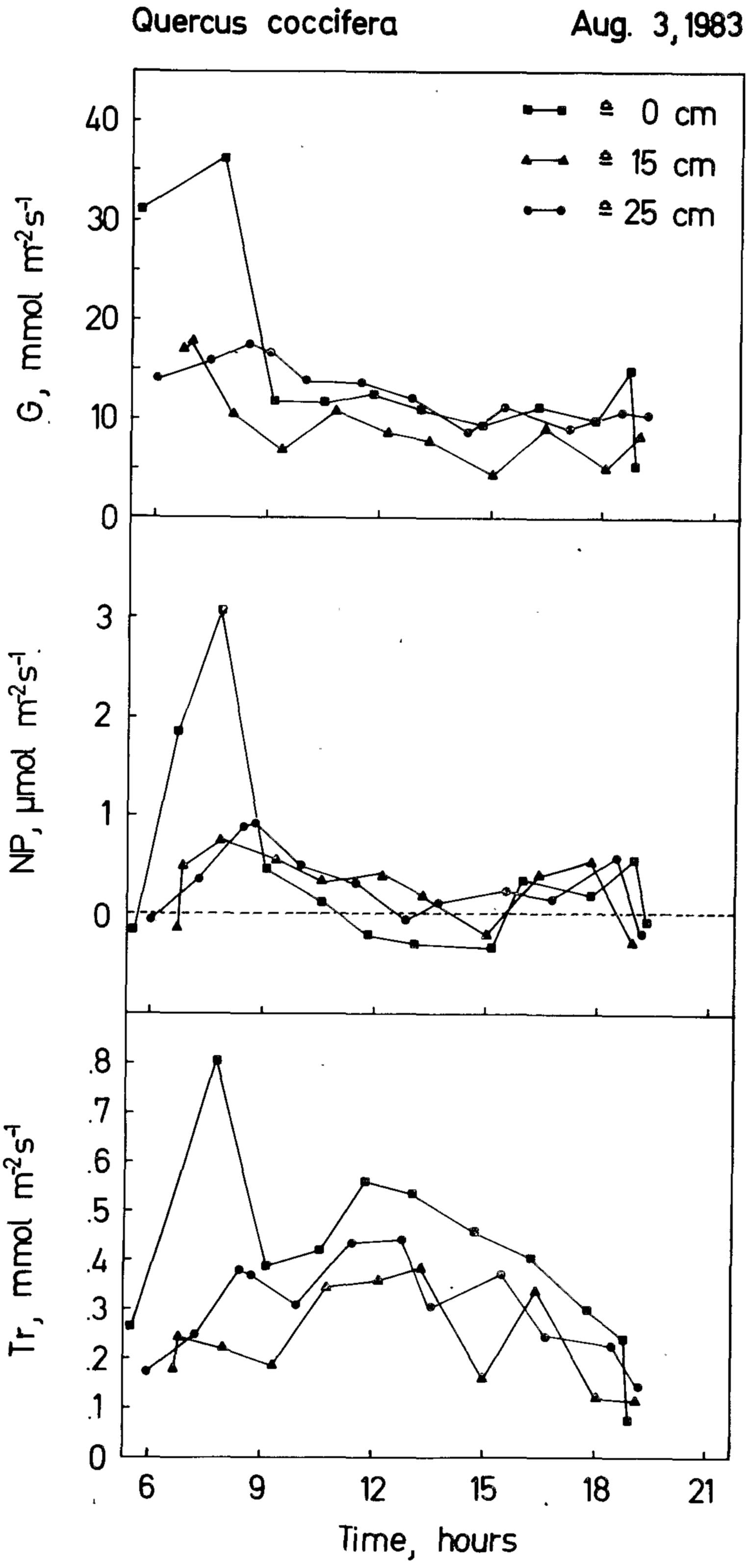


Figure 9. Daily time courses of transpiration rate (Tr), net photosynthesis rate (NP), and leaf conductance (C) measured for leaves of Quercus coccifera *at 0, 15 and 25 cm canopy depth on a clear day during the summer drought. Top of the canopy is indicated as 0 cm depth. Information on leaf microclimate is given in Table 3. Measurements were conducted at Quinta São Pedro, Sobreda, Portugal.*



sents the general situation found throughout the midday period. At 9 o'clock, a total LAI of greater than 0.45 receives approximately 500 μmol m^{-2} s^{-1} PAR (approximate light saturation), while LAI 2.5 remains in deep shade which is, nevertheless, adequate to support positive levels of photosynthesis in all leaves. At 11 o'clock, light intensities reach the daily maximum with LAI 0.8 experiencing PAR greater than 1500 μmol m^{-2} s^{-1} and LAI 3.2 experiencing PAR between 0 and 200 μmol m^{-2} s^{-1}. Most of the leaves experiencing high light intensity are located between 0 and 12 canopy depth. The small bars at approximately 1000 μmol m^{-2} s^{-1} PAR represent small amounts of leaf area lit by direct sun in lower canopy levels. The leaf temperature component of leaf microclimate is established through an iterative solution of the leaf layer energy budgets, using submodel descriptions of stomatal response to determine transpiration rates and transpirational cooling.

Models of leaf photosynthesis and stomatal conductance which accurately simulate leaf function in different canopy levels must be based on a sound understanding of leaf gas exchange behavior in response to environment and coordination of leaf function among different leaf layers within the plant stand. Appropriate gas exchange data often have not been obtained, due to the technical problems which arise when leaves are surrounded by other leaves and twigs. Recently developed CO_2 porometer methods, overcome some of these difficulties and allow us to collect the needed information. For *Quercus coccifera* leaves located at different canopy depths (0, 10 and 20 cm), representative measured net photosynthesis and transpiration rates as well as values of leaf conductance for water vapor are shown in Fig. 8. Data are from Dec. 31, 1982, the winter day for which climate of the canopy was described in Fig. 7 The response of leaves at 0, 15 and 25 cm depth are shown for a late summer day in Fig. 9. Examination of Figs. 7 and 8 indicates that due to the amplification resulting from leaf area distribution, perhaps as much as three fourths of canopy photosynthesis occurs in the first twelve cm during the winter. During other seasons, relative contributions change due to change in radiation incident on the canopy and due to change in leaf response.

Data shown for leaf resonse in Table 3 and in Fig. 9 demonstrate that during drought conditions on August 3, 1983, maxima in photosynthesis were observed in both sun and shade leaves in the early morning and late afternoon. Although sun leaves fixed more CO_2 than shade leaves, the relative differences between sun and shade leaves were much smaller under drought stress conditions than in winter. High light intensity was only of advantage during the early morning; the afternoon maximum in CO_2 fixation occurred at low light intensity and was equal in both sun and shade leaves. Much further experimental work is required to define seasonal influences on leaf function in different canopy levels and to complete the submodels for photosynthesis and stomatal function needed to assess total canopy CO_2 fixation. Under moderate environmental conditions, a comparison of relative distribution of CO_2 fixation in different levels of the canopy may show similarities between *Quercus coccifera* and agricultural crop species (see for example Angus and Wilson 1976). It will be of particular interest to determine the distribution of CO_2 uptake and water use within the canopy of *Quercus coccifera* during summer drought.

LEAF AREA INDEX (LAI)

A leaf area index of approximately 4 results in "complete cover" or nearly complete light interception by a plant canopy. Such leaf area indices are common for canopies of agricultural crops. Even higher leaf area indices increase growth of crops when leaves are steeply inclined, but the greater leaf area index can only be attained when large amounts of fertilizers are used (Loeomis, 1983). The rates of photosynthesis and the actual leaf area index achieved in mature stands of sclerophyll shrub species are limited by water and nitrogen availability and the investment required to obtain increments in these resources (Miller, 1981). Despite nutrient and water limitations, sclerophyll shrub species commonly achieve complete cover (LAI 4), the result being that they remain competitive with regard to the light resource. Partitioning of carbon to rapidly increase leaf area during early stages of growth and community development can strongly determine the standing biomass, and thus the dominance, of a species within mature vegetation (Potter and Jones, 1977; Spitters and Aerts, 1983; Miller, 1981).

Leaf area indices of *Quercus coccifera* are comparable with those reported for other sclerophyll shrubs (Kummerow *et al.*, 1981). Higher LAI values have been suggested to result at locations where lower investment in root materials is possible (Ehleringer and Mooney, 1983). Rambal (1984) reported an LAI value of 2.5 for the extensive *Quercus coccifera* garrigue near Montpellier, France. The value of 4 obtained at our study site near Lisbon suggests an influence of the relatively high precipitation occurring at this

Table 3. Representative gas exchange rates and conductances of sun (0 cm canopy depth) and shade leaves (20-25 cm canopy depth) of Quercus coccifera *on selected days shown in figures 8 and 9.*

		DEC 31, 1982	AUG 3, 1983		
TIME:		**13:45**	**8:00**	**12:00**	**18:45**
Light	sun (0 cm)	1340	1340	2000	100
μmol m^{-2} s^{-1}	shade (20-25 cm)	30	100	200	50
T_L	sun	16.9	23.6	36.6	24.1
°C	shade	16.0	21.7	35.3	26.1
G	sun	158	36	12	15
mmol m^{-2} s^{-1}	shade	18	17	11*	11*
Tr	sun	1.23	0.8	0.5	0.24
mmol m^{-2} s^{-1}	shade	0.14	0.38	0.44	0.22
NP	sun	11.9	3.06	—	0.55
μmol m^{-2} s^{-1}	shade	0.9	0.87	—	0.57
T/P	sun	103	263	—	437
mol mol^{-1}	shade	208	430	—	390

* The measurable cuticular conductance of these leaves is approximately 5 mmol m^{-2} s^{-1}.

northerly extreme of distribution of the Mediterranean zone vegetation in Portugal. In particularly favorable and protected sites in the Serra da Arrabida, large trees of *Quercus coccifera* are found, suggesting that the species may be capable of forming forest stands (Catarino *et al.*, 1982) that might be similar to the *Quercus ilex* forests of Spain and France (Lossaint, 1973; Eckardt *et al.*, 1977). In those evergreen *Quercus ilex* forests, leaf area indices reach 4.5.

Seasonal patterns in water and nitrogen availability influence leaf duration and plant phenological response (Miller 1981, 1983). Seasonal changes in LAI of mediterranean type shrubs have been discussed by Specht and Moll (1983). Two major events occur that affect LAI in uniform stands of sclerophyll shrubs. Spring growth leads to an increase in LAI at that time when photosynthetic rates are highest. The two factors combined result in a maximum in carbon input during April and May in mediterranean areas of the northern hemisphere. Subsequently carbon input decreases with the onset of summer drought. Shedding of leaves and decrease in LAI is correlated with decrease in pre-dawn xylem water potential (Schlesinger and Gill, 1980) as is the decrease in photosynthesis of individual leaves (Fig. 4). During the remainder of the year, LAI remains more or less constant.

RESOURCE SUPPORT FACTOR (SUP)

The proportion of photosynthate respired in maintenance and in turnover of resource supply organs, referred to as SUP, is a measure of the cost involved in supporting the photosynthetic system. This cost is in general relatively high for species adapted to water stress and nutrient limitations when compared to agricultural crop plants because the former have proportionally greater masses of non-green respiring tissues. In a crop such as wheat, leaf material makes up 40 to 70 % of the standing biomass during vegetative growth, the proportion decreasing as the stand develops. Root systems make up about 10 % of the stand-

Table 4. Examples of biomass distribution and portion of annual photosynthate respired in perennial shrubs.

	% of total biomass in:			% of annual photosynthate respired
	leaves	stems	roots	
Mediterranean shrubs				
California:				
Arctostaphylos glauca*	14	57	29	64
Adenostoma fasciculatum*	9	57	34	65
Ceanothus greggii*	8	55	37	65
Rhus ovata*	11	54	35	61
Chile:				
Colliguaya odorifera*	15	59	26	63
Lithraea caustica*	21	26	53	55
Satureja gilliesii*	15	66	19	60
Trevoa trinervis*	6	55	39	59
Desert shrubs				
Utah:				
Atriplex confertifolia[1]	4	15	81	19
Ceratoides lanata[1]	2	11	87	36

* Oechel and Lawrence (1981); respiration cost simulated with models CAPS and MEDECS.

[1] Caldwell *et al.* (1977).

ing biomass (McNeal *et al.*, 1966; Fischer, 1975). Well established perennial shrubs, of arid mediterranean regions may have 5 to 20 % of standing biomass in leaves and 20 to 55 % of biomass in roots (Table 4). In the case of desert shrubs, more than 80 % of the standing biomass may be maintained as root material (Caldwell *et al.*, 1977).

The proportional amount of below-ground biomass maintained by *Quercus coccifera* is similar to that found for other related mediterranean shrub species. Rapp and Lossaint (1981) estimated a root to shoot biomass ratio for *Quercus coccifera* in the garrigue formation in southern France of approximately two. Rambal (1984) has reported even higher values for *Quercus coccifera* of between 4 and 6. The large proportion of root material may in this case be a consequence of frequent burning and resultant resprouting. In any case, relatively little leaf material is present to support the, in comparison, large amount of non-green biomass. A similarly large ratio of root material was reported by Hellmers *et al.* (1955) for oak species native to California

Table 5. Distribution of above-ground biomass per m² ground surface in Quercus coccifera *stand sampled at Quinta São Pedro, Research Station, Sobreda, Portugal in September 1981.*

Height of Layer	Leaves	Twigs and Branches							total dry wt.	Total % above-ground biomass in layer
		0-3 mm dia.		3-6 mm dia.		6-12 mm dia		12-25 mm dia		
(cm)	dry wt. (g)	dry wt. (g)	length (m)	dry wt. (g)	length (m)	dry wt. (g)	length (m)	dry wt. (g)	(g)	
250-265	289.	144.	61.8	15.	1.1	—	—	—	448.	8.
225-250	299.	467.	201.0	168.	12.4	97.	2.7	7.	1038.	19.
200-225	16.	179.	77.1	209.	15.5	313.	8.6	36.	753.	14.
175-200		72.	31.1	102.	7.6	173.	4.8	185.	532.	10.
150-175		40.	17.1	26.	1.9	112.	3.1	244.	422.	7.
125-150		12.	4.7	5.	0.3	66.	1.8	330.	413.	7.
100-125		3.	1.2	—	—	—	—	316.	319.	6.
75-100		3.	1.2	2.	.1	24.	0.7	316.	345.	6.
50-75								436.	436.	8.
25-50								441.	441.	8.
0-25								395.	395.	7.
Total dry wt. (g)	604.	920.	395.2	527.	38.9	785.	21.7	2706.	5542.	
Total above-ground	11.	17.	—	9.	—	14.	—	49.		

(root to shoot ratio of *Quercus dumosa* 2.5) and by Davis and Pase (1977) for oaks of Arizona (root to shoot ratio of *Quercus turbinella* of 3.2). That the large investment in root material contributes greatly to the success of *Quercus coccifera* is evidenced by its widespread occurrence and its frequently dominant position within the scrub communities characteristic of the European Mediterranean region. There, due to its deep rooting and resprouting ability, *Quercus coccifera* is able to withstand fire, grazing, and disturbance by man in addition to extreme drought stress.

A large part of above-ground biomass in *Quercus coccifera* is situated in upper levels of the canopy (Table 5). In the uppermost meter, canopy weight per unit volume was approximately 2600 g m^{-3}, as compared to 2018 g m^{-3} for *Quercus dumosa* and 3312 g m^{-3} for *Quercus agrifolia* reported by Kummerow *et al.* (1981). The large mass of small twig material present is a sizable drain on fixed carbon in these shrub species (Oechel and Lawrence, 1981; Jarvis and Leverenz, 1983). At lower levels, the stem supporting materials are equally distributed in thicker main branches and stems. The California oaks had 15 and 9 % respectively of the above ground biomass in leaf material, while *Quercus coccifera* in Portugal had approximately 11 % in leaf material. Rapp and Lossaint (1981) reported that approximately 18 % of the above ground biomass of *Quercus coccifera* was in leaf material.

A large portion of fixed carbon is necessarily budgeted to continually replace organs supplying resources, for example, fine roots (Caldwell *et al.,* 1977). Estimates of root system respiration are vey difficult numbers to derive. Caldwell *et al.* calculated the total amount of carbon utilized in growth of new shoots and roots of desert shrubs, subtracted this from total carbon fixation, and estimated that 15 to 40 % of annual carbon gain was utilized in respiratory processes (see Table 4). In simulation studies, it was estimated that 55 to 65 % of annual carbon fixation was used by mediterranean shrub species in maintenance and growth respiration (Oechel and Lawrence, 1981). All of these estimates include growth respiration for increment in plant biomass as well as for turnover of plant parts and are not strictly estimates of the factor SUP.

CONCLUSION

Productivity rates of those species naturally occurring in a particular habitat have been suggested to indicate the potential productivity of the site. However, the reason a measured level of productivity is found can only be established through careful study of site inhabitants in an attempt to determine the manner in which physiological and structural adaptations allow effective resource use. Primary production of plants depends on the photosynthetic potential of leaves, arrangement of leaves in the plant canopy, the amount of leaf area which may efficiently be supplied with water and nutrients, and the cost to the plant of acquiring these resources. Since production depends simultaneously on many attributes of the whole plant, efforts have been made to construct physiologically based models of plant growth which can evaluate the significance to production of change in any particular factor, cf. Jones *et al.* (1980), Reynolds *et al.* (1980), Miller (1981), and Penning de Vries (1983). Again, such models depend on accurate assumptions concerning plant response, especially under stress conditions. These assumptions must be altered as new information is gathered and new insight is obtained. In part, this depends on the development of new techniques and methods for gathering and analyzing information on plant physiological response under field conditions. The research described in this paper contributes to this ongoing effort.

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