Effects of Irradiance on Growth, Photosynthesis, and Water Use Efficiency of Seedlings of the Chaparral Shrub, Ceanothus megacarpus

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Summary. The effects of irradiance during growth on biomass allocation, growth rates, leaf chlorophyll and protein contents, and on gas exchange responses to irradiance and CO2 partial pressures of the evergreen, sclerophyllous, chaparral shrub, Ceanothus megacarpus were determined. Plants were grown at 4 irradiances for the growth experiments, 8, 17, 25, 41 nE cm-2 sec-1, and at 2 irradiances, 9 and 50 nE cm-2 sec-1, for the other comparisons.

At higher irradiances root/shoot ratios were somewhat greater and specific leaf weights were much greater, while leaf area ratios were much lower and leaf weight ratios were slightly lower than at lower irradiances. Relative growth rates increased with increasing irradiance up to 25 nE cm-2 sec-1 and then leveled off, while unit leaf area rates increased steeply and unit leaf weight rates increased more gradually up to the highest growth irradiance.

Leaves grown at 9 nE cm-2 sec-1 had less total chlorophyll per unit leaf area and more per unit leaf weight than those grown at 50 nE cm-2 sec-1. In a reverse of what is commonly found, low irradiance grown leaves had significantly higher chlorophyll a/b than high irradiance grown leaves. High irradiance grown leaves had much more total soluble protein per unit leaf area and per unit dry weight, and they had much higher soluble protein/chlorophyll than low irradiance grown leaves.

High irradiance grown leaves had higher rates of respiration in very dim light, required higher irradiances for photosynthetic saturation and had higher irradiance saturated rates of photosynthesis than low irradiance grown leaves. CO2 compensation irradiances for leaves of both treatments were very low, <5 nE cm-2 sec-1. Leaves grown under low and those grown under high irradiances reached 95% of their saturated photosynthetic rates at 65 and 85 nE cm-2 sec-1, respectively. Irradiance saturated rates of photosynthesis were high compared to other chaparral shrubs, 1.3 for low and 1.9 nmol CO2 cm-2 sec-1 for high irradiance grown leaves. A very unusual finding was that leaf conductances to H2O were significantly lower in the high irradiance grown leaves than in the low irradiance grown leaves. This, plus the differences in photosynthetic rates, resulted in higher water use efficiencies by the high irradiance grown leaves. High irradiance grown leaves had higher rates of photosynthesis at any particular intercellular CO2 partial pressure and also responded more steeply to increasing CO2 partial pressure than did low irradiance grown leaves. Leaves from both treatments showed reduced photosynthetic capability after being subjected to low CO2 partial pressures (~100 µbars) under high irradiances. This treatment was more detrimental to leaves grown under low irradiances.

The ecological implications of these findings are discussed in terms of chaparral shrub community structure. We suggest that light availability may be an important determinant of chaparral community structure through its effects on water use efficiencies rather than on net carbon gain.

Introduction

It is widely recognized that primary productivity of ecosystems in Mediterranean-type climates is largely a function of growing season length as determined by water availability (Bauer 1936; Mooney et al. 1975; Miller and Poole 1979; Radojevich and Conard 1980; Schlesinger et al. 1982). Recently, however, it has become apparent that light availability may have important effects on the structure and function of the chaparral communities of California. McPherson and Muller (1967) found strong evidence for the elimination of a chaparral shrub, Salvia leucophylla Greene, by another, Ceanothus cuneatus (Hook.) Nutt., through competition for light. In simulations using data on Heteromeles arbutifolia M. Roem., Miller and Mooney (1974) have demonstrated the possible importance to production and water use efficiency (WUE) of the effects of canopy structure on light availability and leaf temperature. Miller and Poole (1979) have suggested that leaf area in chaparral communities develops in relation to light during periods of high soil moisture. Schlesinger and Gill (1980) have described massive death of branches beneath canopies of dense, evenaged, pure stands of Ceanothus megacarpus Nott. and have suggested light availability may be responsible. Thus, light availability may be a strong determinant of the vertical aspects of chaparral community structure, and, by affecting leaf area, it could also be affecting movements of water and nutrients (Gray 1981) as well as energy flux (Oechel and Mustafa 1979) through these ecosystems.

While there have been measurements of photosynthetic-irradiance responses of some chaparral shrubs (Harrison 1971; Oechel and Lawrence 1979; Oechel et al. 1981), the only study to date of growth responses to irradiance or of the effects of irradiance during growth on gas exchange...
characteristics of chaparral shrubs was on a successional, semi-drought-deciduous shrub of central and northern California (Gulmon and Chu 1981). The purpose of the present study was to investigate the effects of irradiances during growth on growth rates, biomass allocations, leaf thicknesses, leaf gas exchange-irradiance and CO$_2$ responses, and leaf chlorophyll and protein contents of a dominant, evergreen, sclerophyllous, chaparral shrub, *C. megacarpus*.

**Materials and Methods**

**Plant Materials and Growth Conditions**

Newly discharged seeds of *C. megacarpus* were collected from a pure stand at an elevation of about 450 m on the southern slope of the Santa Ynez Mountains, Santa Barbara County, California. To induce germination the seeds were dipped into boiling water for 1 min and then stored on wet filter paper in petri dishes at 2-5°C for two weeks. Seeds ready to germinate became swollen and were planted, one per 15-cm diameter pot, in a 50:50 mixture of sand and vermiculite. Eighty to ninety percent of the seeds germinated. With the appearance of the first true leaves, 20 days after planting, the plants were moved from a greenhouse into two Percival RGW-108-132 growth chambers. Air temperatures in both chambers were maintained at 25°C day/15°C night with 14 h days and relative humidity varying between 35 and 55%. Plants were watered every 2-3 days and fertilized with full strength Hoaglands solution every week. Two irradiance levels were maintained in each chamber with cheesecloth netting over half of the plants. Irradiances, monitored throughout this experiment with a Licor LI-185 quantum sensor (400-700 nm), averaged: 8±2.3; 17±4.5; 25±4.9; and 41±5.8 nE cm$^{-2}$ sec$^{-1}$. For the gas exchange measurements and chlorophyll and protein analyses a second batch of plants was grown under identical conditions during the gas exchange experiments are listed in Table 1. In the irradiance response experiments measurements were first made at an intermediate irradiance, then down in steps to a very low irradiance, back up to the original intermediate irradiance, and then up in steps to the high irradiances. The CO$_2$ response experiments were run both by starting at high CO$_2$ partial pressures and going down in steps and by starting at low CO$_2$ and going up (see Results).

**Harvests and Harvest Data Treatments**

Seedlings in 160 pots were initially divided into 10 size classes, and four pots of each class were randomly assigned to each irradiance treatment. Four harvests were made, the first 20 days after planting and the others 15, 43 and 62 days later. At each harvest, one plant was randomly chosen from each of the size classes in each irradiance treatment. Plants were divided into leaves, stems, and roots, dried at 80°C for 2 days and weighed. Leaf areas were measured from shadows produced on Kodak photographic proof paper. Growth rate indices were calculated for pairs of plants composed of plants in the same size class from 2 successive harvests. These were then averaged for all 10 size classes. All growth analysis calculations followed the formulae presented by Evans (1972).

**Chlorophyll and Protein Analyses**

Chlorophyll was extracted from the youngest mature leaves by grinding leaf disks of known area with a hand homogenizer in cold 90% acetone, 10% water plus a bit of magnesium carbonate for chlorophyll stabilization. The homogenates were centrifuged at 12,100×g for 20 min in a 2RB Sorvall centrifuge, and absorbances of the supernatants were measured at 664 and 647 nm in a Cary 15 dual beam spectrophotometer. From these absorbances total chlorophyll and a/b were calculated following the formulae of Jeffrey and Humphrey (1975).

Soluble protein was extracted from the youngest mature leaves by grinding leaf disks of known area with a hand homogenizer in cold 0.05 M tris-maleic buffer adjusted to a pH of 7.2 with NaOH (Jensen 1962). The homogenates were centrifuged at 17,300×g for 15 min. Concentrations of soluble protein in aliquots (three per sample) of the supernatant were measured using the standard Bio-Rad Protein Assay procedure (Bio-Rad Laboratories, Richmond, California). This procedure involves the binding of a dye, Coomassie Brilliant Blue G-250, to the protein, producing a shift in maximum absorbance of the dye from 465 to 595 nm (Bradford 1976). The changes in absorbance at 595 nm upon mixing the dye reagent with the extracts were measured in a Varian 634 dual beam spectrophotometer and were then compared with those produced by known concentrations of Bio-Rad Protein Standard (lyophilized bovine gamma globulin) to estimate the soluble protein concentrations.

**Gas Exchange Apparatus and Experimental Conditions**

The gas exchange apparatus used in this study was the same open flow system as described by Mahall et al. (1981). The major components included: a Beckman 865 differential infrared gas analyzer; a Wösthoff G27/3F high capacity gas mixing pump; two Weather Measure HMP 14-U relative humidity sensors; a Validyne MP 45-1 electronic pressure transducing flow meter; and a Digitec 1268 Data Logger. During experiments irradiance, provided by a Sylvania 1000 watt metal arc lamp, was filtered through water and various numbers of spectrally neutral screens, and it was continuously monitored in the leaf chamber with a silicon photocell calibrated against a Licor LI-185 quantum sensor. The leaf chamber, similar to that described by Björkman and Holmgren (1963), was stainless steel with a internal volume of 245 ml (10.2 cm diameter, 3 cm high).

Measurements were made on single, attached leaves chosen from among the youngest mature leaves on the plants. Areas of the measured leaves grown under low irradiance averaged 3.78±1.13 cm$^2$, and those grown under high light averaged 2.82±0.31 cm$^2$. The environmental conditions during the gas exchange experiments are listed in Table 1. In the irradiance response experiments measurements were first made at an intermediate irradiance, then down in steps to a very low irradiance, back up to the original intermediate irradiance, and then up in steps to the high irradiances. The CO$_2$ response experiments were run both by starting at high CO$_2$ partial pressures and going down in steps and by starting at low CO$_2$ and going up (see Results).

**Results**

**Growth Analyses**

Root/shoot (root weight per unit shoot weight, R/S) declined by about 70% during growth under all irradiances between harvests 1 and 4 (Table 2). This decline was nearly linear except between harvests 3 and 4 when the rate of decline decreased. Averages of data from all harvests indi-