

The Acclimation Ability of
The Shale Barren Endemic Eriogonum alleni
to Light and Heat.

by

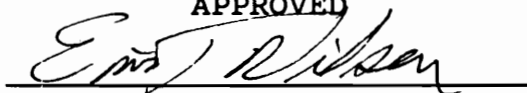
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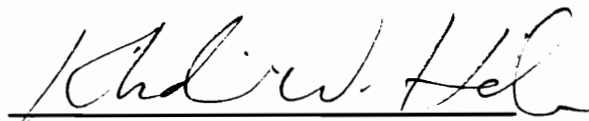
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ABSTRACT

Shale barrens are unique habitats located throughout the southern Appalachians. They are characterized by a south or south west aspect, a steep slope, and an exposed rocky surface (Platt, 1951). They have a high total irradiance and can experience temperatures higher than the surrounding deciduous forest.

A variety of plant species, several of which are rare or endangered, are endemic to the shale barren habitat. One reason proposed for their endemism is that the plants are obligate heliophytes (Keener, 1983). The purpose of this dissertation is to examine the acclimation ability of the shale barren endemic Eriogonum alleni to shade and high temperature.

The woody vegetation of the shale barren is dominated by Quercus prinus, Q. ilicifolia, Pinus virginiana, and Junniperus virginiana. This composition is somewhat different from other regional south facing slopes which are dominated by

Pinus rigida, additional Quercus species and understory species such as Kalmia latifolia.

In order to assess shade acclimation ability, E. alleni was shaded in the field for two consecutive growing seasons at 3 levels: full sun, 47% shade and 73% shade. Photosynthesis declined for both the moderately and heavily shaded treatments, while internal carbon dioxide concentrations increased. Stomatal conductance declined for shaded plants. Additionally, plants maintained in 73% shade did not flower, and died during the second growing season. Light response curves were obtained for plants maintained in the garden and greenhouse and receiving either full light or 73% shade. E. alleni showed no acclimation to shade. There was no increase in quantum yield, and no differences in light saturation levels or light compensation points between treatments.

To examine heat acclimation, plants were maintained in growth chambers at either control (25°C day/18°C night) or elevated (37°C day/28°C night) temperatures. Acclimation to elevated temperatures was determined by examining electrolyte leakage and by measuring photosynthetic response.

Electrolyte leakage studies revealed no increase in membrane integrity at elevated temperatures. Plants maintained at higher temperatures in fact tended to have

membranes more susceptible to ion leakage. Maximum photosynthetic rates were considerably lower for plants maintained at elevated temperatures as were the temperatures where net photosynthesis reached zero.

E. alleni is clearly an obligate heliophyte, but is unable to withstand prolonged exposure to heat. Although this study answers in part why E. alleni occurs on shale barrens, it does not address why E. alleni is restricted to the shale barren habitat. Future work addressing the distribution pattern of this species and its competitive ability would be useful to further explain its endemic life history.

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CHAPTER 1: INTRODUCTION TO ENDEMISM AND SHALE BARRENS

Endemism is the quality of being restricted in geographic location (Stace, 1980). An endemic species is one which is considered characteristic of a particular location. In a sense, then, all plants are endemic; however, endemism has overtime acquired a context whereby it is used to refer to species which are restricted in distribution and are also frequently rare or endangered.

What are the causes of endemism? Although botanists are intrigued by the rare plants they encounter, determining the reason for a taxon's rarity is not an easy task. The ancestry of a species, while perhaps helpful in determining relationships between the different taxa of a group, is not always useful as a causal mechanism to explain a species restriction. A species which is narrowly distributed may either be a relict or a species on the verge of expansion (Richardson, 1978).

Isolation is often touted as one of the driving forces for speciation. Islands perhaps provide the best example of this; by virtue of their being separated from a mainland they have provided ideal evolutionary laboratories (Greuther, 1972) for the study of speciation. Islands are by definition, geographically isolated relative to continental land masses;

however, the plant species of an island, while obviously restricted, are not always different from that of the original continental flora. Instead, one could view isolation as a force for maintaining endemism after geographic restriction has occurred, rather than the actual causal mechanism for endemism (Mason, 1946). Geographic restriction is an event which results in a population being unable to transfer genes with other populations of its species. Isolation is the consequence of restriction. Other isolating mechanisms might include temporal differences in flowering time such as has been found in sympatric endemic species of Sedum (Denton, 1979).

Genetics have also been considered in the quest for understanding potential causes of endemism (Stebbins and Major, 1965; Babbel and Selander, 1974). It has been suggested (Stebbins and Major, 1965) that populations which are genetically depauperate (little variability) are also likely to be geographically restricted. Intuitively, this makes sense; if a species has a low threshold of allelic combinations, one might expect it to be limited in its choice of habitat. However, if low allelic variation is associated with high plasticity, then wide distribution can result.

Another aspect of population genetics that could be a

determining factor for endemism might be reflected in a plants inherent dispersal ability. Lack of migration or immigration would prevent new allele combinations from being introduced into a restricted population. Babbel and Selander (1974) conducted a study of Lupinus in which they compared the genetic variation between the widely occurring species Lupinus texensis compared to the highly restricted Lupinus subcarnosus. They found greater genetic variability in the widely spread Lupinus as opposed to its restricted counterpart.

There are several potential causes for species to have restricted distributions. These include poor dispersal ability, interspecific competition, allelopathy, and herbivory. Ultimately, however, it is selection pressures which result from environmental conditions which determine a population's genetic makeup. Thus, it is reasonable to infer that the environment is an important factor at the root of a species endemism. This is the view espoused by Mason, (1946) who gives particular emphasis to edaphic factors which he defines as involving ". . . the physical and chemical nature of the substratum together with the effects of these on the various aspects of water relations and aeration of soils. . . . the edaphic factor presents the possibility of enormous

diversity of habitats in any given area." (Mason, 1946). He goes on to point out that all plants are in a sense endemic as they are all geographically restricted by the environment acting on their physiology and genetic composition. Thus endemism, as it is understood and applied to plants which are rare or restricted in distribution, is really a matter of scale (Mason, 1946; Stace, 1980). Although Mason's postulate is straightforward, and intuitively appealing, it is not simplistic. Certainly, a wide variety of environmental factors may interact to promote endemism; however, it is probably rare that any single cause would provide the reason for species restriction.

If one accepts that environmental characteristics are the driving forces behind endemism, then research on the ecology of a given endemic species is a worthy pursuit. Knowledge about the environment can provide important information about mechanisms controlling species with a restricted distribution. Both Mason (1946 I, II) and Stebbins and Major (1965) have done so for the California flora. With its diversity of habitat type, from mountain to desert, California boasts a high percentage of endemics among its native species (Stebbins and Major, 1965). These authors found a high correlation between environmental diversity and proportion of endemic

species. Perhaps the most notable example of endemism as a result of ecology/edaphic factors is that of the serpentine endemics. Serpentine environments are areas in which the soil contains high concentrations of chromium, manganese, and nickel (Stebbins and Major, 1965; Hull, pers. com.). The levels of these metals are so high in fact that most plants cannot tolerate the serpentine habitat.

Raven (1964) suggests that catastrophic selection is a potentially driving force to edaphic endemism. He argues that if a population existing in an already marginal environment were to undergo catastrophic selection, the resulting genetic shift would lead to narrow endemics. Thus, the severity of a given habitat, as well as a diversity of different habitats may play a role in establishing species as endemics. It is with this concept of environmental severity in mind that one may consider the shale barrens of the eastern United States and the shale barren endemic Eriogonum alleni (Polygonaceae).

Shale barrens occur throughout the southern Appalachians, from south central Pennsylvania through western Maryland, into south western Virginia and eastern West Virginia. As early as 1911, botanists noticed that shale barrens supported an herbaceous flora with a variety of endemic plants that were distinct from the species found in the surrounding eastern

temperate deciduous forest (Platt, 1951; Allard, 1948; Artz, 1937, 1948; Wherry, 1935; Keener, 1983).

Shale barrens are defined geologically by the Brallier formation, of the upper Devonian (Platt, 1951). This formation is characterized as being "...micaceous green shale commonly with uneven or dimpled surfaces in which are interbedded layers of finely grained, evenly bedded and blocky jointed greenish sandstone." (Butts, 1940). It generally weathers into rocky fragments and is easily eroded. According to Platt (1951), the layer of rock fragments formed by the Brallier shale is an important aspect of maintaining the shale barren condition. Therefore, it is the structural characteristics of the root zone that sets them apart from the surrounding sandstone ridges and limestone valleys.

In addition to their geologic parent material, shale barrens are characterized by various physical aspects. The barrens generally occur on south facing slopes with an incline of 20 degrees or more. They may be undercut by streams at the base and have little vegetation (Keener, 1983). The climate of the shale barrens is fairly consistent throughout their range, and is described as warm temperate and rainy (Platt, 1951).

Shale barrens do not seem to have a soil chemistry different

from the surrounding deciduous forest; however, soil depth is shallow and there is little to no organic layer. The soil surface is covered by shaly rock fragments instead of leaf litter and soil surface temperature often reaches 60 degrees celsius (Platt, 1951), making the barrens inhospitable to most eastern temperate plants. Herbaceous plants receive almost full irradiance as the shale barren canopy is sparse at best (pers. observation) although the shale barrens support some xeric woody species (Pinus virginiana, Quercus ilicifolia).

The distribution of shale barrens is disjointed; each barren is spatially isolated from the others. A question of considerable interest to some botanists is; how did shale barren endemics become distributed throughout the shale barren range (Keener, 1983)? Additionally, most of the shale barren endemics are disjuncts; none of them have related species in the eastern United states closer than Kentucky (Keener, 1983,) and little is known about their dispersal abilities.

Eriogonum alleni Wats. (Strasbaugh and Core, 1978) occurs in the southern range of the shale barren distribution. It has been hypothesized that E. alleni is an obligate heliophyte, or high light requiring plant, and is therefore restricted to the shale barren habitat (Keener, 1983). Eriogonum alleni does have morphological characters commonly

associated with high light adapted plants such as reflective leaf hairs.

The purpose of this dissertation is to address the potential mechanisms whereby the shale barren endemic Eriogonum alleni tolerates or avoids the potentially stressful environment of the Southern Appalachian shale barrens; however, it does not attempt to address the question of why E. alleni is endemic. Although a considerable amount of work has been done on the shale barren flora from a natural history standpoint (Allard, 1948; Artz, 1937, 1948; Keener, 1983; Wherry 1935), little work aside from Platt (1951) has been carried out on the ecology of the shale barren endemics (Platt, 1951; Kaltenbach, unpublished) and no research has been done on the physiological characteristics of any shale barren endemic. Specifically, this dissertation focuses on the light requirements and heat acclimation ability of E. alleni. There were three objectives to this study. The first was to establish the vegetative communities of shale barren versus non shale barren sites. This provided a frame of reference for light and temperature studies, and characterized the shale barren community beyond the level of a species list. The second objective was to determine the light requirements of E. alleni by testing whether or not the

species could acclimate to various light regimes. The third objective was to establish the ability of E. alleni to acclimate to high heat conditions; the temperatures reported for and measured on shale barrens suggest the ability to withstand temperatures well above the optimum for the Eastern Temperate Deciduous Forest. The literature suggests that the shale barren endemics are high light requiring plants; the temperatures of the shale barrens implies that the endemics can withstand high temperatures (Keener, 1983; Platt, 1951); however, no data exist to confirm or refute these ideas. This dissertation supplies basic data about the physiological ecology of a plant from a poorly understood habitat. Since several of the shale barren endemics are rare or endangered at state and federal levels, this study will aid in establishing future management strategies.

CHAPTER 2: VEGETATION STUDY

Introduction

The vegetation of Southwestern Virginia falls into the ridge and valley province as defined by Braun (1950). It is generally considered a mixed-oak association with changes in vegetation resulting from either slope and/or elevation (Ross, 1982).

Canopy dominants include Quercus prinus, Q. velutina, and Q. coccinea in mid slope areas with Nyssa sylvatica and Cornus florida in the understory (Ross et. al., 1982). Lipscomb and Nilsen (unpublished.) found that abrupt changes in slope affected vegetation; opposing north and south slopes can have different vegetation communities.

Although the vegetation in the eastern deciduous forest is continuous on a broad scale, it is interspersed with several rock outcrop communities (Baskin and Baskin 1989). These communities tend to have a somewhat lower species diversity than the surrounding forest; however, they all support a variety of endemic species.

One such environment is the shale barrens. These sites range from south central Pennsylvania through western MD and into south western VA and West Va (Platt, 1951). The substrate is derived from the Braillier shale formation which dates to the upper Devonian. The Braillier shale breaks easily into rock fragments; these cover the soil surface in

the place of leaf litter. Commonly, shale barrens have a shallow soil depth but soil chemistry is not unusual compared to other non barren sites (Baskin and Baskin, 1989). In fact shale barren, and other rock outcrop endemics are easily grown in ordinary potting soil; there is no unusual soil requirement (Baskin and Baskin, 1989; pers, obs). Baskin and Baskin (1989) report that no unusual edaphic changes limit the distribution of endemic species in the southeastern deciduous forest.

Shale barrens have attracted considerable attention from a floristic standpoint because they support a variety of endemic species (Artz, 1937; 1948; Allard 1948; Wherry, 1963). However, little work beyond Platt's studies in the 40's and 50's (Platt, 1951) has been done on the community structure of the shale barrens. Although the overall purpose of this dissertation is to examine the physiological ecology of the shale barren endemic Eriogonum alleni, an important first step was to determine the barren vegetation community. Thus, the purpose of this chapter was to characterize the woody vegetation of shale barren sites. Data from the literature (Lipscomb 1991, Murphy, 1992; Schiffman, 1989; Williams, 1990) pertaining to regional north and south non shale barren sites on Brush Mt. and a wooded non barren site opposite the Ironto shale barren were used as regional and local references.

Materials and Methods

SITE DESCRIPTION

Two shale barrens were sampled with respect to woody vegetation. The first of these, the Ironto shale barren is located in Montgomery County, Virginia on Ellet rd (Rt. 603) between the town of Ironto and Interstate 81. The barren is 64 acres in size and is owned by the Nature Conservancy. It is considered by the Nature Conservancy to be one of the best representations of a typical shale barrens community. It ranges from 1300 - 1600 feet in elevation (determined from a US Geological survey map, Ironto quadrangle), is south west facing, and has an average slope of 32°. The Ironto shale barren is undercut by the North Fork of the Roanoke river. This shale barren was selected as the primary site for all field studeies as it has an abundant population of E. alleni and receives little human disturbance.

The Craig Co. shale barren is located on route 612 on the border of Craig and Botetourt Counties, Virginia. It is 1200 - 1400 feet in elevation(US Geological Survey Map, Oriskany Quadrangle), faces southeast, and has an average slope of 31.4°. The shale barren is undercut by a small stream which runs into Craig Creek, and by a forest service road. It is privately owned by Dr. Ernest Senneca of North Carolina State University.

Both sites have a thin layer of rock fragments covering

the soil surface, are sparsely vegetated, and contain several shale barren endemics. At the Ironto site, the shale barren is complemented by a wooded slope of the same geologic formation, on the north side of the ridge. The wooded side has approximately the same slope as the shale side, has a well developed litter layer, and is undercut by a small creek. This slope was sampled as a local reference site to the Ironto shale barren. The Ironto sites were sampled in 1989 and the Craig Co. site in 1991.

SAMPLING METHODS AND DATA ANALYSIS

This study was first initiated by direct sampling of the Ironto and Craig County sites in order to establish the woody vegetation community of shale barrens. When data were analyzed, information on regional non barren sites (Brush Mt.) was added for additional comparison purposes.

Twenty-five by 25 meter adjacent plots were established using rebar and string as plot boundaries, for each of the three directly sampled sites (Ironto shale, Ironto woods, Craig co. shale). This plot size was selected to encompass as much of the shale slope as possible. In order to ensure consistency, plot boundaries were determined by sighting along a compass. Five plots were established at the Ironto shale site, 3 at the Ironto woods site, and 4 at the Craig Co. site. The number of plots sampled at each site was determined by

their accessibility.

Environmental data consisting of air temperature at @ 1.5 meters, air temperature at plant height (@ 0.2 m) around E. alleni leaves, soil surface temperature, relative humidity, and light intensity were taken at the Ironto shale and wooded sites during the summer of 1989. A Campbell scientific datalogger was used. Temperatures were measured using copper/constantin thermocouples, humidity was measured with a Visalia Humicap sensor, and light intensity was determined with a pyranometer. Data presented in Figures 1-5 are hourly means calculated from measurements made at 10 minute intervals at the Ironto shale and wooded sites. Daily means were calculated for each parameter and analyzed for statistical significance using the T-test for paired samples.

Soil samples were collected for the Ironto shale site in the Spring of 1991. Because of the steepness of the shale barren slope, the soil's shallow depth, and its large quantity of rock fragments, digging a soil pit and collecting samples from each horizon was not feasible. Therefore, soil samples were collected as a combination of the entire soil strata. Three samples were collected from each study plot for a total of 15 samples.

Both physical and chemical soil characteristics were assayed. Particle size distribution, texture, capillary porosity and bulk density were determined by methods outlined

in Burger, 1991. Soil mineral nutrients, nitrates, and pH were determined at the Virginia Tech Soils Testing Laboratory. Data are presented as means and standard deviations for the shale site.

All woody vegetation greater than or equal to 1 cm in diameter at breast height (DBH) was sampled within each plot. If a plant was too short to have a DBH, its diameter was measured below the lowest branch or visible branch scar (Parker et.al., 1993). Density, frequency, and basal area were determined for each species. The Importance value (IV) for each species was then calculated (IV = relative frequency + relative density + relative basal area).

Vegetation data from the Ironto shale and wooded sites, the Craig Co. shale site, Platt's 1951 shale sites, and north and south slopes on Brush Mt. (Platt, 1951; Lipscomb and Nilsen, unpublished; Murphy, 1992; Schiffman, 1990; Williams, 1989) were analyzed on a per site basis, using two different approaches, with the Numerical Taxonomy System for personal computers (NTSYS-pc), a multivariate statistical analysis system (Rohlf, 1988). Data were initially analyzed using species importance values per site. Sites were reanalyzed on a species presence or absence per site basis. NTSYS was originally designed as a means of analyzing taxonomic data; however, it has been found useful for analyzing data in a wide variety of fields, including ecology (Rohlf, 1988). Cluster

and principal component analyses were performed. The cluster analysis groups similar sites, while the principle component analysis allows one to determine the species that cause sites to cluster together. The Platt, Williams and Schiffman sites were analyzed for presence and absence only as no importance values were reported.

Results

I. ENVIRONMENT (IRONTO SITES):

Ambient air temperature did not differ significantly ($p > .05$) between shale and wooded sites throughout out the day (Fig. 1). Mean daily air temperature on the shale site was 25.6 degrees Celsius, while on the wooded site mean daily air temperature was 25.8 degrees. Additionally, air temperatures between the shale and wooded sites at the approximate height of Eriogonum allenii only differed at midafternoon, at which point the peak temperature on the shale site was approximately 34° C versus about 31° C on the wooded slope (Fig. 2). Air temperature declined for both sites after 3:00 pm. Mean daily temperatures at plant height were 27.04 and 26.13 degrees for the shale and woods sites respectively.

Soil surface temperature differed significantly ($p < .05$) between the two sites (Fig. 3). The average daily soil surface temperature on the shale site was 31.56 degrees, while on the woods slope it was 23.85 degrees. The shale barren

experienced sharply increasing soil surface temperatures through the day with a peak temperature of almost 50° C in the mid afternoon, almost double the soil surface temperature found in the woods at the same time. Platt (1951) reports soil surface temperatures of 55 - 60° C during the warmest part of the day.

Both the shale and wooded sites experienced a decline in relative humidity throughout the day, with the lowest humidity reached in the mid-afternoon (Fig. 4). The shale site experienced a low relative humidity of 39.1%; and a mean daily humidity of 72.84%; the woods site had a daytime low of 46.2%, and a mean of 72.55%.

Light intensity was significantly higher ($p < .05$) on the shale slope as opposed to the wooded slope (251.27 Watts per meter squared vs. 34.11). Figure 5 represents light intensity for each site during peak photosynthetic hours. Throughout most of this period, the shale site received more than four times the amount of light than did the wooded slope. Canopy photographs for the two sites (Fig. 6) reveal that the shale slope has a sparse canopy, allowing more light to reach the barrens herbaceous layer. The wooded slope has a closed canopy, thus irradiance reaching the herbaceous layer is reduced.

II. SOIL (IRONTO SHALE SITE):

The soil at the Ironto shale barren is classified as a sandy loam as determined by particle size distribution (Table 1). It had a bulk density of 1.18 g/cm^3 . The capillary porosity, an indication of available water (Brady, 1984), was 17.9%.

The average soil pH was 4.6. This corresponds to data reported for shale slopes by Platt (1951), and is comparable to pH data for both north and south slopes within the region (Brush Mt., and Salt Pond Mt; Schiffman, 1990; Stephenson, 1982 respectively).

Soil nutrient concentrations determined for the Ironto shale barrens (Table 1) were within the range of nutrient concentrations reported for the region for both North and South facing slopes (Hicks and Frank, 1984; Schiffman, 1990; Stephenson, 1982). Additionally, Platt (1951) recorded similar nutrient concentrations for North slopes and shale barrens.

III. VEGETATION:

The shale barrens selected for study were largely dominated by the following species: at Ironto; Pinus virginiana, Quercus prinus, and Quercus ilicifolia; at Craig Co.; Junniperus virginiana, Quercus rubra, Q. prinus, Carya species, and P. virginiana. The wooded slope at Ironto which

was sampled as a reference site was dominated by Q. prinus, Amelanchier arborea, Ostrya virginiana, and Q. rubra. Although P. virginiana and Q. ilicifolia were present in the wooded stand, they appeared only at the crest of the ridge dividing the shale and wood slopes and were completely absent well into the wooded stand. Table 2 provides a list of species with their importance values for each site.

Dominance ranks of species for the Ironto and Craig Co. sites indicate that shale barrens have only a few dominant species, with other species occurring with relatively little importance. This trend is reflected in the steep slopes for these sites in figure 7, particularly between species ranks 6 and 14. The Dominance rank of species for the wooded Ironto site, however, indicates a more even distribution of species importance; its slope as seen in figure 7 is gentler relative to the two shale sites with more codominant species of intermediate importance. Additionally, the wooded site supports a somewhat greater species diversity than either of the shale slopes (18 species vs. 11 or 14 respectively).

Figure 8 shows the phenogram generated by the NTSYS cluster analysis using species importance values as character states. Sites with species of similar composition grouped together. The Ironto shale (IRS), Ironto woods (IRW), and Craig Co. (CCO) sites formed a cluster distinct from the Brush Mt. reference sites. Oddly, although the Brush Mt. sites

clustered together, they grouped by experimenter rather than by aspect (ie Lipscomb's sites, LBMN and LBMS, clustered together and Murphy's sites, MBMN and MBMS, clustered together, but their North and South slopes did not). This may have been the result of each study using different plot sizes and shapes. A small plot may exclude some species, thus the importance of these species within a stand might go unnoticed. Additionally, some species may have been misidentified. Of all the sites examined, Craig Co. had the least percent similarity to any of the others (Table 3, column 3). This was probably due to the occurrence of Junniperus virginiana and Celtis occidentalis at Craig Co. and not at any of the other sites. (J. virginiana was recorded at IRS, but was of little importance.)

Principle component analysis of these sites supported the cluster analysis. IRS, IRW, and CCO grouped together, as did LBMN, LBMS, and MBMN, MBMS (Fig. 9). Within the first dimension, all Brush Mt. sites were distinguished from the Ironto and Craig Co. sites. This is probably the result of species either present with high importance on Brush Mt and absent on the shale barrens or species present on the shale barrens with high importance values, and absent on Brush Mt. These species would include Quercus prinus, Sassafras albidum, Nyssa sylvatica, Vaccinium species, Quercus species, Pinus rigida, P. strobus, and Kalmia latifolia on Brush Mt., and P.

virginiana, and Junniperus virginiana for the shale sites. The Ironto woods site is separated from the shale barren sites by the importance of Ostrya virginiana, Amelanchier arborea, Quercus alba, and Prunus serotina.

The Murphy Brush Mt sites MBMN, MBMS are separated from the rest in the second dimension. This separation is probably influenced by the following species: Q. ilicifolia (on the shale barrens), Q. rubra, Rhus species, Cercis canadensis, Vitis, Castanea dentata, Pinus rigida, P. strobus, Kalmia latifolia, Mensezia pilosa, and Viburnum acerifolium. These species were either not present on the Murphy sites or occurred with very low importance values (Murphy, 1992). (Appendix 1, Table 1 contains the Eigen vectors for each species in each dimension used to determine site separations.)

The cluster analysis for presence/absence data showed all shale barren sites grouping together, with an 82% similarity (Fig. 10). This is probably due to the inclusion of Platt's (1951) data set which incorporated species presence over a wide range of shale barren sites. Since his species list included plants common to both Ironto and Craig Co., his data effectively act as a link joining these two sites. The shale sites are only 67% similar to the Ironto wooded site (IRW). As with the Importance value cluster analysis, all Brush Mt. sites clustered together. The additional north (PBMN) and south (CBMS)slope data (Schiffman, 1990; Williams, 1989)

included, clustered with Murphy's sites and Lipscomb's sites respectively. The Brush Mt. sites are only 49% similar to the other stands. Table 4 presents the similarity values for each site.

The principle coordinate analysis using presence/absence supports the phenogram obtained: the Brush Mt. sites group separately from the shale sites in the second dimension (Fig. 11). As with the importance value analysis this separation is accounted for by the presence of species either only on Brush Mt. or only on the shale sites (ie on Brush Mt.: P. pungens, P. rigida, P. strobilus, Menzesia pilosa, Rhododendron species; on shale sites: P. virginiana, J. virginiana, Q. ilicifolia). Table 2 in Appendix 1 presents the species Eigen vectors for each dimension.

Discussion

The most striking environmental differences between shale and non shale sites are seen in soil surface temperatures and light intensity experienced by the shale barrens. The shale barrens had a much greater soil surface temperature, and experienced considerably higher irradiance. Both of these traits can be attributed to the south facing aspect of the shale barrens and to the sparsity of overstory canopy (Fig 6). The aspect of the barren and the lack of canopy permit increased insolation. This in turn raises soil surface

temperature. Although no environmental data was collected for the Craig Co. site, it seems reasonable to assume that it experiences similar environmental conditions as Ironto. Platt (1951) states that shale barrens are climactically consistent, and Kaltenbach (unpubl.) reports soil surface temperatures for a shale barren in western MD which are comparable to those found at Ironto.

The high soil surface temperature and high light intensity of the shale barrens, may contribute to their lack of vegetation. It is possible that the sparse vegetation allows for an increased evaporative surface. However, one could also argue that a site that is heavily vegetated offers a large surface area for water loss due to transpiration. Shale barren species do not seem to experience water stress. Most endemic species have a deep root system, capable of tapping water reserves not available in the upper soil layer (Platt, 1951, pers obs.).

Platt (1951) does raise the point that low soil moisture could impact nutrient availability. Although nutrient data obtained from the Ironto shale barren was comparable to the region, a study examining nutrient availability and use efficiency by shale barren species would be enlightening.

It has been suggested that the shale barren vegetation is reflective of a xeric environment (Allard, 1948). It certainly is markedly different from that of the surrounding

non-barren region. While most south facing slopes are dominated by species such as P. pungens, P. rigida, Q. rubra or Q. prinus, the shale slopes are dominated by P. virginiana or J. virginiana. Additionally, Q. ilicifolia is present with some importance. The species found at Ironto and Craig Co. were also noted by Platt (1951) who stated that shale barren vegetation was consistent throughout. However, the relative dominance of species between shale barrens can be different. This difference in dominant species between Ironto and Craig Co (P. virginiana vs J. virginiana) may indicate that although shale barrens are similar in climate, geology, and aspect they have site specific variation in vegetation. Since shale barrens are disjunct throughout their range this may be reflective of species distribution patterns at a local level or stochastic events (Schiffman, 1990).

The impact of woody vegetation on Eriogonum alleni may be important insofar as areas below trees could provide favorable microsites for seedling colonization. Any shade provided could potentially lower soil surface temperatures enough for establishment. A study examining the microhabitat preference of E. alleni within a shale barren would supply this information. Conversely, woody species dominants such as Q. ilicifolia and P. virginiana have an open canopy which allows considerable irradiance to reach the herbaceous layer. If E. alleni is an obligate heliophyte, the high light intensity

provided on the shale barren would be of considerable importance.

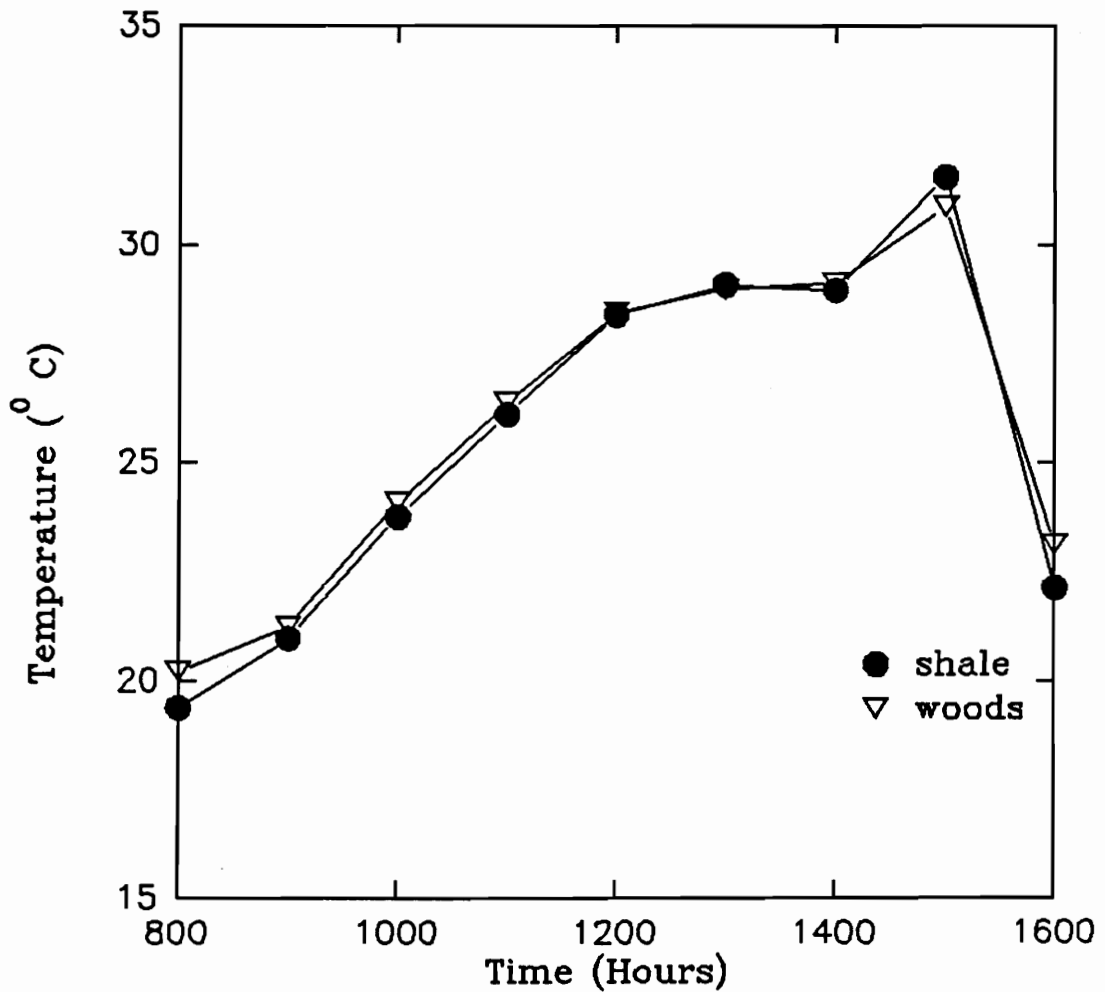


Figure 1: Air temperature at 1.5 m of a shale and a wooded site at Ironto Virginia on August 29, 1989. shale (o) = the Ironto shale slope, woods () = the Ironto wooded slope.

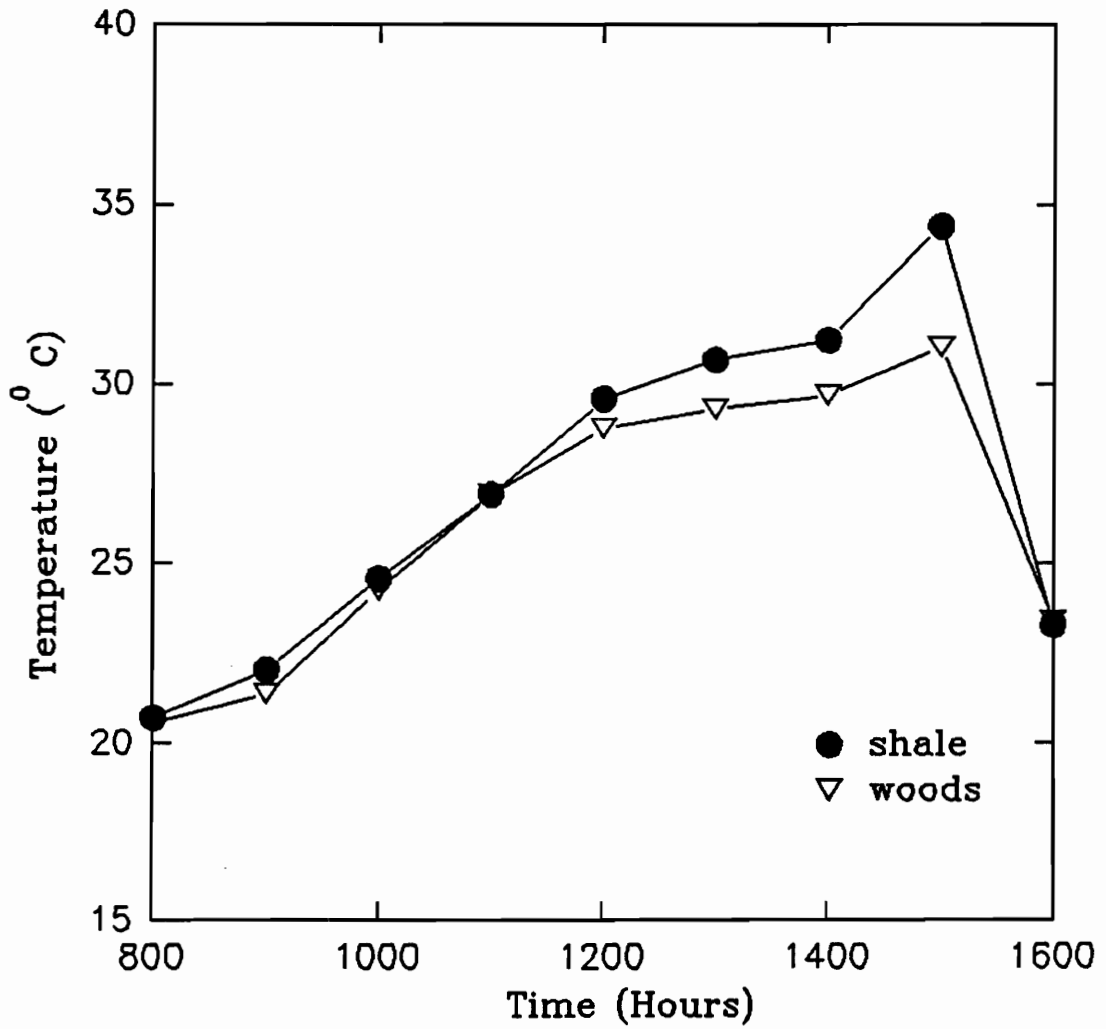


Figure 2: Air temperature at plant height (@ 0.2 m) on a shale and a wooded site at Ironto, Virginia on August 29, 1989.

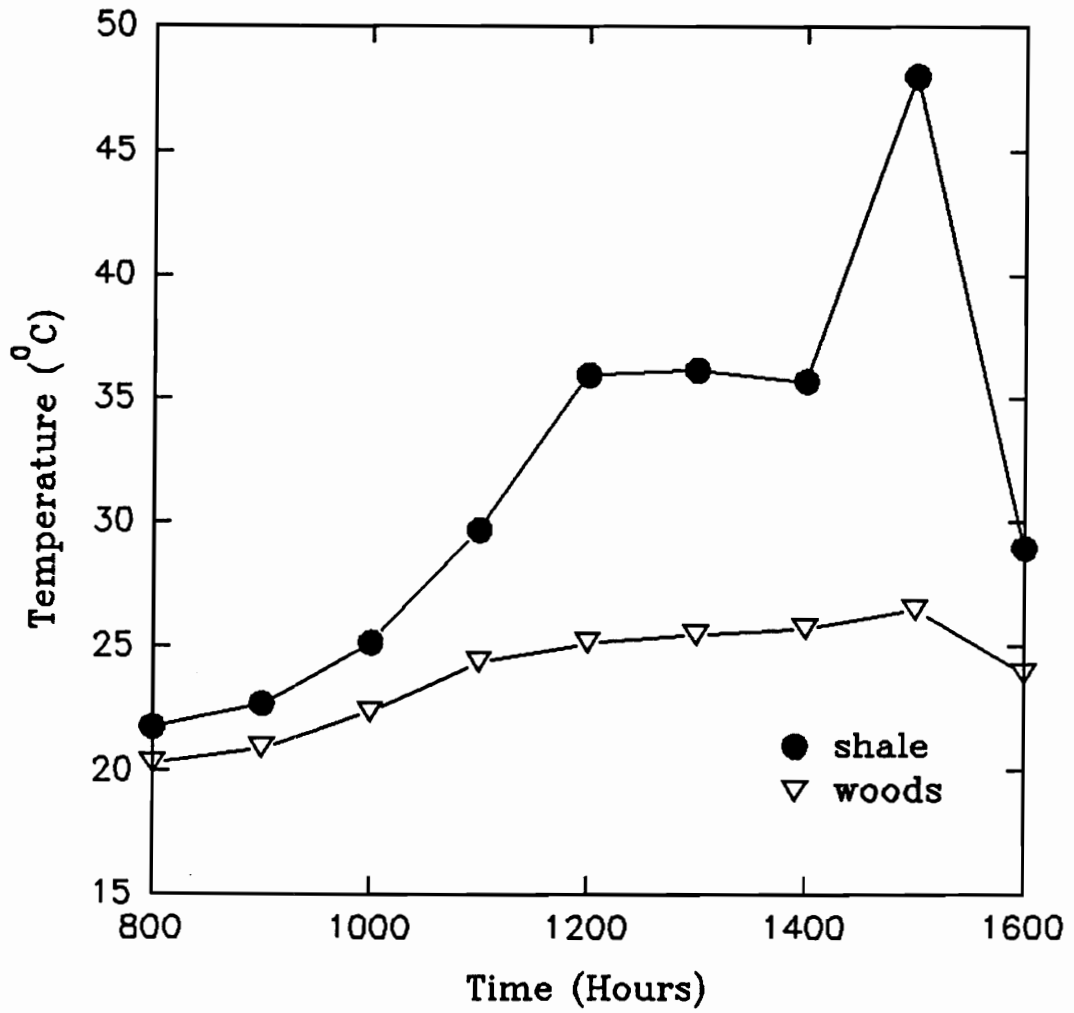


Figure 3: Soil surface temperature at a shale and a wooded site at Ironto, Virginia on August 29, 1989.

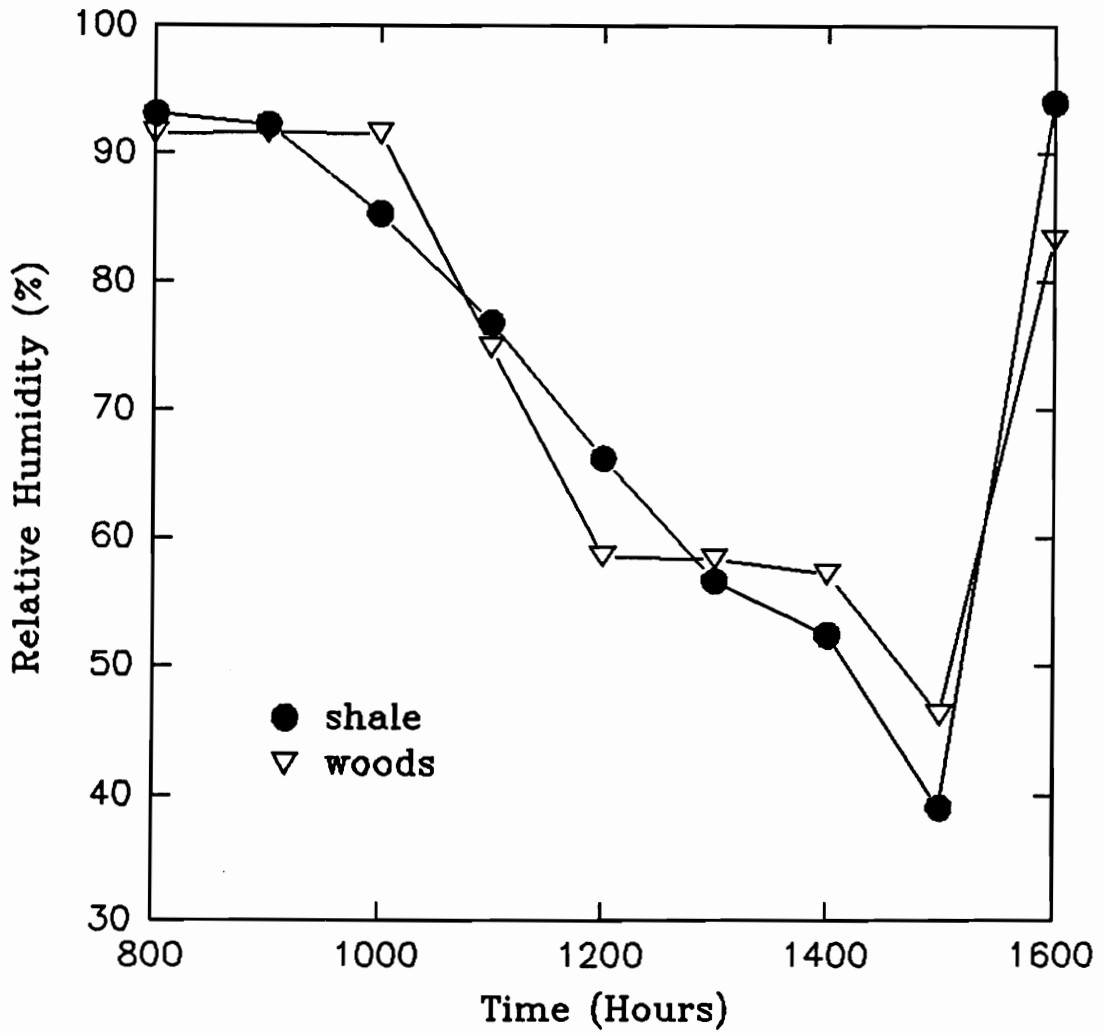


Figure 4: Percent relative humidity at a shale and a wooded site at Ironto, Virginia on August 29, 1989.

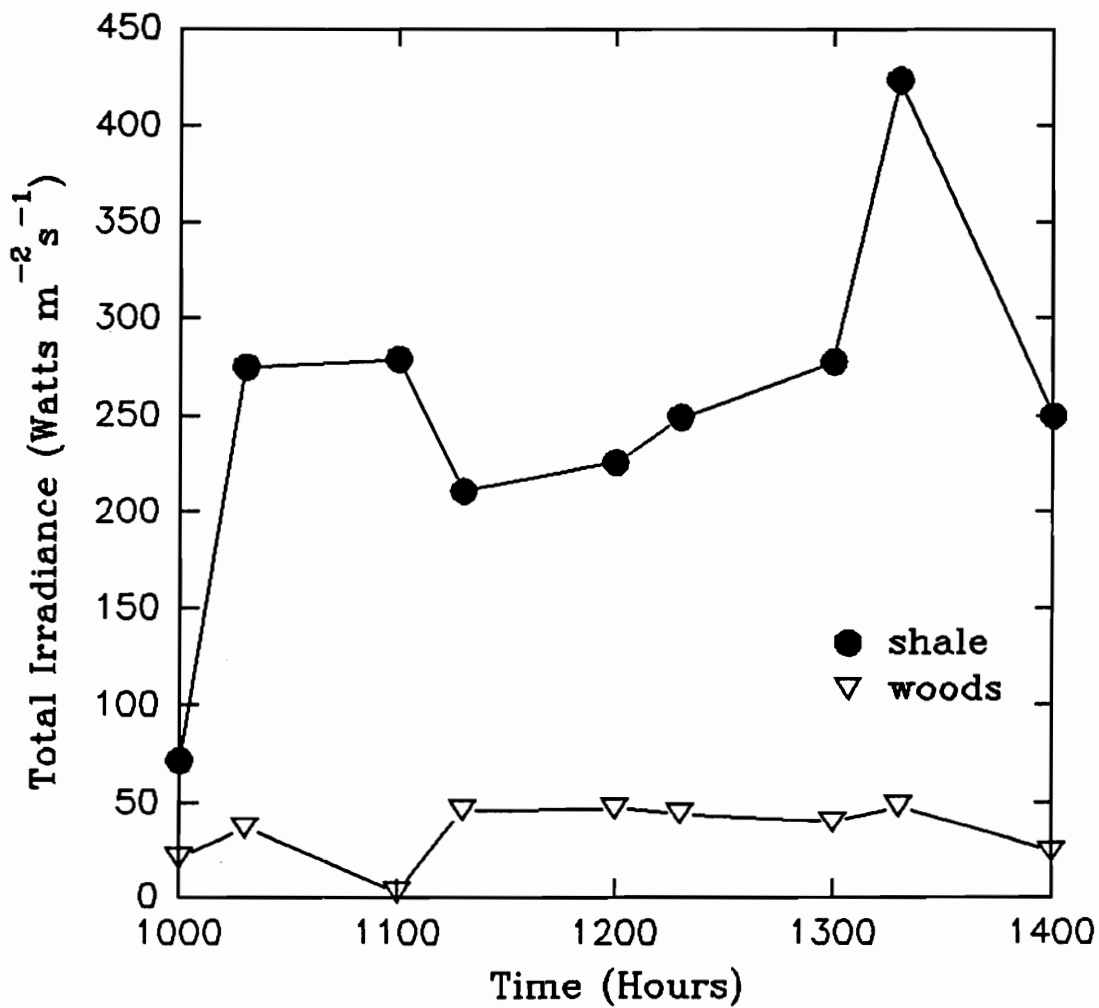


Figure 5: Total irradiance at a shale (August 21) and a wooded (August 29) site at Ironto, Virginia in 1989.



Figure 6: Canopy photographs from a shale (a) and a wooded (b) site at Ironto, Virginia.

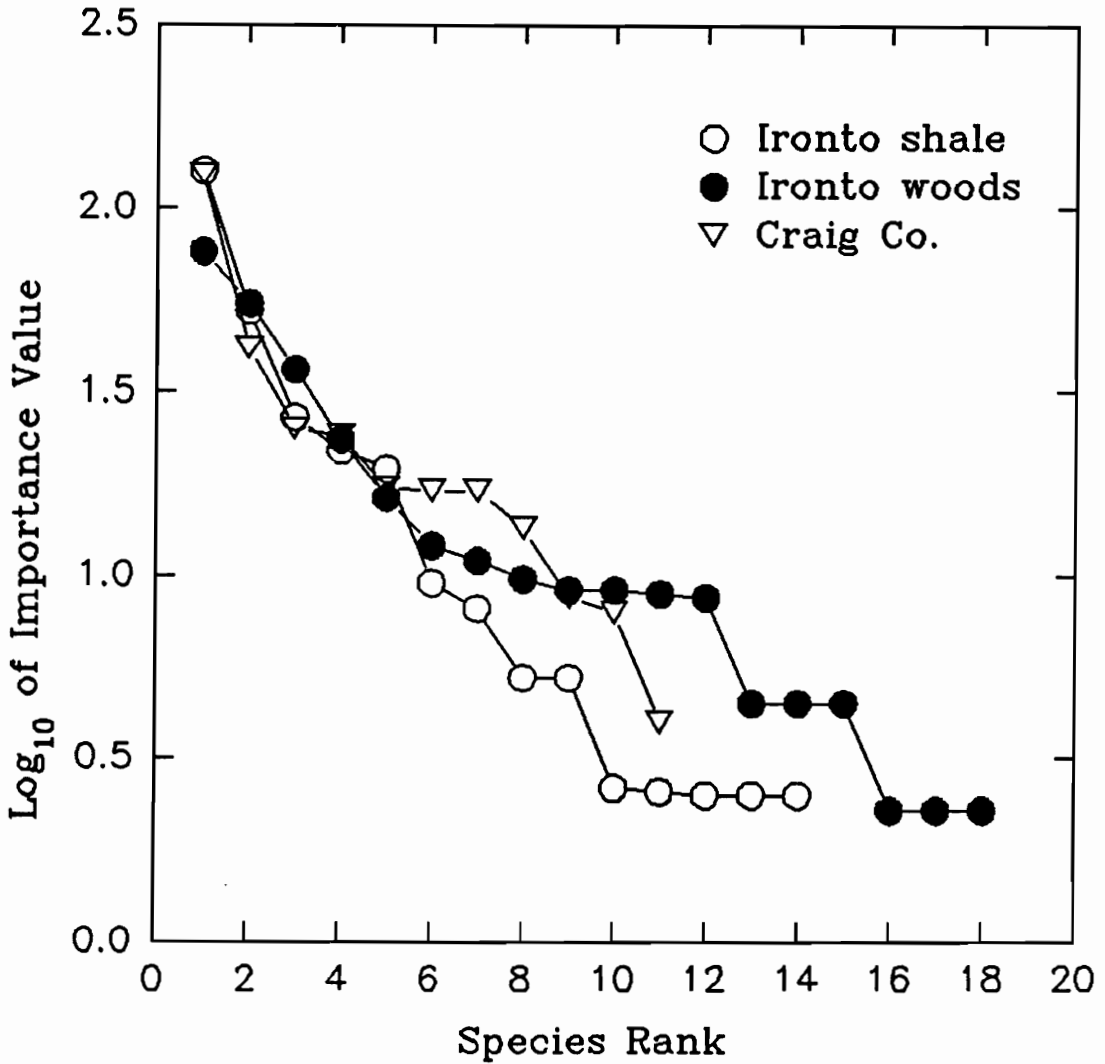


Figure 7: Dominance rank of woody species at the Ironto shale and woods sites and Craig Co.

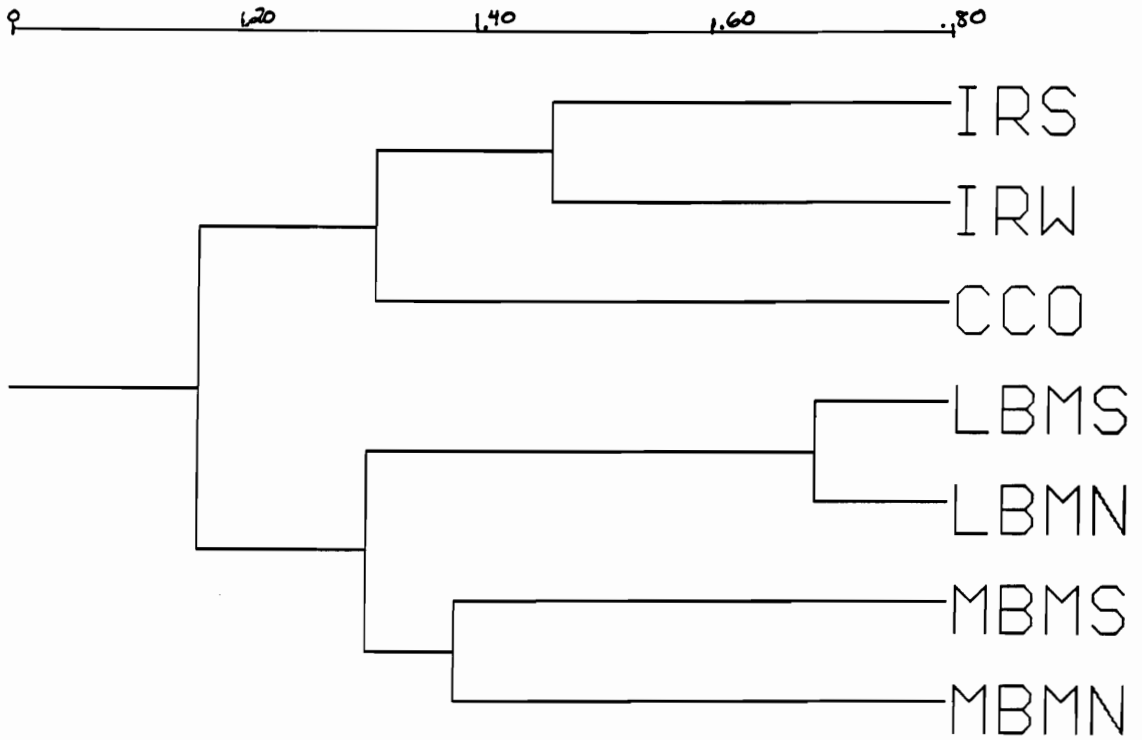


Figure 8: Phenogram generated by NTSYS analysis using species importance values as character states (IRS = Ironto shale south slope; IRW = Ironto woods north slope; CCO = Craig Co. shale south slope; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy Brush Mt. north slope). The top scale indicates percent similarity.

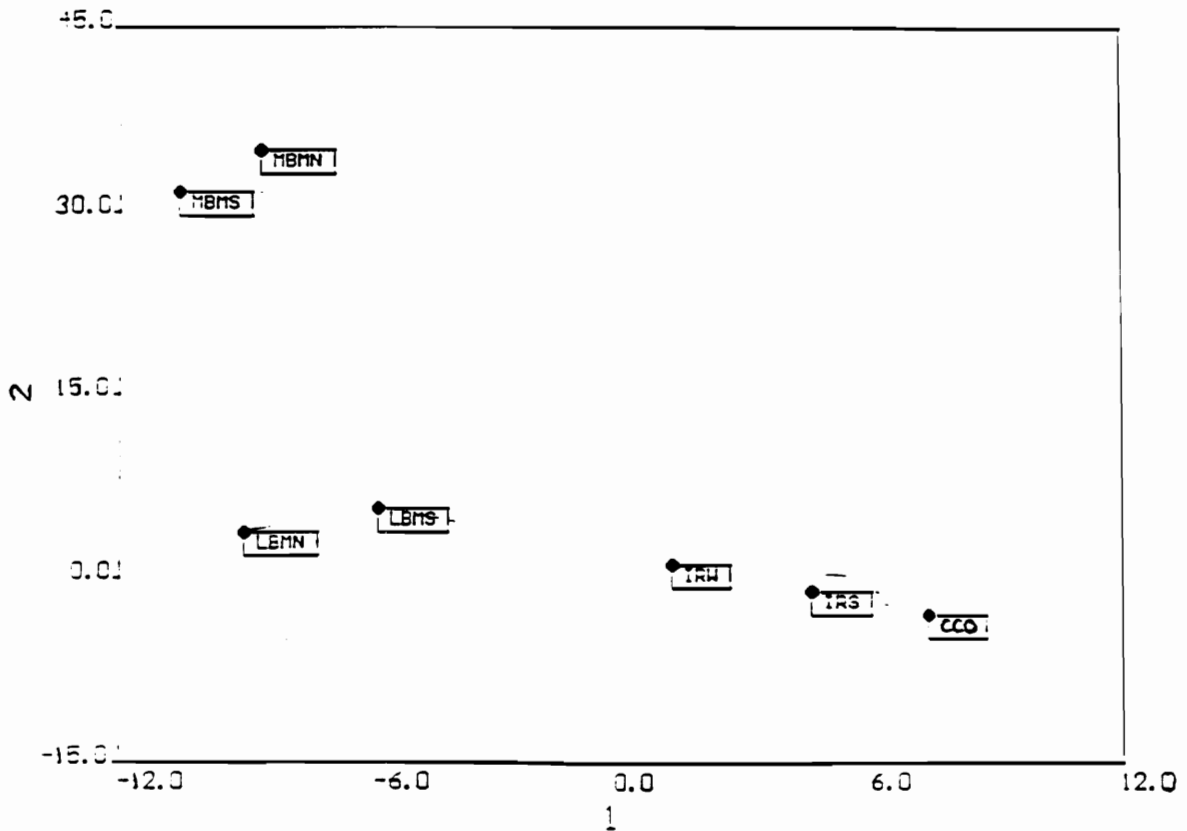


Figure 9: Vegetation community grouping generated by NTSYS principle component analysis using importance values as character states (IRS = Ironto shale south slope; IRW = Ironto woods north slope; CCO = Craig Co. shale south slope; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy Brush Mt. north slope).

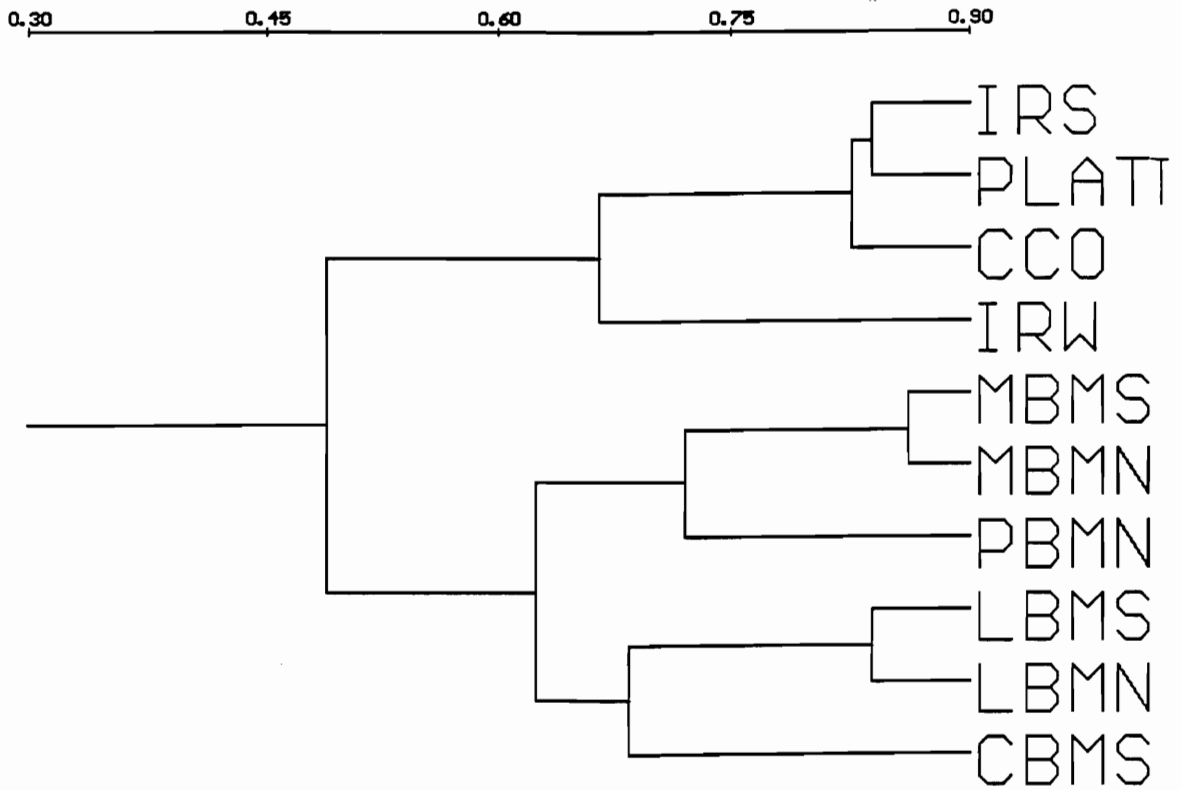


Figure 10: Phenogram generated by NTSYS analysis using species presence/absence as character states (IRS = Ironto shale south slope; IRW = Ironto woods north slope; CCO = Craig Co. shale south slope; PLA = Platt shale sites; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy Brush Mt. north slope; PBM = Schiffman Brush Mt. north slopes; CMB = Williams Brush Mt. south slopes). The top scale indicates percent similarity.

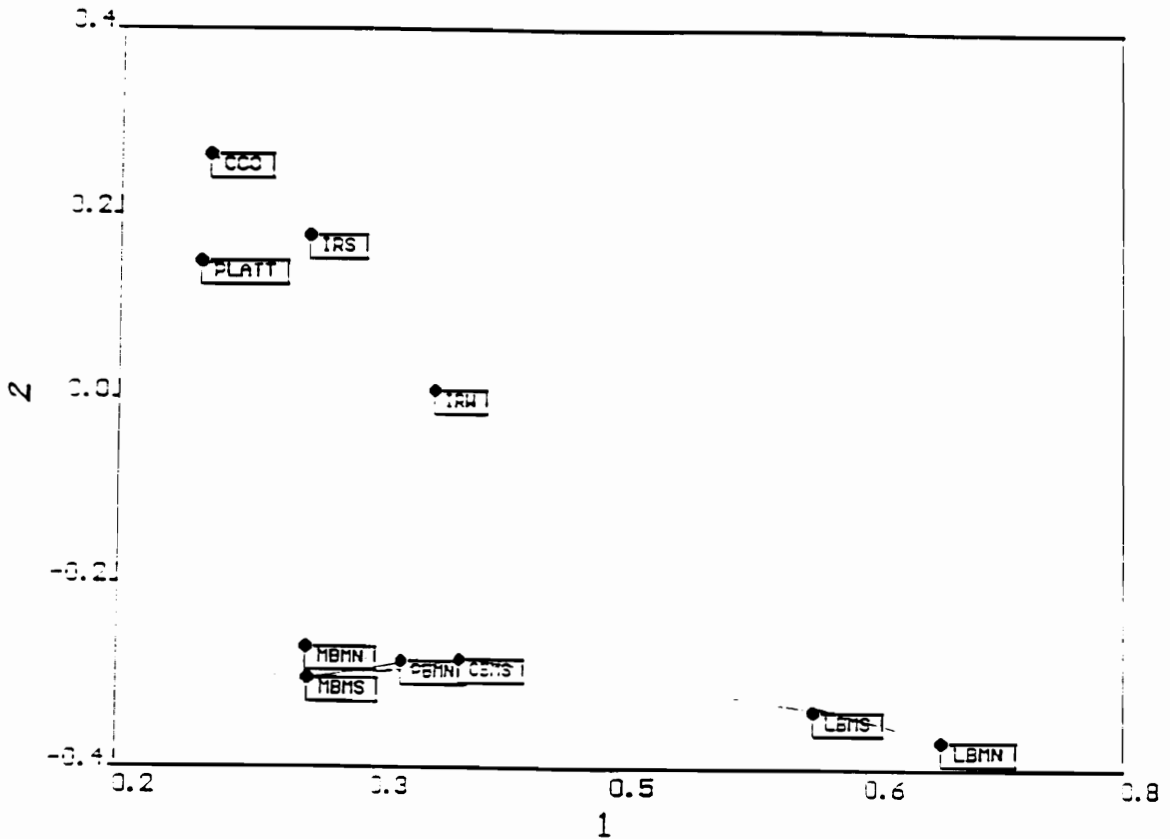


Figure 11: Vegetation community grouping generated by NTSYS principle component analysis using species presence/absence as character states (IRS = Ironto shale south slope; IRW = Ironto woods north slope; CCO = Craig Co. shale south slope; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy Brush Mt. north slope).

Table 1: Soil characteristics at the Ironto shale Barren. Data are expressed as mean (std.dev.) site values (n = 15).

Physical Characteristics	
Particle Size Distribution (%)	Sand: 60.49 (2.06) Silt: 29.61 (5.14) Clay: 9.89 (2.06)
Texture	Sandy Loam
Capillary Porosity (%)	17.9 (5.51)

Soil Nutrients (parts per million):

NO3	P	K	Ca	Mg	Zn
3.8 (1.01)	4.4 (1.04)	76.95 (9.16)	325.5 (88.2)	107.8 (19.2)	3.52 (.622)
Mn	Fe	Al	Cu	B	
59.63 (12.9)	107.2 (17.8)	363.7 (37.7)	1.47 (.317)	.220 (.021)	

Table 2: Importance values for all woody species found at the Ironto shale barren (IRS), the Ironto woods (IRW), and the Craig County shale barren (CCO). Importance values = (relative density + relative frequency + relative basal area) for each species.

	IRS	IRW	CCO
<u>Acer rubrum</u>	-	9.8	-
<u>Amelanchier arborea</u>	22.1	54.6	0
<u>Carya glabra</u>	-	8.7	-
<u>Carya tomentosa</u>	2.52	12.1	-
<u>Carya sp.</u>	8.11	9.1	24.0
<u>Cercis canadensis</u>	5.24	-	8.7
<u>Celtis occidentalis</u>	-	-	17.4
<u>Cornus florida</u>	-	8.9	-
<u>Fraxinus americana</u>	-	-	17.1
<u>Hamamelis virginiana</u>	-	9.1	-
<u>Junniperus virginiana</u>	2.57	2.3	124.0
<u>Kalmia latifolia</u>	-	4.5	-
<u>Nyssa sylvatica</u>	9.6	-	-
<u>Ostrya virginiana</u>	-	36.4	-
<u>Pinus virginiana</u>	126.2	16.1	25.2
<u>Prunus serotina</u>	-	4.5	-
<u>Quercus alba</u>	-	10.9	-
<u>Quercus ilicifolia</u>	19.5	2.3	17.0
<u>Quercus prinus</u>	53.0	75.6	13.6
<u>Quercus rubra</u>	27.2	23.3	41.3
<u>Quercus sp.</u>	5.3	4.5	-
<u>Rhus sp.</u>	2.52	-	4.0
<u>Sassafras albidum</u>	2.54	-	-
<u>Vaccinium sp.</u>	-	2.3	-
<u>Vitis sp.</u>	2.61	-	7.9

Table 3: Similarity matrix for shale and non-shale sites, using species importance value as character states. (IRS = Ironto shale; IRW = Ironto woods; CCO = Craig Co.; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy brush Mt. north slope)

	IRS	IRW	CCO	LBMS	MBMS	LBMN	MBMN
IRS	1.0						
CCO	.464	1.0					
LBMS	.355	.272	1.0				
MBMS	.240	.312	.08	1.0			
LBMS	.107	.148	.031	.364	1.0		
LBMN	.230	.349	.066	.688	.308	1.0	
MBMN	.120	.207	.059	.254	.383	.301	1.0

Table 4: Similarity matrix for shale and non-shale sites, using species presence/absence as character states. (IRS = Ironto shale; IRW = Ironto woods; CCO = Craig Co.; LBMS = Lipscomb Brush Mt. south slope; MBMS = Murphy Brush Mt. south slope; LBMN = Lipscomb Brush Mt. north slope; MBMN = Murphy brush Mt. north slope; PLA = Platt sites; PBM = Schiffman, Brush Mt. north slopes; CBM = Williams Brush Mt. south slopes)

	IRS	IRW	CCO	PLA	LBMS	MBMS	LBMN	MBMN	PBM	CBM
IRS	1.0									
IRW	.698	1.0								
CCO	.837	.628	1.0							
PLA	.837	.674	.814	1.0						
LBMS	.442	.558	.326	.419	1.0					
MBMS	.558	.581	.535	.581	.651	1.0				
LBMN	.326	.442	.209	.302	.837	.581	1.0			
MBMN	.558	.581	.535	.581	.558	.860	.581	1.0		
PBM	.465	.581	.442	.535	.605	.721	.628	.721	1.0	
CBM	.558	.535	.488	.581	.698	.721	.674	.674	.628	1.0

CHAPTER 3: ACCLIMATION TO LIGHT

Introduction

The ability of a plant to adjust to its environment is of inherent necessity if the plant is to survive. One of the most basic abilities a subcanopy plant must have is that of maximizing photosynthesis in varying light intensities. A high photosynthetic rate translates into energy for growth and reproduction and thus into a competitively superior individual.

Plants found in high light environments are generally characterized by high maximum photosynthetic rates, high light compensation points, and somewhat lower quantum yields than plants found in shade environments (Bjorkman et.al., 1975). Morphologically, high light adapted plants tend to have thicker leaves than their shade counterparts. (Hanson, 1917).

In the eastern temperate deciduous forest, high light environments are created by disturbance events such as canopy gap formation. Naturally occurring high light environments are old fields and rock outcrops such as shale barrens.

Shale barrens are exposed rock outcrops which occur on south west facing slopes. They are characterized by a suite of endemic plant species, several of which are considered rare or endangered at state and federal levels. A common shale barren endemic in southwestern Virginia and West Virginia is Eriogonum alleni (Polygonaceae). It is a disjunct species for

the genus and is considered a strict shale barren endemic.

Keener (1983) suggests that one factor causing shale barren endemism is that these species are obligate heliophytes or high light requiring plants. However, there is little to no data to confirm or refute this hypothesis. Thus, the objective of this study was to determine the light requirements of E. alleni and to test Keener's hypothesis that E. alleni is an obligate heliophyte.

The approach taken for this study was to test the ability of E. alleni to acclimate to various light conditions. Plants were shaded in the field for two consecutive growing seasons and photosynthesis was monitored. Additionally, plants were grown from seed and shaded in the experimental garden and greenhouse. Light response curves were then obtained in the laboratory.

The following null hypotheses were tested:

HO: If E. alleni is not an obligate heliophyte it will show acclimation to shaded conditions.

There will be no difference in field photosynthesis between shaded and unshaded plants.

Light response curves will show acclimation to shade; quantum yield efficiency will be higher, light compensation point will be lower and the light intensity

at maximum photosynthesis will be lower for shaded vs. non shaded plants.

Materials and Methods

FIELD STUDY, 1990 and 1991:

Field treatments were initiated in 1990 and continued in 1991. One of three levels of light was given to E. alleni in the field. A control group was left unshaded, a moderately shaded group received 47% shade and a heavily shaded group received 73% shade. The 73% shade level was selected to correspond to light levels similar to what was found in a closed canopy forest, while the 47% shade level provided an intermediate treatment between full sun and closed canopy conditions. There were three replicates of each treatment type. Shade was provided by tenting plants with a PVC framework covered with shade cloth obtained from a nursery supply company. E. alleni was covered with tents in mid June 1990. Shade treatments were left in place through the growing season (until late September). Shade treatments were removed during the winter months and re-introduced to the field in March of 1991, before the plants leafed out. Photosynthesis was monitored during both field seasons using a LiCor portable photosynthesis system. All measurements were made at midday during peak photosynthetic activity.

GARDEN/GREENHOUSE:

Seeds were obtained from the field in the fall of 1989 and planted in vermiculite. After germination, plants were transplanted into individual pots containing a mixture of Promix and Perlite in about a 1:2 ratio.

During the summer of 1991, potted plants were placed in the Experimental Research Garden at Virginia Tech and either shaded with 73% shade or left unshaded. In the fall, all the plants were moved into the greenhouse, and were maintained in the shaded or unshaded condition. Four plants were used for each treatment. Five leaves were used from each plant to determine light response curves. Light response curves were obtained by exposing plants to saturating light intensity and then reducing available light with neutral density shade cloth until they were in darkness.

After light response curves were obtained, the leaves used were harvested and fixed for TEM observation. Leaves were preserved in an alcohol glycerol solution, stained with osmium tetroxide and infiltrated with resin. Samples were scanned for changes in chloroplast structure.

Results

ENVIRONMENT:

Mean air temperature, leaf temperature, relative humidity, and light intensity measured during the summer of

the 1991 field season are presented for each treatment in figures 1-4.

There was no significant difference in air (Fig. 1) or leaf (Fig. 2) temperatures between the full sun (control) and 47% shade treatment or between the control and 73% shade treatment. However, air and leaf temperatures in the 47% shade treatment were significantly lower ($p < .05$) than the 73% treatment. Leaf temperatures were significantly lower within each treatment than air temperature. E. alleni maintained a leaf temperature at about 2 degrees below that of ambient air temperature.

Relative humidity was significantly different between the control (@ 32%) and 47% shade (@ 30%) treatments and between the control and 73% (@ 29%) treatments. Relative humidity was highest for the control treatment (Fig. 3). Light intensity differed significantly between all treatments (Fig. 4).

FIELD 1990:

Plants which received full sun (control treatment) had a higher photosynthetic rate than did plants receiving 47% or 73% shade (Fig. 5). There is a trend of decreasing photosynthesis as the season progresses. The plants maintained under heavy shade had a photosynthetic rate of only one third that of full sun plants; by August this was reduced to a quarter of the photosynthetic rate of full sun plants.

Mean seasonal photosynthetic rates are significantly different between treatments (Table 1).

When all data are plotted together, a light response curve is generated. Plants receiving full sun have a similar photosynthetic rate as plants maintained in shade, at low light intensities (Fig. 7). Plants maintained in 73% shade had a range of internal CO₂ of 200-350 parts per million (ppm). Most leaves maintained in 47% shade had an internal CO₂ of 200-300 ppm, while plants maintained in full sun had an internal CO₂ of less than 250 ppm (Fig. 9). Mean seasonal internal CO₂ showed that plant maintained in full sun maintained significantly lower C_i than either plants kept in 47% or 73% shade ($p < .05$; Table 1). This result combined with similar photosynthetic rates between shaded and unshaded plants at low light indicates little physiological adjustment by E. alleni under shaded conditions.

Figure 11 shows that plants receiving 73% shade had a stomatal conductance below 0.2 $\mu\text{mol}/\text{m}^2/\text{s}$ for the season. This was significantly lower than the conductance of either the plants receiving full sun or 47% shade (Table 1).

In addition to reduced photosynthesis, high internal CO₂ and higher conductance, plants maintained in 73% shade did not flower. All plants maintained in full sun produced flowers; plants kept in two out of three 47% shade treatments flowered.

FIELD 1991:

Shade treatments were introduced in March. Plants receiving 73% shade flushed out with smaller leaves than plants receiving full sun or 47% shade. All plants receiving 73% shade died partway through the growing season. As in 1990, there is a seasonal decrease in photosynthetic rate (Fig. 6).

Generally, plants receiving full sun maintained a higher photosynthetic rate than plants maintained in the shade, even if the sun plants received comparable incidental irradiance as the shade plants (Fig. 8). Mean seasonal photosynthesis was significantly higher in the sun plants than in either shade treatment (Table 1).

As in 1990, sun plants maintained a lower internal CO₂ than shaded plants (Fig. 10). Mean seasonal internal CO₂ was significantly lower for the unshaded plants ($p < .05$; Table 1). Additionally, mean seasonal conductance was significantly greater for unshaded vs, shaded plants ($p < .05$; Table 1).

GARDEN/GREENHOUSE:

Plants maintained under shaded conditions in the experimental gardens and the greenhouse showed no acclimation to reduced irradiance. Figures 13 and 14 show representative light response curves obtained for a shaded vs. a non shaded plant. Plants maintained in the shade had lower

photosynthetic rates at saturating light than did sun plants (Table 2). Quantum yield was also lower for plants maintained under shaded versus unshaded conditions. Both mean maximum assimilation and mean quantum yield were significantly lower in shaded plants (Table 2). Had the shade plants acclimated, an increased efficiency in quantum yield would have been expected. There was no significant difference in either light compensation point or light saturation point for shaded vs. non shaded plants (Table 2), although shade plants had somewhat lower values than did sun plants.

TEM photographs of leaves from shaded and unshaded treatments reveal some adjustment to reduced irradiance. Chloroplast of plants receiving shade tended to have thicker, but fewer, thylakoid stacks than plants receiving full sun (Fig. 16a, 16b).

Discussion

The results of this study indicate that E. alleni cannot acclimate to shaded conditions. In the field shaded plants experienced lower photosynthesis, high internal CO₂, and lower stomatal conductance than plants not receiving shade. None of the heavily shaded plants flowered in the 1990 growing season, and had died during the second (1991) field season. It may be that light is an important factor in determining flowering capability. Additionally, plants maintained in 73% shade may

not have been able to accumulate sufficient resources in 1990 to enable them to survive a second field season in low light. The inability to accumulate sufficient resources or flower under low light would certainly have an influence on E. alleni's distribution. It would clearly be unable to survive in the closed canopy situation of the eastern temperate deciduous forest, where most of the total irradiance is absorbed by the overstory canopy. The lowered conductance and high internal CO₂ values of shaded plants indicates that E. alleni closes its stomata in low light conditions. Plants maintained in 73% shade had an internal CO₂ as high as 450 ppm. Eventually, respiration will exceed photosynthesis. It may be that E. alleni was experiencing some biochemical inhibition in low light. The resultant high internal CO₂ levels induced stomatal closure and thus lowered stomatal conductance.

Light response curves obtained also support the hypothesis that E. alleni is an obligate heliophyte. Plants maintained in 73% shade showed no shift towards the light response curves characteristic of shade adapted plants such as improved quantum yield, lower light compensation points or saturating photosynthesis at moderate light intensity. In fact, plants maintained in the shade had lower photosynthesis at low light than did plants maintained in full sun. This suggests that the prolonged exposure to low light may have

actually induced irreparable damage to the plant and made it unable to utilize available light efficiently at any level.

TEM photographs revealed an increased thickness in thylakoid stacks in shaded plants. This is a common response of plants when exposed to reduced irradiance (Osmond et.al., 1980; Ballantine and Forde, 1970). The increased thickness in membranes corresponds to an increase in photosystem II. This in turn leads to an increased efficiency in light harvesting ability. However, the shift in chloroplast structure was not reflected in gas exchange measurements.

E. alleni's inability to acclimate to shaded conditions is a reasonable explanation for why it is not found on the forest floor community; however, it does not explain why the plant is not found in other exposed habitats such as old fields or other rock outcrop environments. Shale barrens are isolated from one another. It may be that there is no means of dispersal that could transport E. alleni seeds away from the shale barren and onto an equally suitable non-barren site. Since E. alleni is found on disjunct shale barrens the history of its distribution and means of dispersal is of interest.

Additional studies of the shale barren endemics tolerance to low light levels would also be helpful. Are other endemics also obligate heliophytes as Keener suggests they all must be? Preliminary data obtained for the endemics Sennecio antennarifolius and Clematis coactilus suggests that this may

be the case. Work has been done looking at light tolerance of species within a genus (Lipscomb, 1991) and of species that are different ecotypes (Gauhl, 1975; Bjorkman 1968; Bjorkman and Holm, 1966). Bjorkman et.al. (1966) and Bjorkman (1968) found that different ecotypes of the same species had different light tolerance abilities similar to sun and shade species. This implies that light acclimation ability is fixed genetically as a result of natural selection. Additional work with E. alleni could also examine its long term adjustments to low light. It may be possible to gradually lower light intensity over several generations and ultimately produce plants capable of surviving shaded conditions.

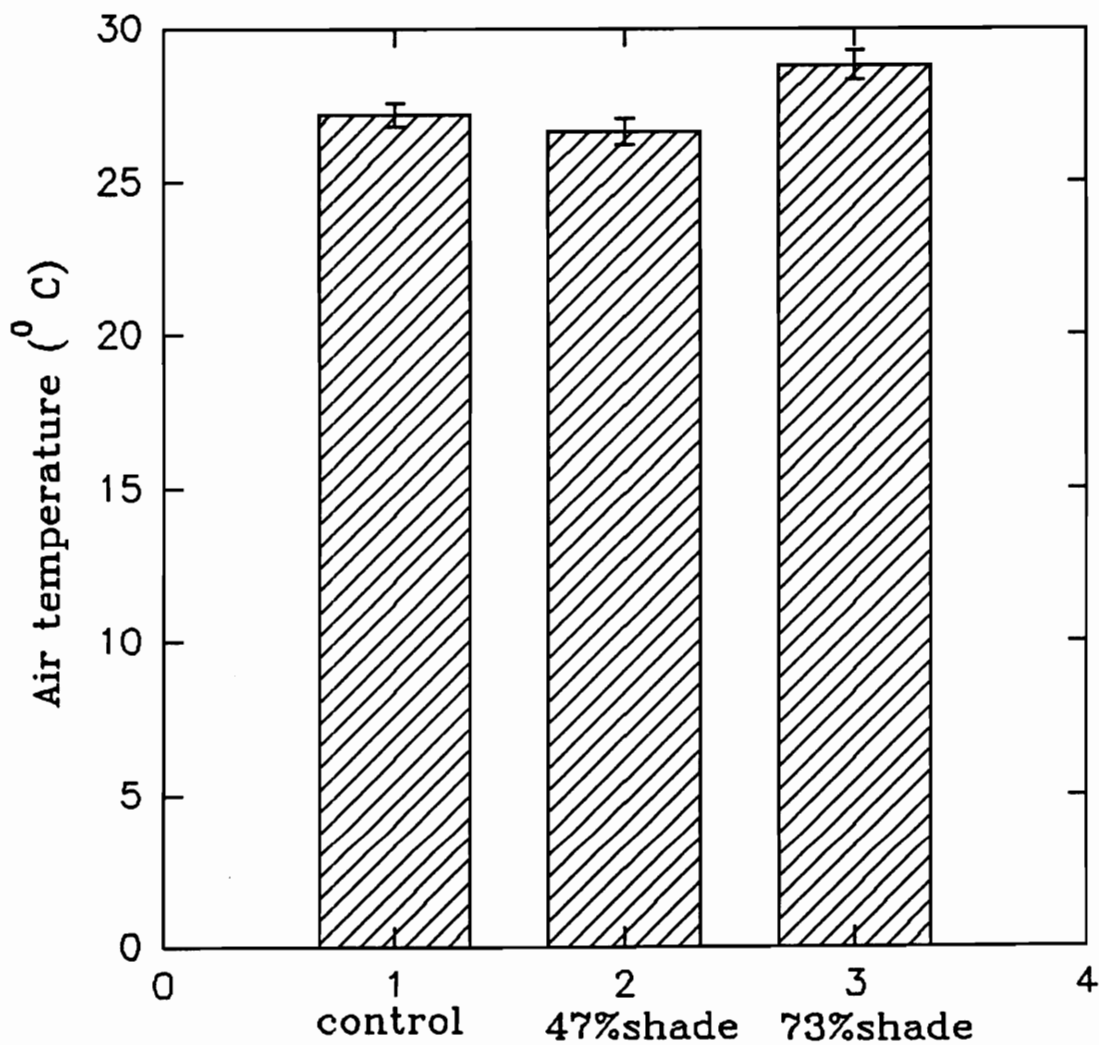


Figure 1: Seasonal mean air temperature at Ironto for each shade treatment (control, 47% shade, 73% shade).

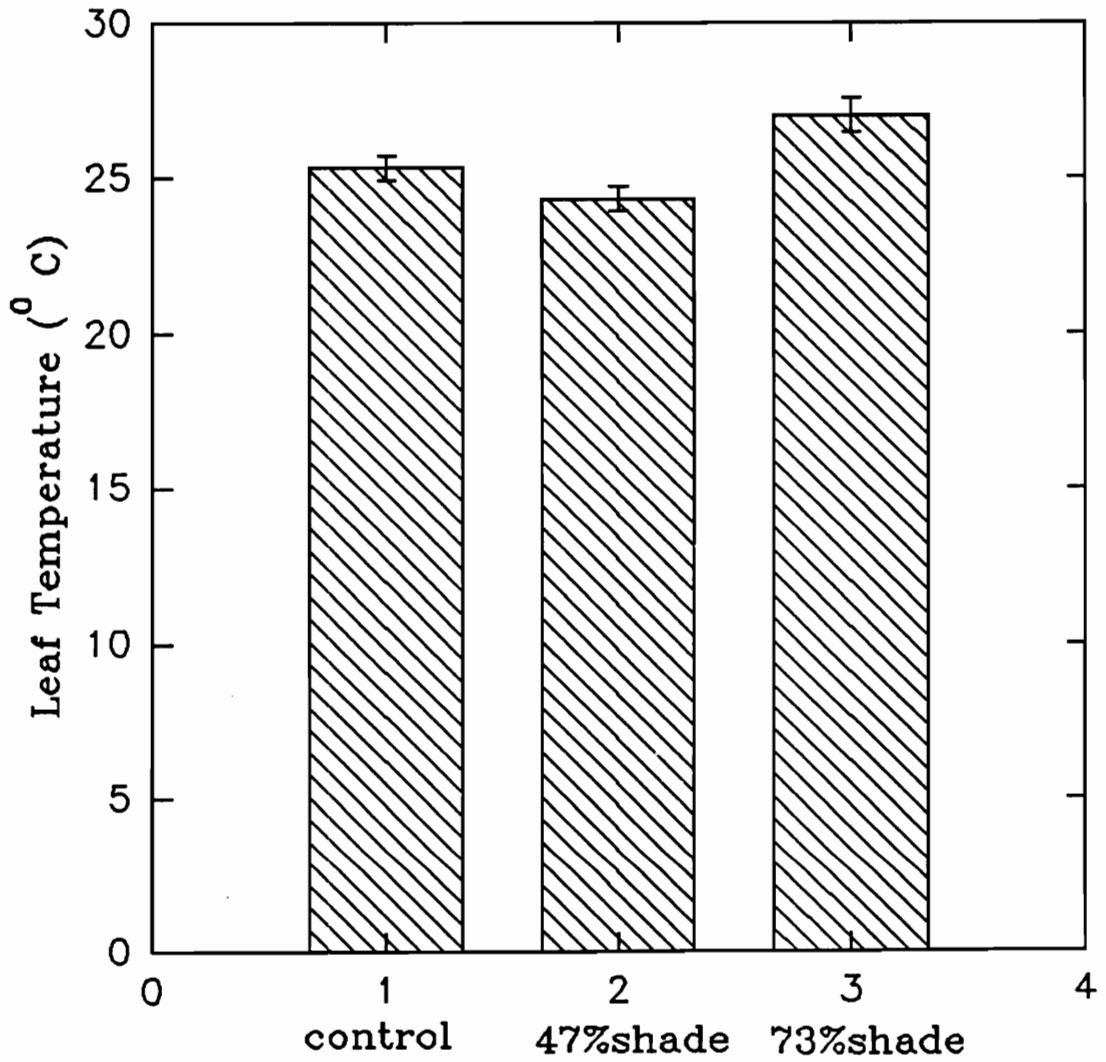


Figure 2: Mean leaf temperature of *E. alleni* at Ironto for each shade treatment (control, 47% shade, 73% shade) during the summer of 1991.

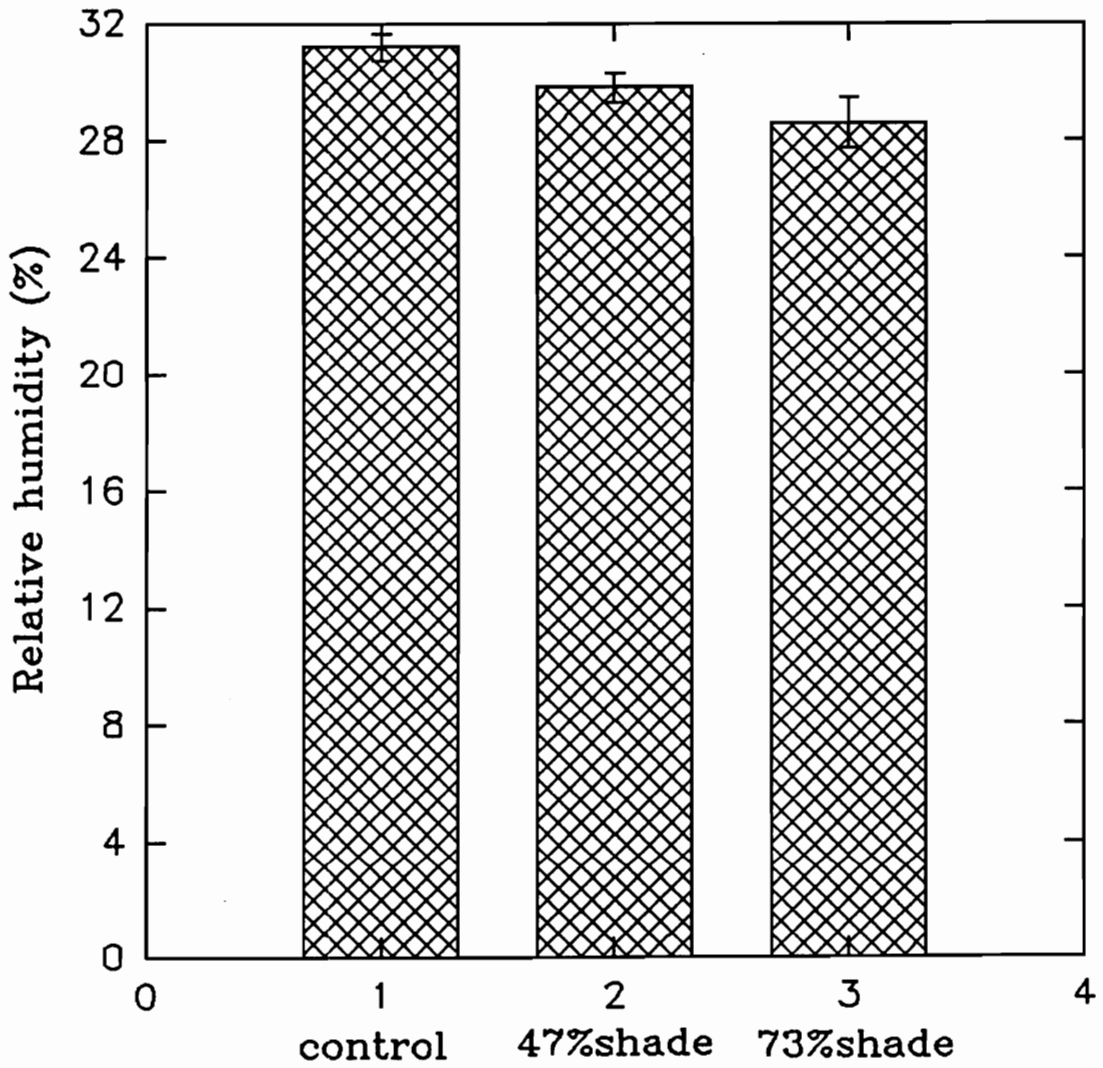


Figure 3: Relative humidity (%) at Ironto for each shade treatment (control, 47% shade, 73% shade) during the summer of 1991.

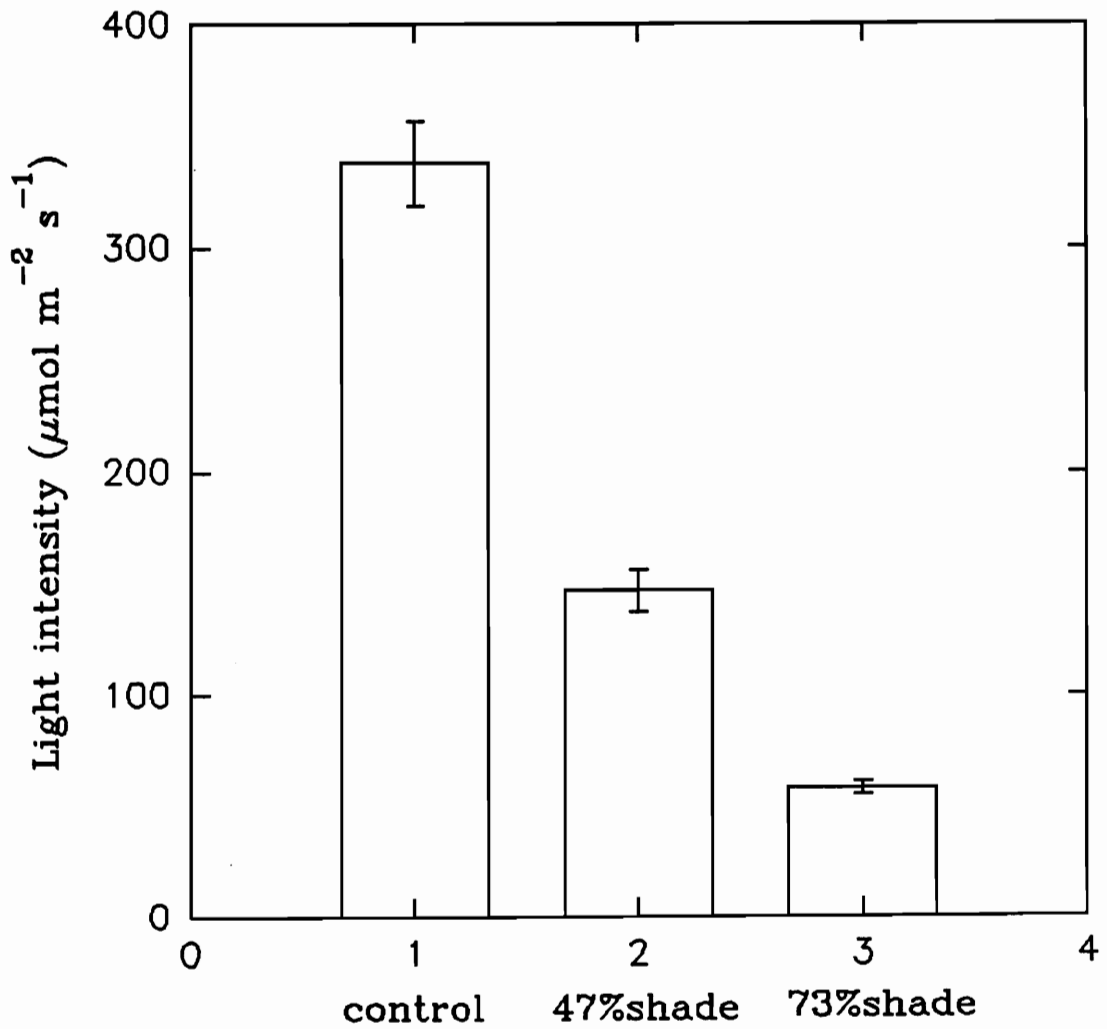


Figure 4: Light intensity at Ironto for each shade treatment (control, 47% shade, 73% shade) during the summer of 1991.

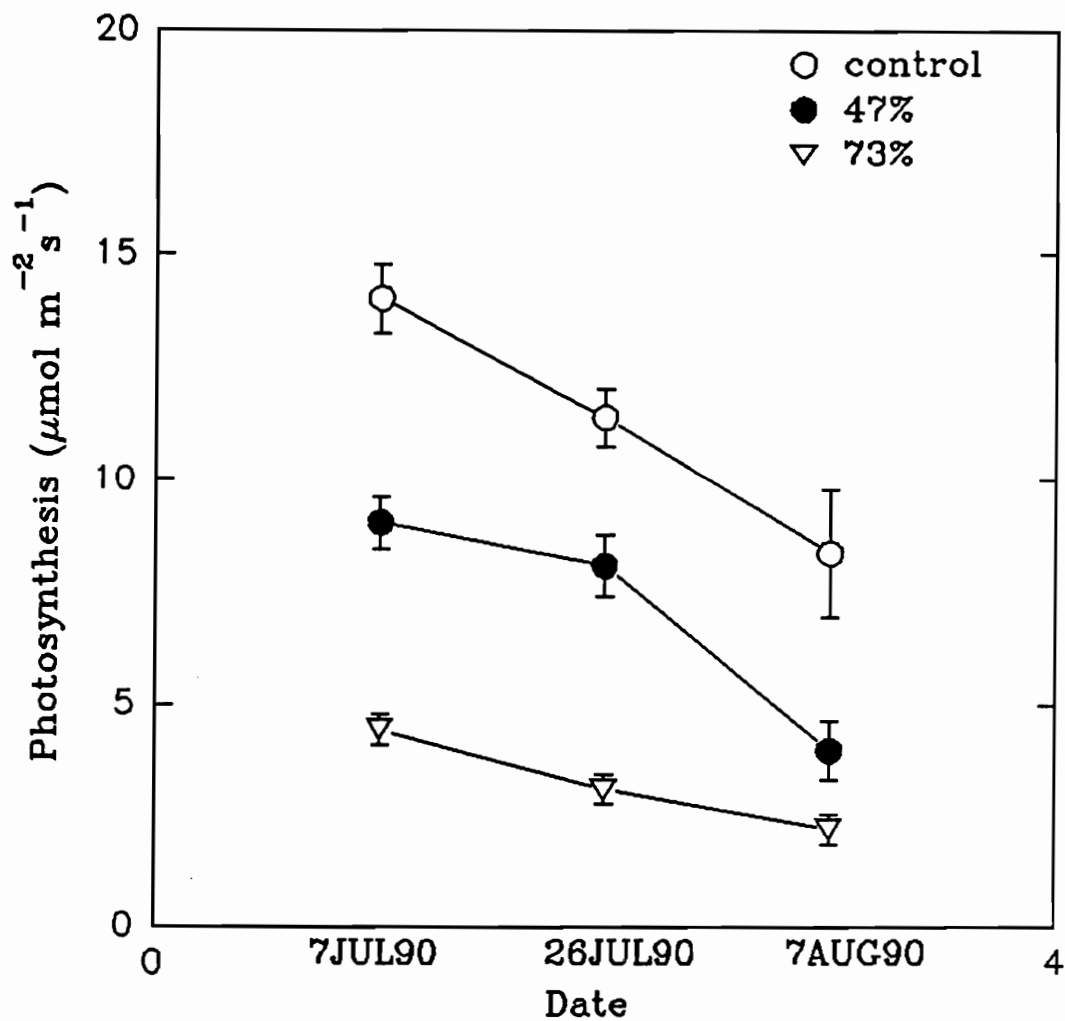


Figure 5: Mean photosynthetic rate for each treatment (control, 47% shade, 73% shade) on each date measured in 1990. $n = 15$ per treatment

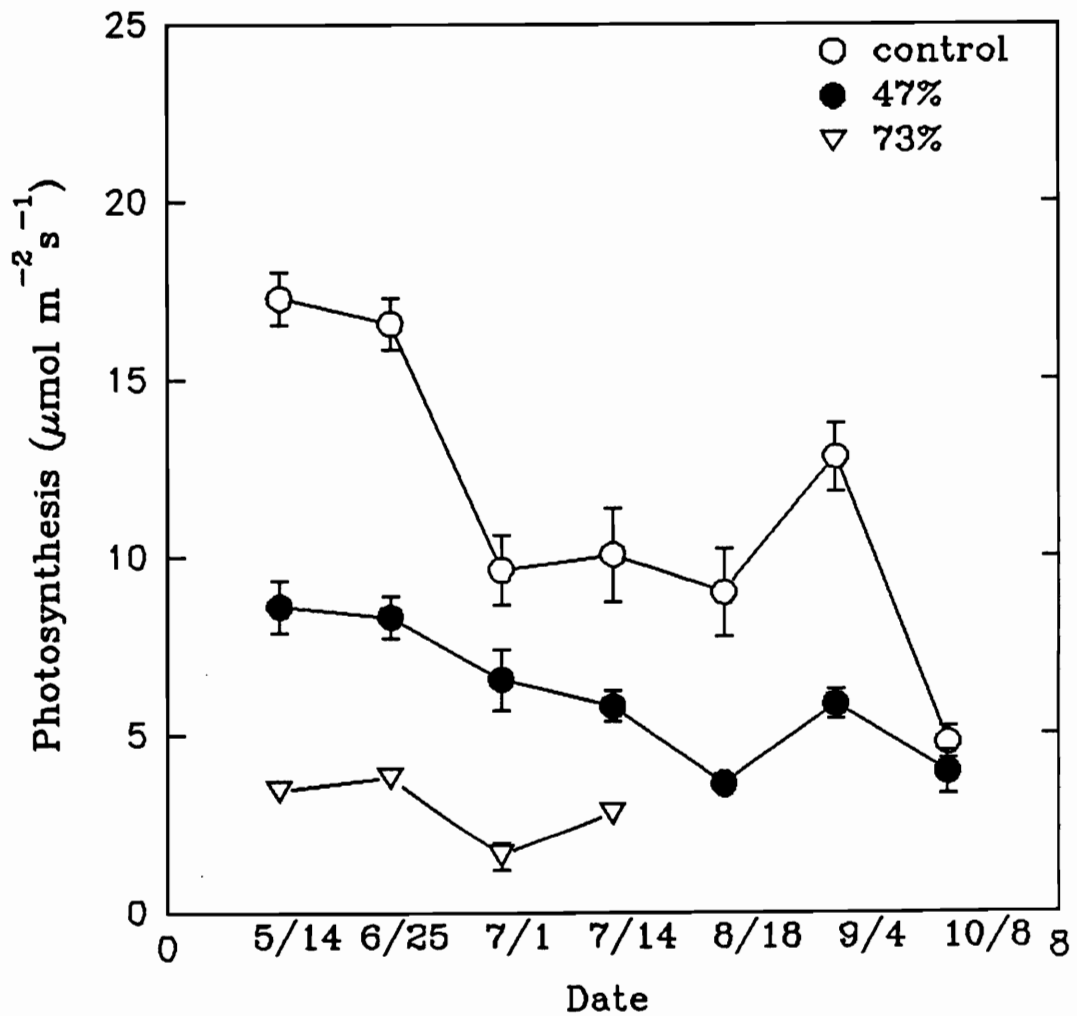


Figure 6: Mean photosynthetic rates for each treatment (control, 47% shade, 73% shade) on each date measured in 1991. $n = 15$ per treatment.

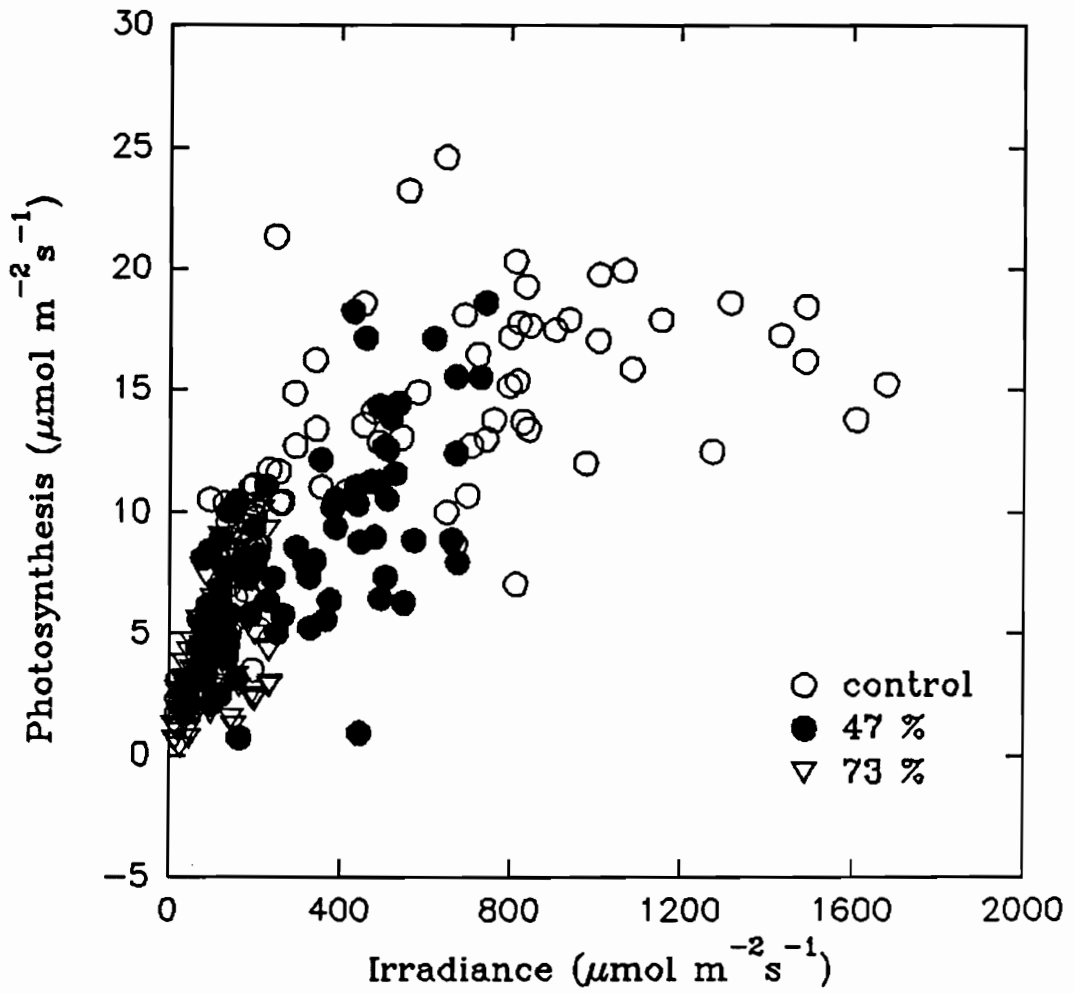


Figure 7: Summer photosynthetic rates measured in the field for all treatments (control, 47% shade, 73% shade) during 1990.

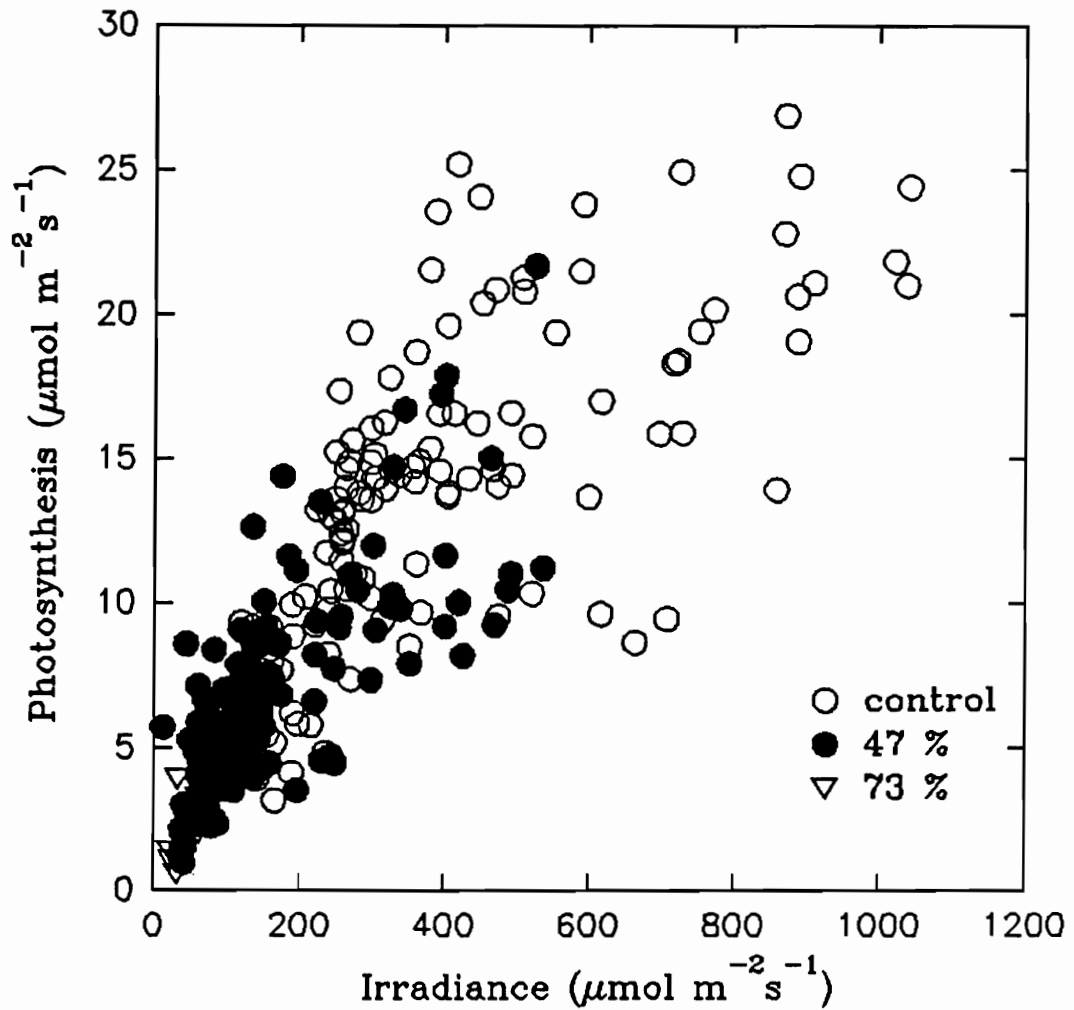


Figure 8: May-October photosynthetic rates measured in the field for all treatments (control, 47% shade, 73% shade) during 1991.

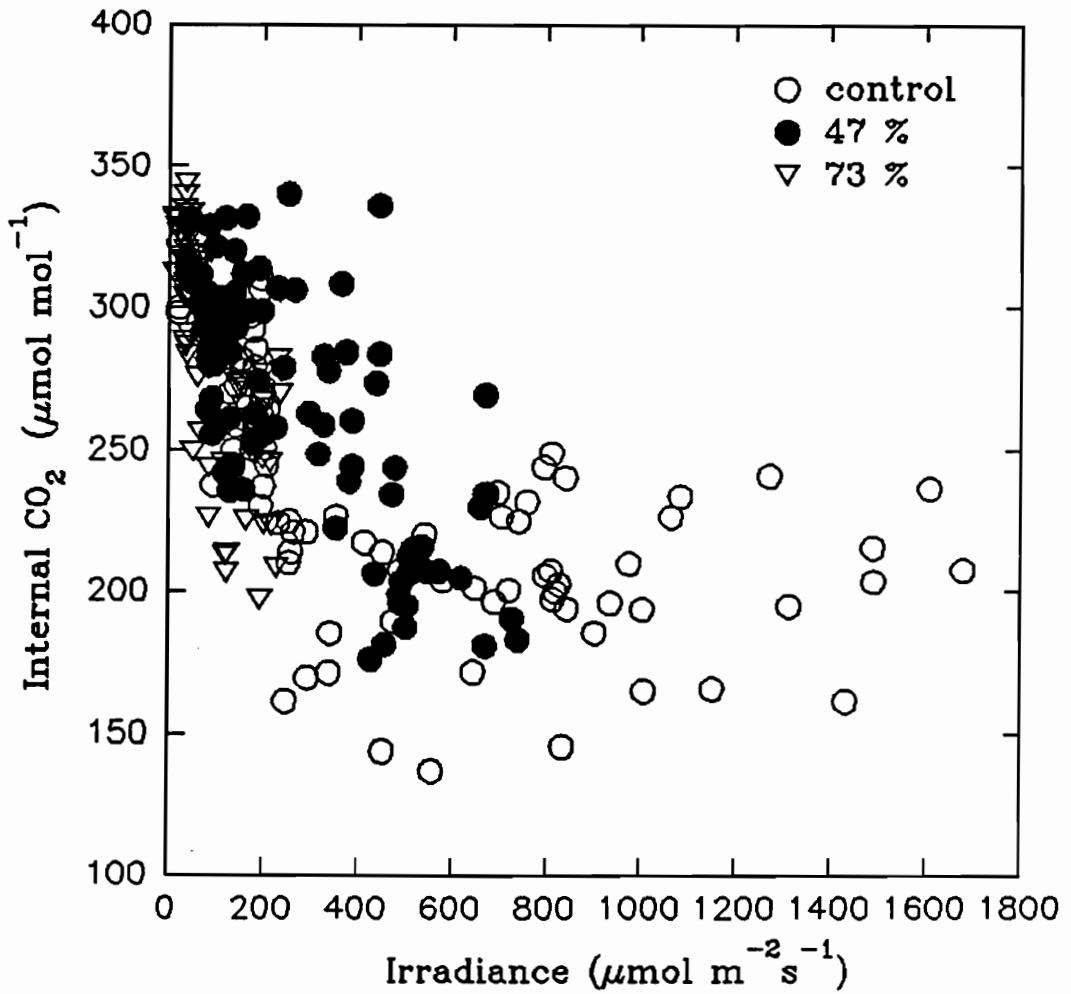


Figure 9: Internal carbon dioxide measured in the field for each treatment (control, 47% shade, 73% shade) during 1990.

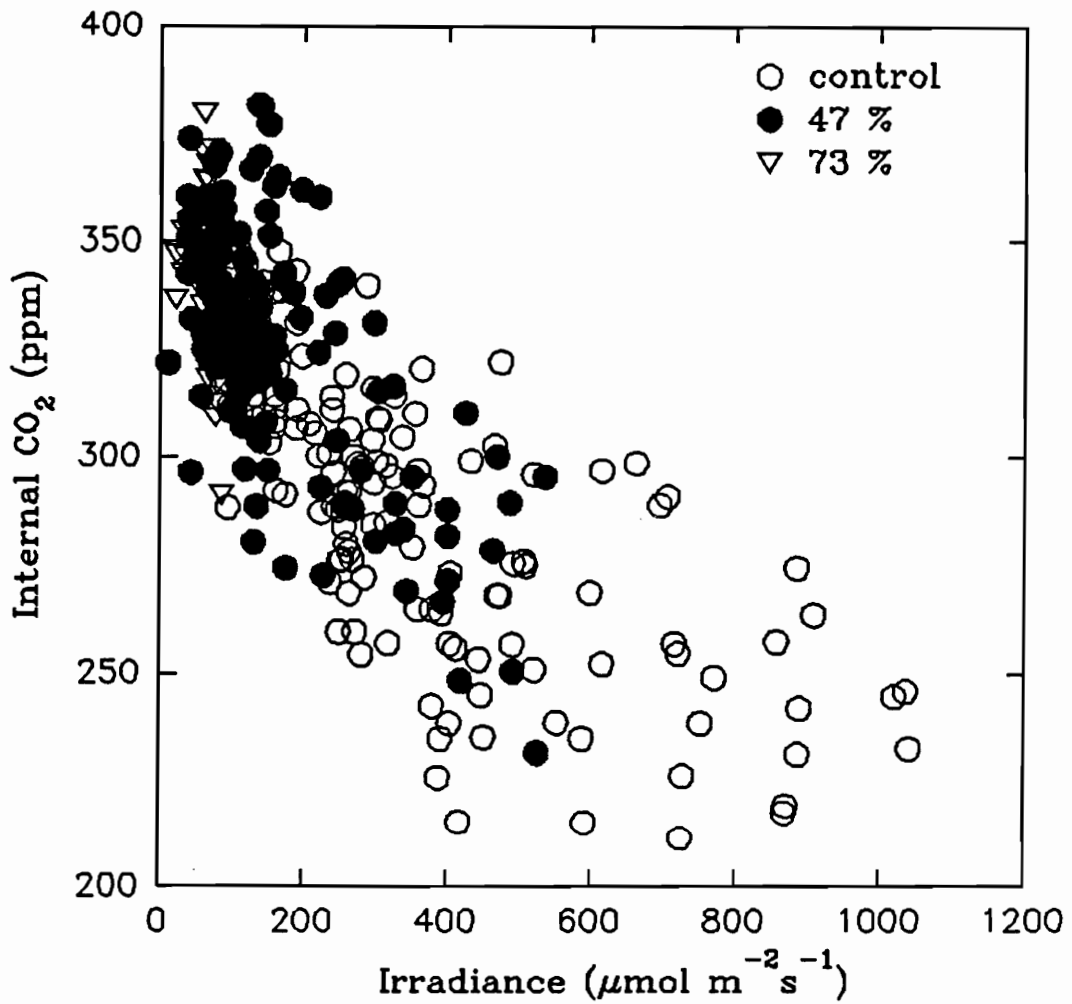


Figure 10: Internal carbon dioxide measured in the field for each treatment (control, 47%shade, 73% shade) during 1991.

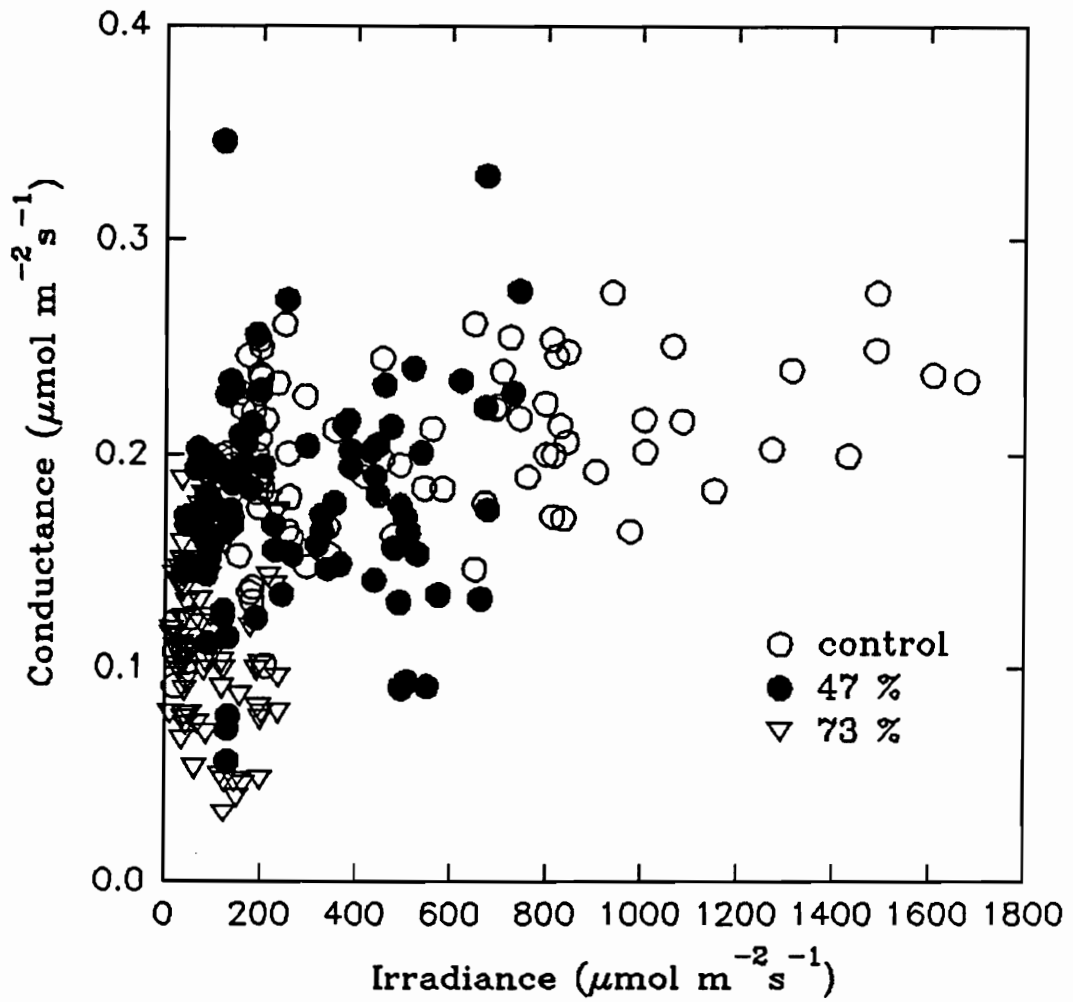


Figure 11: Stomatal conductance measured in the field for each treatment (control, 47% shade, 73% shade) during 1990.

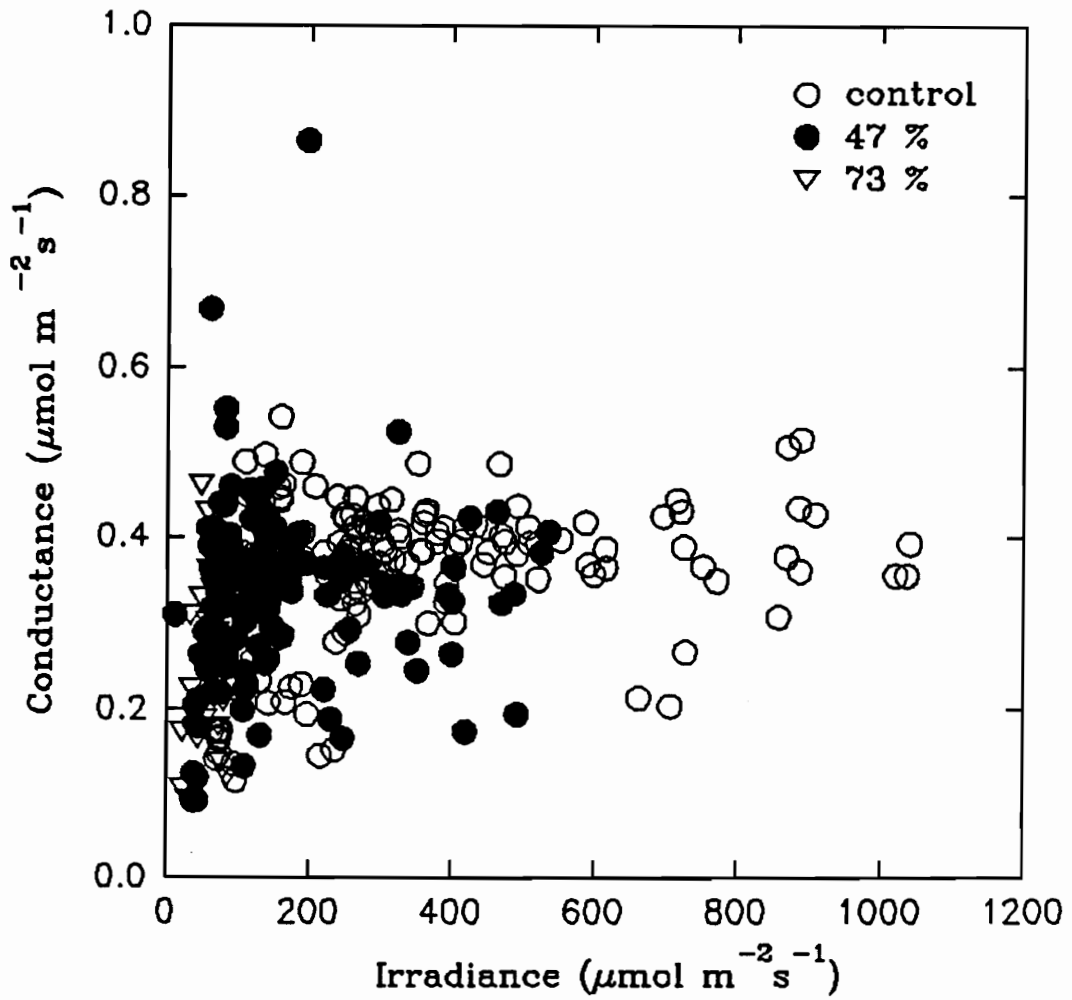


Figure 12: Stomatal conductance measured in the field for all treatments (control, 47% shade, 73% shade) during 1991.

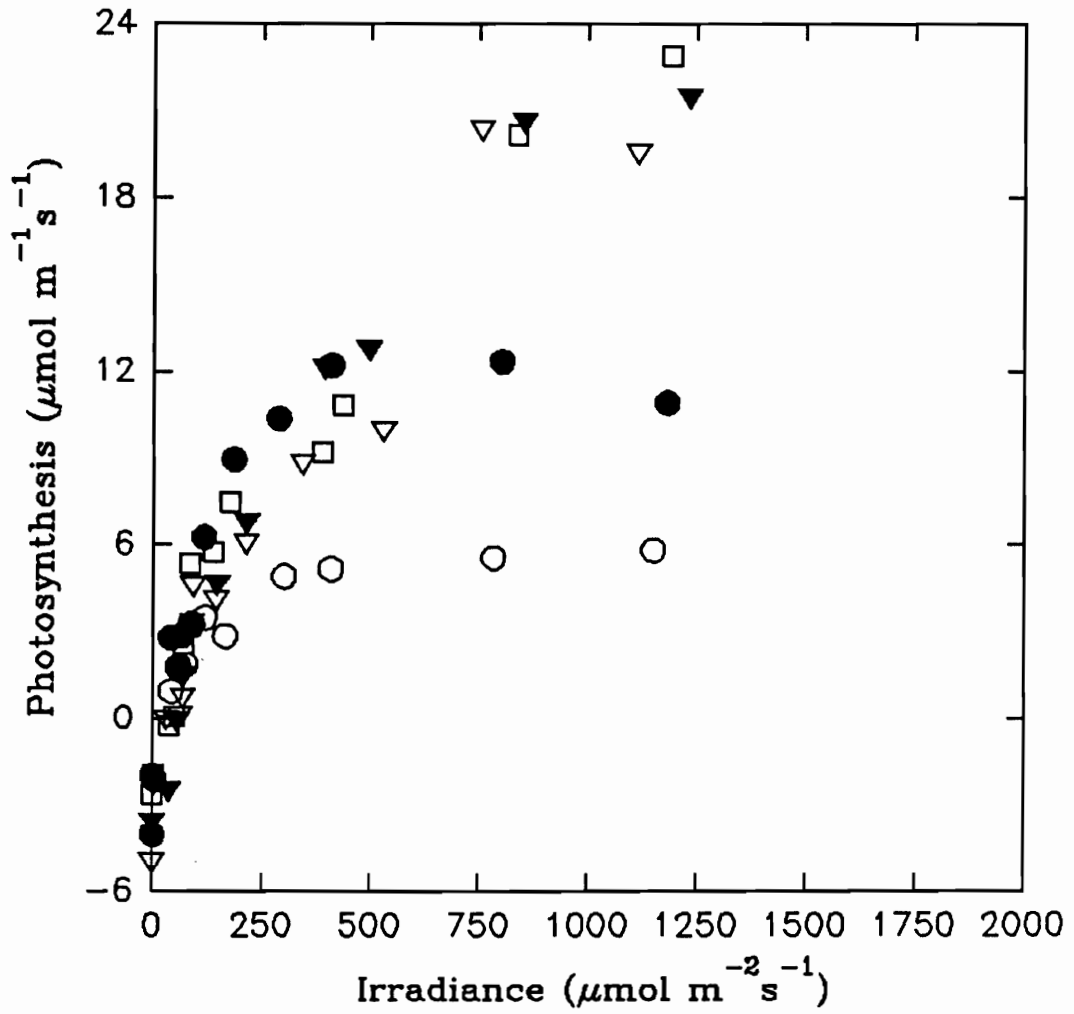


Figure 13: A representative light response curve for a plant maintained in unshaded conditions.

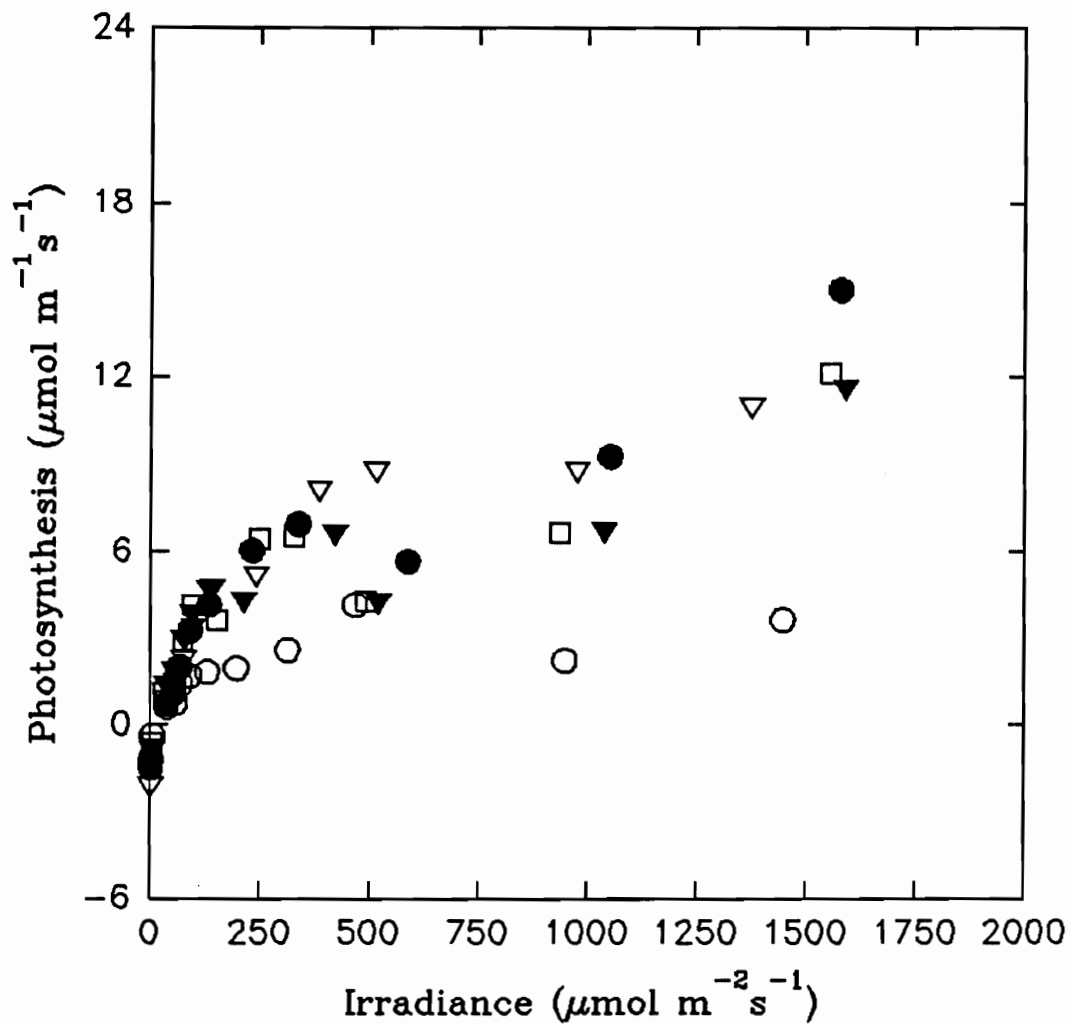


Figure 14: A representative light response curve for a plant maintained in shaded conditions. Each symbol represents a curve obtained from a single leaf.

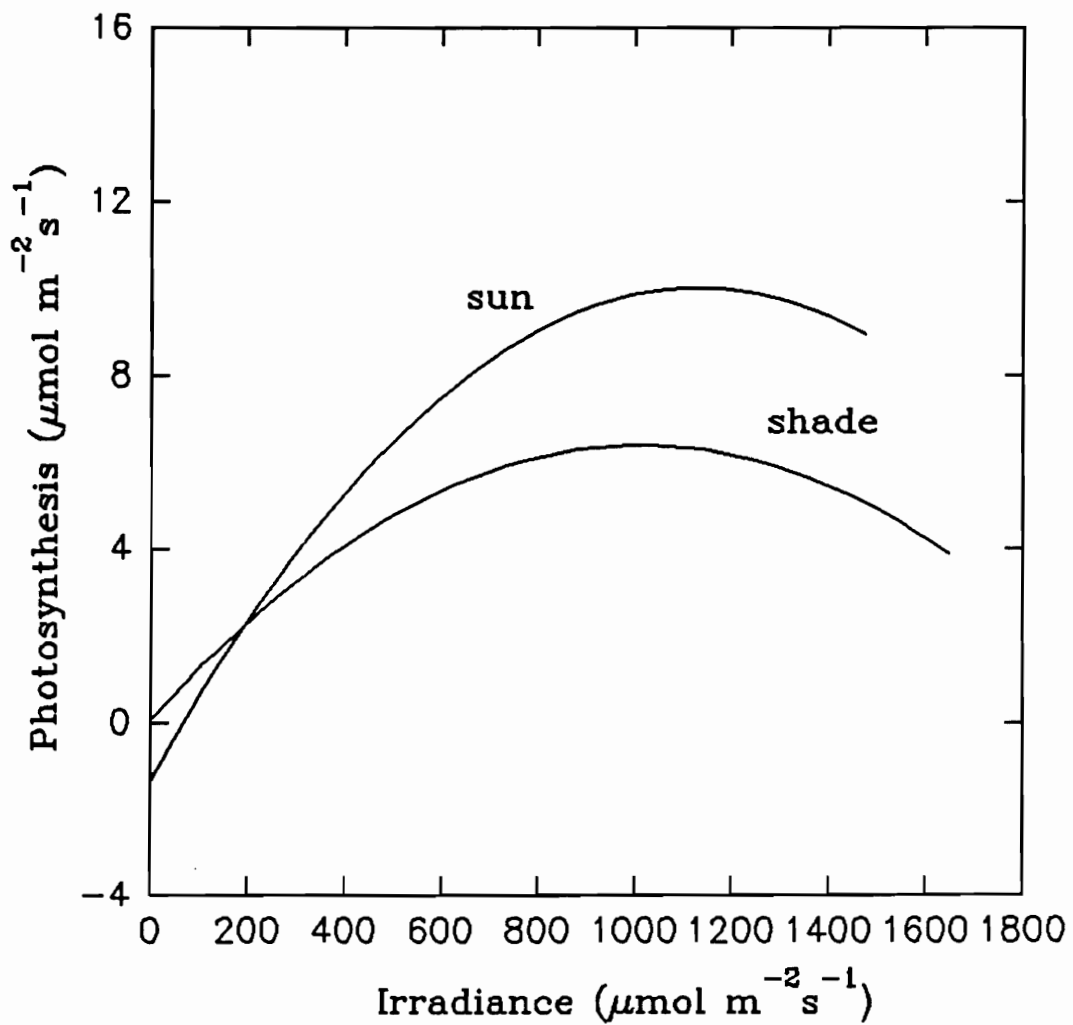
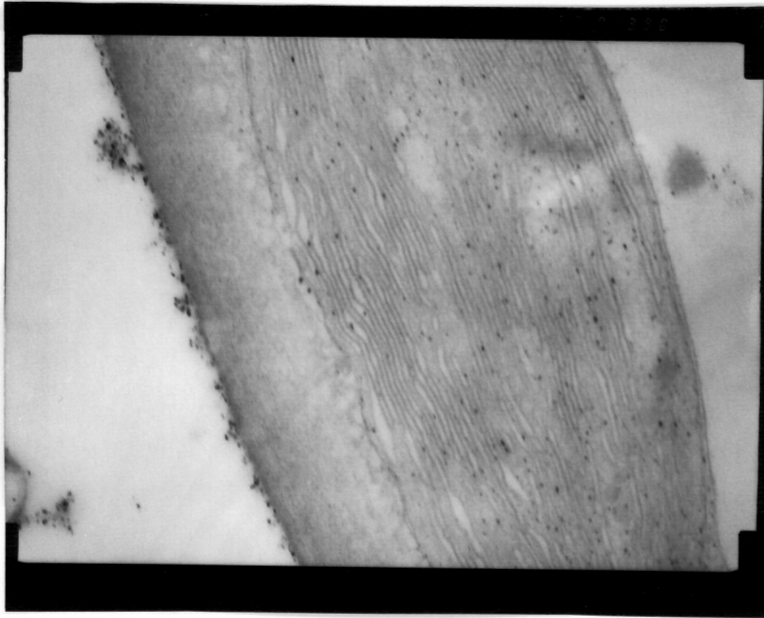


Figure 15: Light response curves generated from plants maintained in shaded or unshaded conditions.

a



b

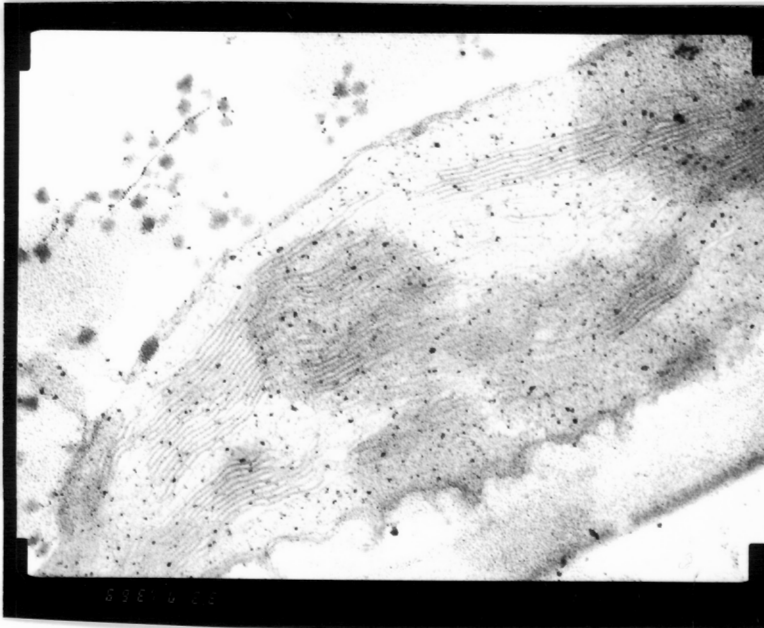


Figure 16: Representative chloroplast photographs from plants maintained in unshaded (a) or shaded (b) conditions. Magnified 33,000 times.

Table 1: Seasonal means (std.dev.) of photosynthesis, conductance, and internal carbon dioxide for plants shaded in the field during 1990 and 1991.

Year	Treatment	Photosynthesis ($\mu\text{mol}/\text{m}^2/\text{s}$)	Conductance ($\mu\text{mol}/\text{m}^2/\text{s}$)	Internal CO_2 ($\mu\text{mol}/\text{m}^2/\text{s}$)
1990	control	11.87 ** (5.09)	.196 ** (.041)	233.10 ** (43.33)
	47% shade	7.67 ** (4.04)	.178 ** (.050)	264.92 ** (44.11)
	73% shade	3.49 ** (2.11)	.847 ** (.085)	304.7 ** (53.27)
1991	control	12.31 ** (5.96)	.360 ** (.087)	291.78 ** (35.38)
	47% shade	6.55 ** (3.49)	.333 ** (.100)	327.36 ** (28.31)
	73% shade	3.14 ** (1.13)	.264 ** (.091)	344.22 ** (20.56)

** All treatments (within a field season) were significantly different from each other at the .05 level, using a t-test, for photosynthesis, conductance, and internal carbon dioxide.

Table 2: Mean (std. dev.) light response curve (LRC) values for sun and shaded Eriogonum alleni.

LRC values	Unshaded plants	Shaded plants
maximum photosynthesis ($\mu\text{mol}/\text{m}^2/\text{s}$)	15.259 ** (5.922)	6.738 ** (4.84)
light saturation ($\mu\text{mol}/\text{m}^2/\text{s}$)	1094.38 (195.79)	937.88 (408.7)
Light compensation pt. ($\mu\text{mol}/\text{m}^2/\text{s}$)	41.41 (17.2)	32.05 (17.72)
quantum yield	.063 ** (.025)	.037 ** (.013)

** Maximum photosynthesis and quantum yield were significantly different between treatments at the .05 level, using a t-test.

CHAPTER 4: ACCLIMATION TO HEAT

Introduction

Plants can experience a multitude of temperatures through their lifetime, both on a seasonal and diurnal basis. Thus the ability to withstand a variety of temperatures can be a valuable adaptive strategy. Lange et.al. (1974) state that changing temperature optima must be a part of the adaptive ability of plants occupying habitats with variable temperature environments.

Heat stress is a common risk faced by many plant species. Levitt (1980) declares that potentially dangerous high temperatures occur in natural habitats. Heat stress may be acute or chronic: acute heat stress is exposure to high temperatures of short duration, while chronic heat stress is prolonged exposure to temperatures that just exceed the temperature optimum for that plant. Plants have developed numerous ways of dealing with heat stress, through avoidance or tolerance mechanisms.

Heat avoidance can take several forms. Plants may rely on increased insulation (bark), on decreased photorespiration, on reflectance or transmittance, or on transpirational cooling (Levitt, 1980). More drastic efforts at heat avoidance are dropping leaves, or going dormant. Dormancy has been shown to be an effective method of surviving extreme stresses (Salisbury and Ross, 1992).

Heat tolerance is manifested in plants by changes in membrane structure, by the production of heat shock proteins, or by change in photosynthetic thermal tolerance. Alteration of membrane structure can result in changes in membrane fluidity, which is in turn influenced by the level of unsaturation in the fatty acids of the phospholipid bilayer. Plants adapted to high temperatures can have membranes containing a high proportion of saturated to unsaturated fats (Hadley, 1985). A high level of saturation would reduce membrane fluidity and would allow the plant to maintain membrane stability at high temperatures. In addition to alteration of fatty acids, membrane integrity may be maintained by sugars. Santarius (1973) found that during temperature stress thylakoid functioning was maintained by the presence of sugars. He hypothesized that the sugars stabilized membrane functioning by binding to proteins and preventing denaturation.

Heat shock proteins are also produced by plants in response to temperature stress (Burke et.al. 1985, Kee and Nobel 1986, Lin et.al. 1984). These authors hypothesize that heat shock proteins confer temperature stability by protecting transcription, translation, and energy production. Heat shock proteins are located in association with the nucleus, ribosomes, and mitochondria (Lin et.al. 1984).

Finally, the overall photosynthetic pathway employed by

a plant may allow it to tolerate high temperatures. Cyclic photophosphorylation is believed to be the most primitive form of photosynthesis (Raven et.al. 1981). Its appearance in a wide variety of organisms (prokaryotes, algae, higher plants) implies that it is a highly conserved form of producing energy. The broad range of environments in which organisms with cyclic-photophosphorylation are found implies the ability to withstand high temperatures.

Additionally, C_4 and CAM pathways of photosynthesis are often found in plants from hot arid environments, and are traditionally associated with plant ability to withstand high temperatures (Barbour et.al. 1987). Berry (1975) however, points out that many C_3 plants are also found in hot environments.

Mid-day temperatures on shale barrens can approach 37-40 degrees Celsius. This is comparable to temperatures found in the four desert regions of North America (Barbour et.al., 1987). In addition shale barrens experience high soil surface temperatures, in excess of 50 degrees C (Platt, 1951, Kaltenbach, unpubl., pers. obs.). Platt (1951) postulated that most plants found in the eastern deciduous forest could not tolerate the shale barren environment in part because of high temperatures. The implication is that the shale barren endemics are capable of withstanding such temperatures; however, there are no data to support or deny this hypothesis.

Thus, the purpose of this study was to provide some basic data on the physiological heat tolerance and acclimation ability of the shale barren endemic Eriogonum alleni. The approach taken for this study was to examine membrane integrity as determined by electrolyte leakage studies, and photosynthetic acclimation ability in growth chamber maintained plants. These physiological characteristics were selected because the ability to maintain photosynthesis and membrane integrity are essential for plant survival in hot conditions.

Hypothesis (General): E. alleni is capable of acclimating to elevated temperatures at the physiological and/or cellular level.

Specific Hypotheses:

Ho: There is no difference in the ability to maintain membrane integrity between E. alleni plants maintained at elevated or control temperatures.

Ho: There is no difference in temperature optimum of photosynthesis between E. alleni plants maintained at elevated or control temperatures. There is no higher temperature tolerance for photosynthesis of E. alleni plants maintained at elevated vs. ambient temperatures.

Materials and Methods

GROWTH CHAMBER STUDY:

Eriogonum alleni plants were initially grown from seed in a perlite/Pro-Mix potting medium. Mature plants were transferred to into two growth chambers (Sherer Model CEL 25-7HL), one of which was maintained at control temperatures (25°C day/18°C night) and the second of which was maintained at elevated temperatures. The temperature of the elevated growth chamber was started at 25°C day/18°C night and gradually raised to a final temperature of (37°C day/25°C night) over about a two week period. The slow increase in temperature was to prevent shocking the plants. The temperature of the elevated growth chamber was selected to correspond to high daytime temperatures as measured at the Irono shale barren.

Five plants were placed into each growth chamber. All leaves on each plant were tagged. Any leaves produced during the interval of increasing temperature in the elevated growth chamber were also tagged. Campbell Scientific Dataloggers were placed in each chamber to monitor air, soil, and leaf temperatures, as well as relative humidity and irradiance. All plants were of the same age, and all studies were carried out on leaves as similar in size as possible.

Electrolyte leakage was measured with a conductivity meter. Leaves from each plant in each growth chamber were

harvested. Five leaf disks (6mm diameter) from each leaf were cut out with a hole punch. Care was taken to not crush the disks. The leaf disks were rinsed in distilled water to remove electrolytes released from cells during cutting. The leaf disks were then placed into test tubes containing double distilled water; the test tubes were placed in to a 25°C waterbath and allowed to equilibrate for 30 minutes. Conductivity was measured at 5 degree increments through to 55 degrees. Leaf disks were allowed to re-equilibrate for 30 minutes with every temperature increase. This procedure established the approximate temperature at which electrolyte leakage occurred. A second trial was conducted with new leaf disks to pinpoint the temperature at which membrane breakdown occurred. Leaf disks were again equilibrated at 25°C, transferred to a 40°C waterbath and allowed to re-equilibrate. Temperature was increased at 2-3 degree increments to 60 degrees, with conductivity measured at each interval.

Photosynthetic rates were measured for all plants from each growth chamber, and temperature response curves obtained. The PACsys-9900 gas exchange system was used. Plants were provided with photosynthetically saturating light intensity. To obtain temperature response curves each plant was oriented with leaves inside a cuvette. Temperature was initially established at as low a level as possible, and increased at 2-3 degree increments. Leaves were allowed to equilibrate at

each temperature before photosynthesis was measured. Temperature was increased until photosynthetic rates were at or below zero. At this point the curve was considered complete.

DATA ANALYSIS:

Mean air, soil and leaf temperatures, relative humidity, and light intensity during both the day and night were determined for each growth chamber. For electrolyte leakage, conductivity was plotted vs. temperature for each plant from each growth chamber. Regression equations were calculated (Sigma Plot4.1), and slopes were obtained to provide an indication of each sample's membrane integrity.

The slopes of samples from each growth chamber were compared using the Mann-Whitney Rank Sum test. This test is analogous to the t-test, but does not assume a Gaussian, or normal, distribution (Zar, 1984). This test was used instead of the parametric t-test because of the small sample size in each growth chamber (n=5 plants). The temperature at which membrane integrity completely broke down was also determined for each sample from each growth chamber; the Mann-Whitney test was again used to determine statistical significance.

Mean maximum photosynthetic rates for plants from each growth chamber were calculated, as well as the mean temperature at which photosynthetic rates were at or below

zero. The Mann-Whitney test was used to determine statistical significance between treatments.

Results

Environmental data consisting of air temperature, soil temperature, leaf temperature, % relative humidity and light intensity from each growth chamber are presented in Figures 1 through 9. Air and soil temperatures in the elevated growth chamber stayed well above the temperatures for the control growth chamber during both the day and the night over several days (Figs. 1-4). Additionally, the temperatures in each growth chamber stayed consistent over time. The daytime temperatures are closely related to those found in the field during midday. Air, soil and leaf temperatures stayed close to one another in the control growth chamber, however, in the elevated growth chamber leaf temperature was about 5 degrees above air and soil temperature (Figs. 7,8). Relative humidity in the elevated growth chamber was between 30 and 35%; this is comparable to seasonal relative humidity found in the field during 1991. Humidity over several days stayed fairly stable in the elevated growth chamber, but fluctuated in the control growth chamber. At night relative humidity fluctuated in both growth chambers (Figs. 5,6) but was higher in the control growth chamber than in the elevated growth chamber. Light intensity in both growth chambers was considerably lower (Fig.

9) than irradiance found in the field (see Chapter 2, Fig. 5). The low light level was unfortunately a function of the growth chamber.

The electrolyte leakage study revealed no acclimation to elevated temperatures by plants maintained in the elevated growth chamber. There was no significant difference ($p > .05$) between treatments (control vs. elevated temperatures) of the temperature at which conductivity sharply increased, for either the trial conducted at broad (5° C) temperature increments or narrow ($2-3^{\circ}$ C) temperature increments (Table 1). Plants maintained at elevated temperatures did not show acclimation to heat by maintaining membrane integrity.

Figures 10 (a-e) and 11 (a-e) present electrolyte leakage plots at broad temperature intervals from each plant from the control and elevated growth chambers. Regressions calculated for both before and after the break temperature are shown. The slopes of the regression lines provide an indication of membrane leakiness, and are presented in Tables 1 and 2. As with break temperatures there was no statistically significant difference ($p > .05$) between control and elevated temperature treatments. Figures 12 (a-e) and 13 (a-e) present conductivity vs. temperature for plants from each growth chamber measured at narrow intervals. As with the first trial, regressions and slopes were determined for each sample. There was no statistically significant difference ($p > .05$) in

membrane leakiness for plants maintained at elevated or control temperatures. Plants subjected to increasing temperature at narrow intervals did have a slightly higher break temperature than did plants exposed to temperature increases at 5 degree intervals.

Temperature response curves for plants maintained at elevated temperatures indicate a lower photosynthetic rate, overall, than plants maintained at control temperatures. (Figs. 14 and 15). Figure 16 is a summary of all plants for each treatment temperature. Plants from the elevated growth chamber had negative net photosynthetic rates at lower temperatures than did plants from the control growth chamber (Table 3); however, these differences were not significant.

Although physiological measurements showed no statistically significant differences between plants maintained in control vs. elevated conditions, plant kept in the elevated growth chamber did show a marked difference in leaf morphology as compared to plants in the control growth chamber. Leaves from the elevated growth chamber were long and slender as compared to those from the control growth chamber (Fig. 17). Leaves on plants in the field, while larger than the laves produced in the elevated growth chamber, are also elongate in shape.

Discussion

Both the results from the electrolyte leakage study and from the temperature response curves indicate no acclimation to prolonged elevated temperatures on the part of Eriogonum alleni. Although there were no statistically significant differences in the electrolyte leakage study, there were potentially important biological differences between the plants maintained at elevated vs. control temperatures. The plant kept at higher temperatures had slightly lower break temperatures than the plants maintained under control conditions. The prolonged exposure to high temperatures that they experienced may have in fact been detrimental to the point that they experienced a decreased ability to maintain membrane integrity as compared to their control counterparts. This is also supported by the slopes obtained from regressions calculated from each sample. Plants maintained in the elevated growth chamber had steeper slopes than plants in the control growth chamber, indicating that their membranes were essentially "leaky". The increased electrolyte leakage experienced by the plants maintained at elevated temperatures could be an indication of an increase in membrane fluidity. Membrane fluidity to a large extent is controlled by the degree of saturation of the fatty acid tails in the phospholipid bilayer. The greater the level of saturation, the greater the membrane fluidity. It is possible that the

E. alleni plants maintained under elevated temperatures could not adjust fatty acid saturation to maintain the selective permeability of its membranes.

E. alleni is a C₃ plant. Osmond et. al. (1980) found that the cold adapted Atriplex sabulosa experienced electrolyte leakage at approximately 52 degrees , similar to E. alleni when measured at narrow temperature intervals. Tidestromia oblongifolia, a C₄ desert species, however, did not undergo electrolyte leakage until 55 degrees Celsius. Both these species as well as E. alleni experienced photosynthetic shutdown at temperatures well below the point they experienced electrolyte leakage. this implies that the photosynthetic apparatus is more sensitive to high temperature than is the plasma membrane (Levitt, 1980, Osmond et.al., 1980).

Interestingly, when Levitt (1980) examined electrolyte leakage in response to freezing injury he found no change in actual membrane permeability. Electrolyte leakage was the result of potassium efflux from the cells. He attributed this loss to a breakdown of ion pumps. It may be that heat damage affects membrane ion pumps as well as phospholipid structure.

Photosynthesis may be affected by high temperature in a variety of ways. The photochemical reactions may be influenced through the breakdown of thylakoid membranes. Quinn (1988) found that temperatures from 35-45 degrees

celsius caused unstacking of grana. Additionally, the deterioration of the proton gradient responsible for driving photophosphorylation may occur. Armond et.al. (1978) postulate that high temperature can damage light harvesting complexes, thereby reducing quantum yield.

Mooney et.al. (1978) define photosynthetic acclimation potential as "...the ability of a given genotype to change its photosynthetic characteristics in an adaptive manner in response to changes in environmental conditions...." The results obtained from temperature response curves imply that E. alleni is not tolerant of prolonged high temperature exposure. If it were capable of acclimation, a shift towards a higher temperature optimum of photosynthetic rates would have been expected (Osmond et.al., 1980). Mooney et.al. (1978) point out that a shift in temperature optimum is not a sign of acclimation if photosynthetic rates are lower than they would have been at ambient temperatures. Since E. alleni not only had lower photosynthesis but a temperature shift towards lower instead of higher temperatures it was indicating no acclimation to elevated temperature conditions.

Weiss and Berry (1988) have found that RuBisco activity decreases precipitously in cotton past 30 degrees celsius. Thus E. alleni in the elevated growth chamber was probably experiencing biochemical inhibition in the form of being unable to fix Carbon dioxide. Bjorkman et.al. (1975)

determined that photorespiration and oxygen inhibition increase with high temperatures. Oxygen could have been out competing carbon dioxide for available RuBisco, thus lowering photosynthesis.

In addition to being heat stressed, the plants in the elevated growth chamber (and in the control growth chamber) were light limited. E. alleni is a high light requiring plant and growth chamber conditions could provide only a fraction of what the plants experience in the field. Thus the photosynthetic rates for plants in both chambers was considerably less than what the plants are capable of under high light conditions. Repeating this study with additional available light would eliminate the confounding effects of low light and clarify E. alleni's responses as a function of temperature.

Levitt (1980) states that plants experiencing prolonged high temperature are ultimately water stressed. Although E. alleni plants in the growth chambers were well watered, they may have maintained a heavy transpiration rate in an effort to remain cool. Leaf temperatures in the elevated growth chamber remained near 40 degrees (Fig 10)

This study indicates that E. alleni is not capable of acclimating to prolonged high temperatures. Extended exposure to elevated but sub-lethal temperatures may undermine heat tolerance by draining carbon resources (Levitt, 1970). Over

time E. alleni in the elevated growth chamber produced smaller and smaller leaves. Essentially, the plant was caught in an unbreakable circle; it did not have the available resources to manufacture normal leaves, and the small leaves, when faced with elevated temperatures and low light levels, could not photosynthesize enough to re-establish a carbon reserve. However, the plant flourishes in the field where it routinely experiences daily temperatures equal to or exceeding those experienced in the growth chamber. It may be that E. alleni is capable of sustaining short periods of high temperature (eg midday temperatures) but cannot tolerate prolonged exposure. Thus it can handle acute heat stress (of short duration) as opposed to chronic heat stress (long term high temperatures). Additionally, E. alleni in the field may employ some heat avoidance strategies. The elongate leaf shape increases edge and decreases surface area available for absorbing a heat load. Also the extensive white trichomes on the leaves of E. alleni may serve to reflect light away from the leaves and thus heat as well. The leaves are densely hairy on their undersides. Since E. alleni grows close to the ground, this may be a means of reflecting heat radiated from the hot soil surface of the shale barrens.

Table 1: Electrolyte leakage of *E. alleni* maintained at two different temperatures (control or elevated) measured at broad temperature intervals. Slopes are an indication of the rate of membrane leakage.

Control Growth Chamber:

Break Temperature	Slope before break temperature	Slope after break temperature
49.5	.394	2.92
49.75	.362	8.14
49.5	.486	8.34
49.75	.370	6.34
49.75	.450	8.46
mean = 49.65	mean = .412	mean = 6.84

Elevated Growth Chamber:

Break Temperature	Slope before break temperature	Slope after break temperature
48.5	.620	6.42
49.5	.382	4.72
49.75	.320	1.92
47.75	1.56	5.9
49.0	.500	5.36
mean = 49.3	mean = .676	mean = 4.86

Table 2: Electrolyte leakage of *E. alleni* maintained at two different temperatures (control or elevated) measured at narrow temperature intervals. Slopes are an indication of the rate of membrane leakage.

Control Growth Chamber:

Break Temperature	Slope before break temperature	Slope after break temperature
53.0	.420	10.10
53.5	.631	13.17
52.2	.806	14.35
53.4	.440	10.85
53.5	.597	14.23
mean = 52.12	mean = .579	mean = 12.54

Elevated Growth Chamber:

Break Temperature	Slope before break temperature	Slope after break temperature
50.8	3.08	9.67
53.9	.991	12.3
53.1	.966	8.83
52.0	3.53	13.3
53.6	3.02	14.3
mean = 52.68	mean = 2.32	mean = 11.69

Table 3: Maximum photosynthetic rates and temperatures at zero net photosynthesis for *E. alleni* maintained at control or elevated temperatures.

Maximum Photosynthesis ($\mu\text{mol}/\text{m}^2/\text{s}$)		Temperature (celsius) at zero photosynthesis	
Control	Elevated	Control	Elevated
2.94	1.76	31.0	33.0
2.62	2.40	31.3	26.1
8.75	2.80	40.0	27.9
6.22	2.76	38.0	32.0
mean = 5.13	mean = 2.43	mean = 35.07	mean = 29.75
std = 2.91	std = .482	std = 4.61	std = 3.29

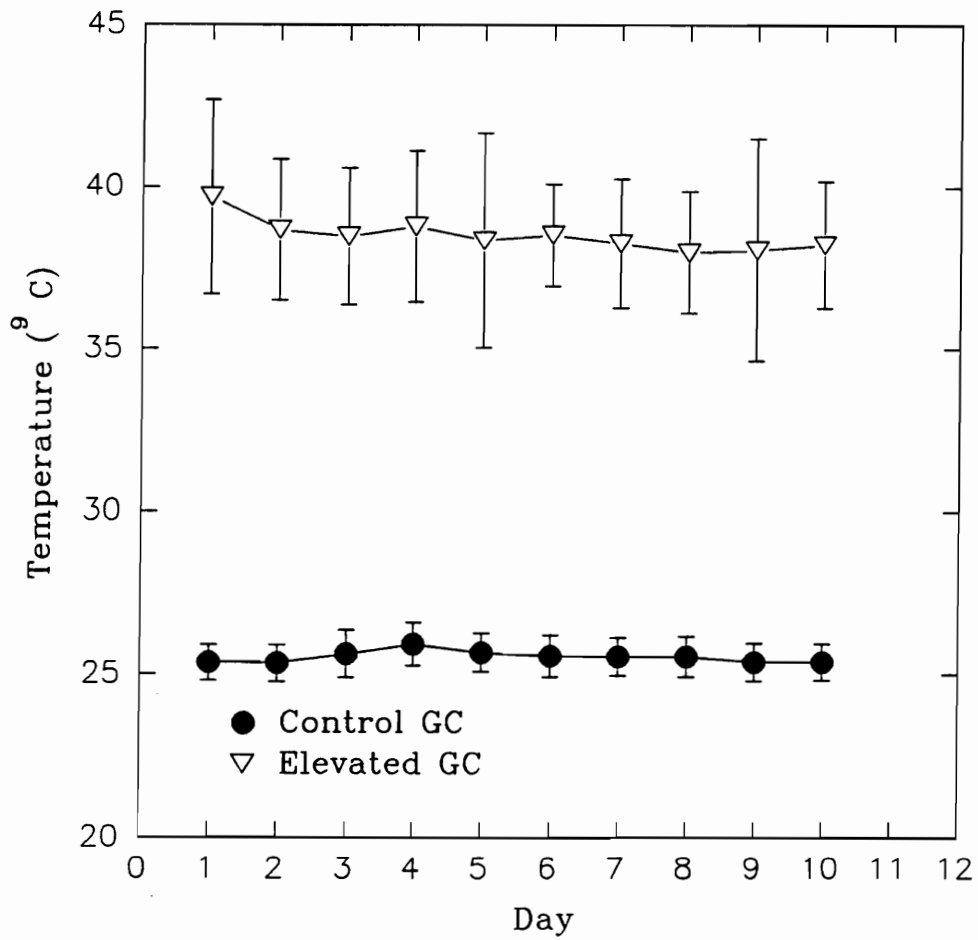


Figure 1: Average daytime temperature in the control and elevated temperature growth chambers.

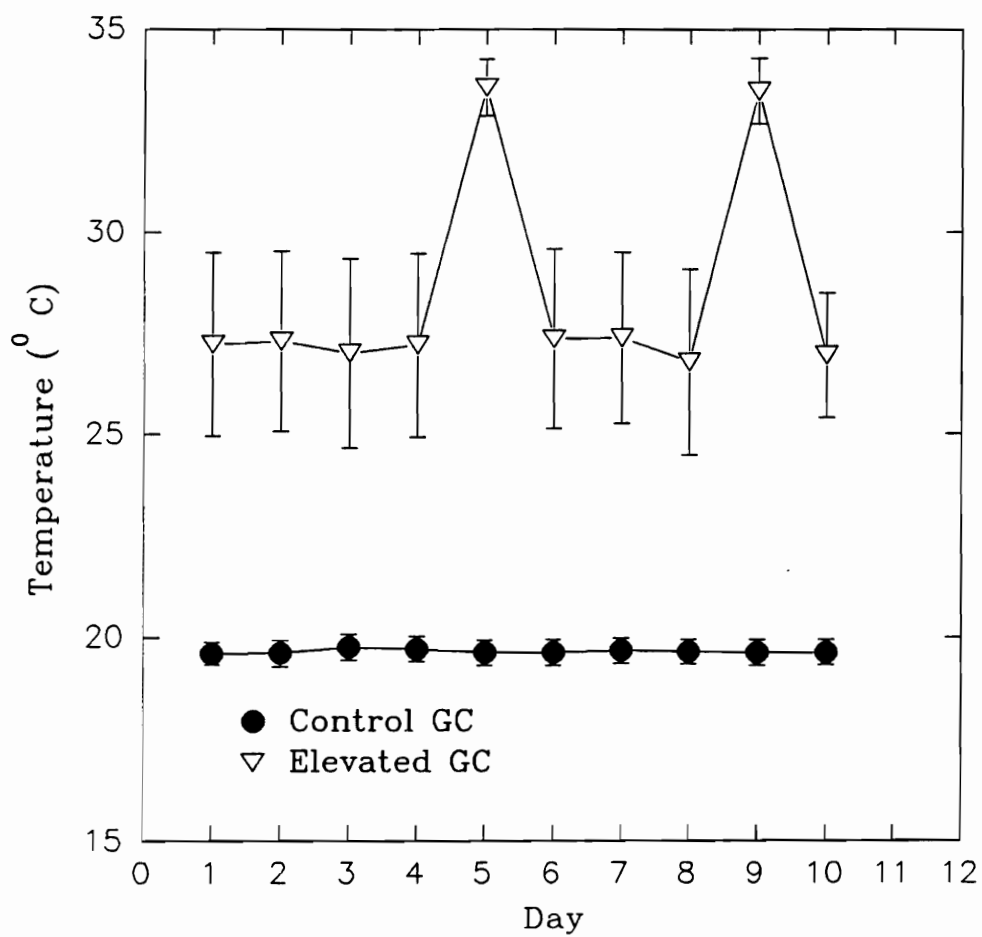


Figure 2: Average nighttime air temperature in the control and elevated temperature growth chambers.

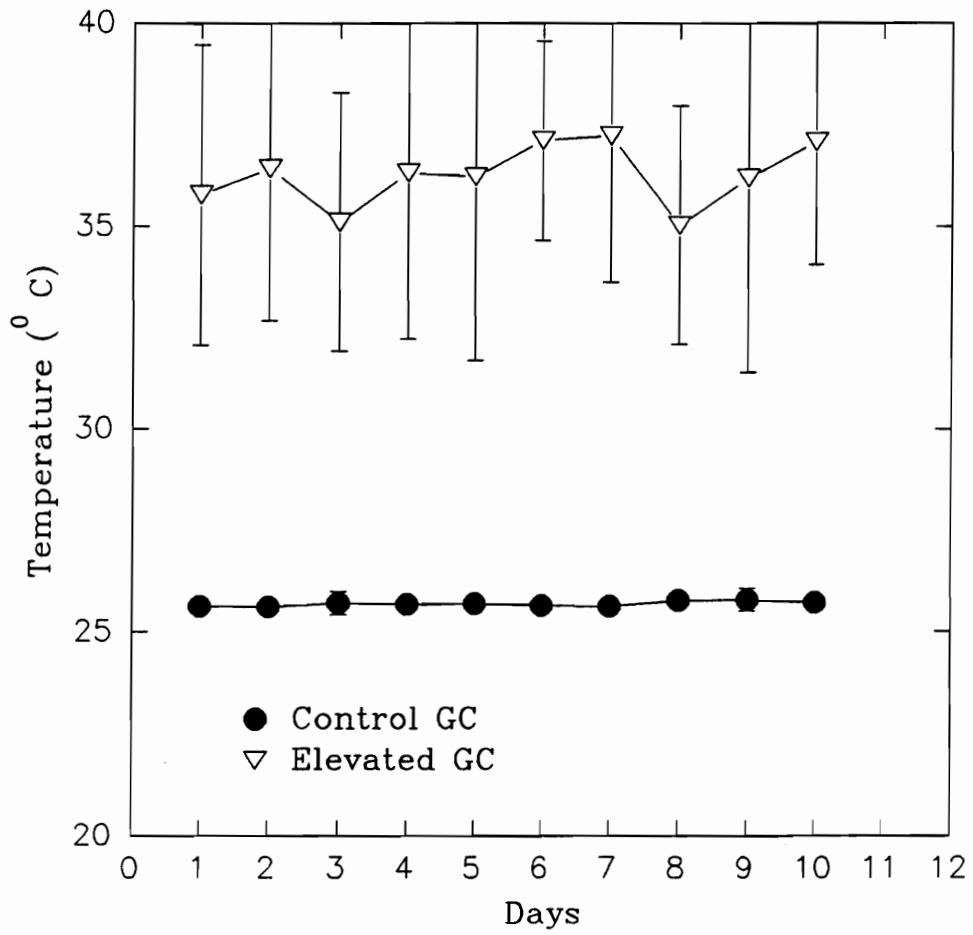


Figure 3: Average daytime soil temperature in control and elevated temperature growth chambers.

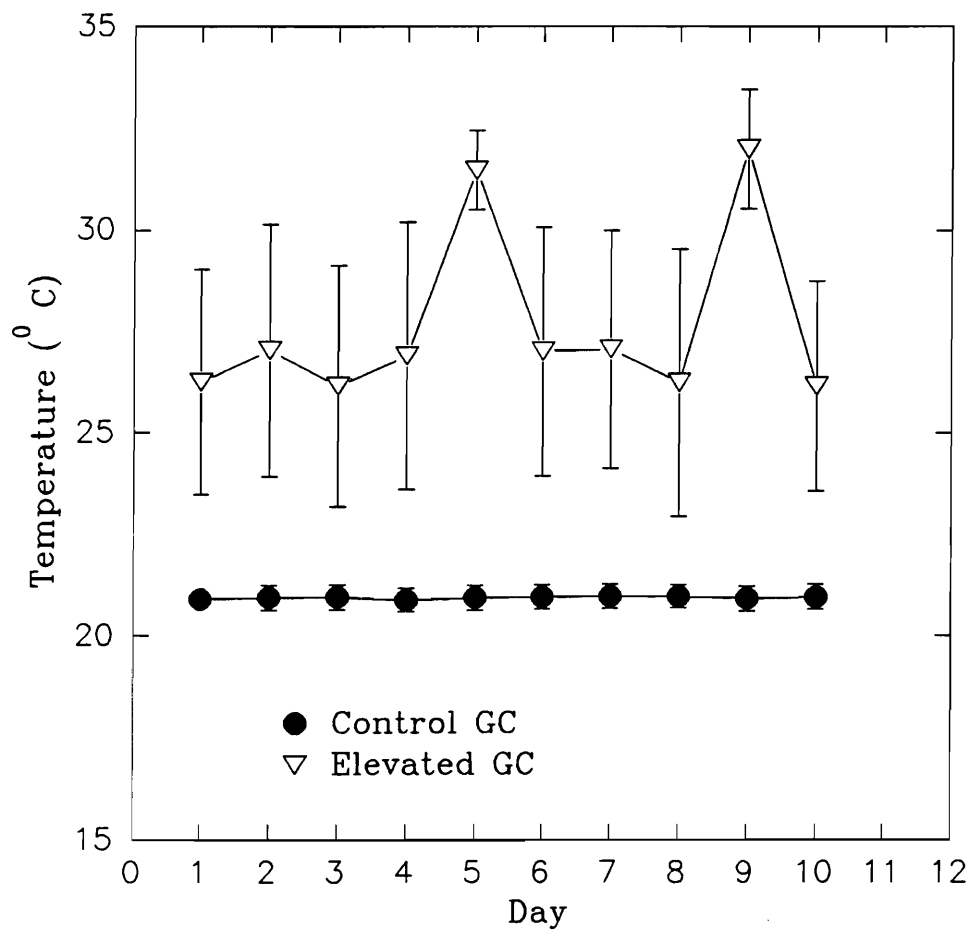


Figure 4: Average nighttime soil temperature in control and elevated temperature growth chambers.

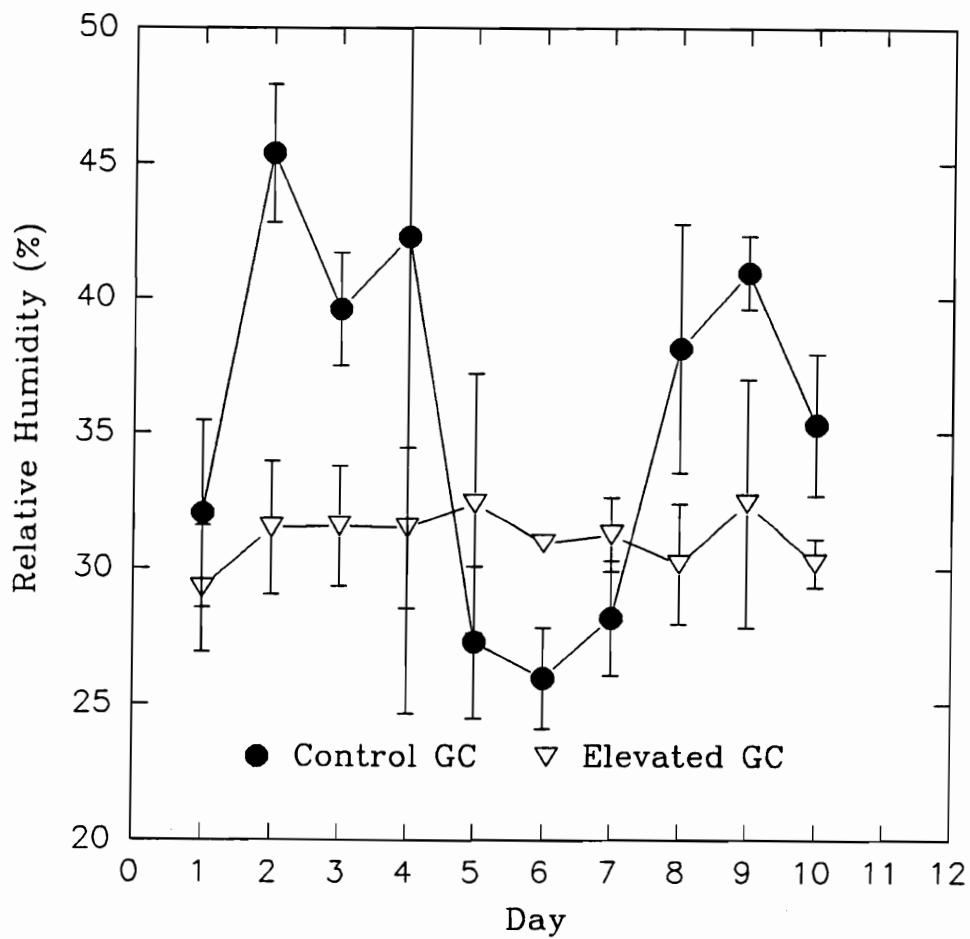


Figure 5: Average daytime relative humidity (%) in control and elevated temperature growth chambers.

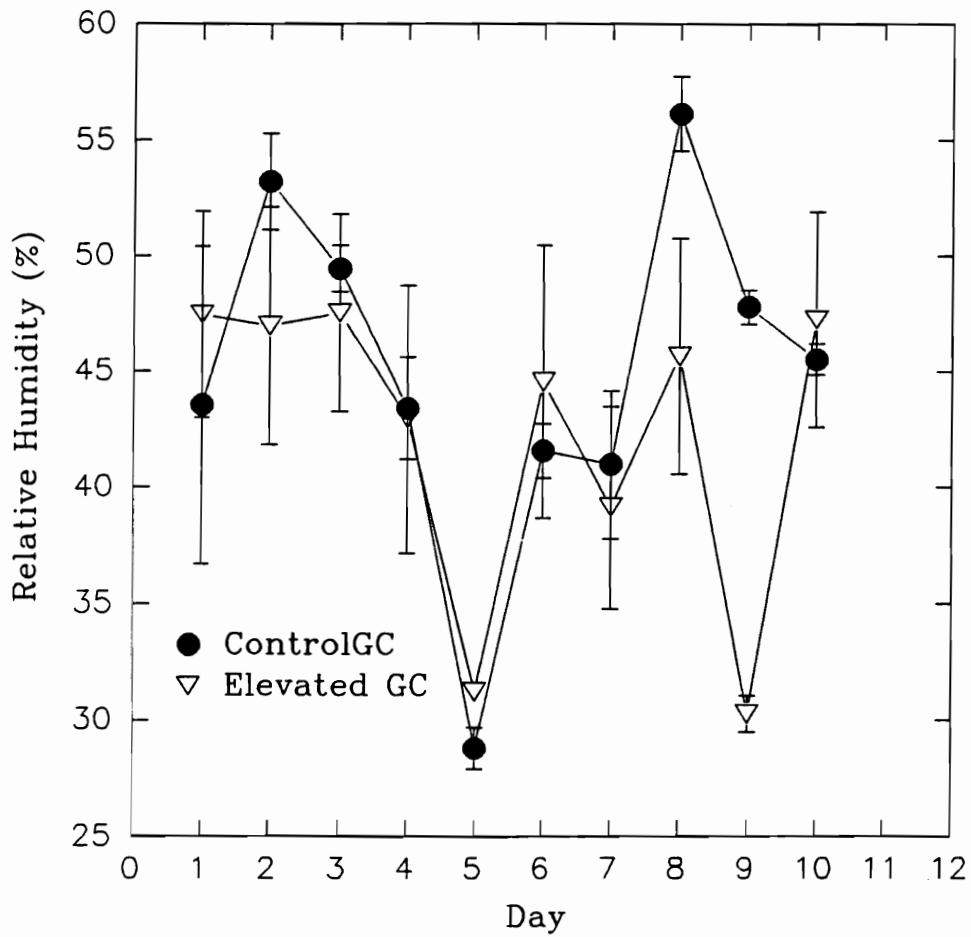


Figure 6: Average nighttime relative humidity (%) in control and elevated temperature growth chambers.

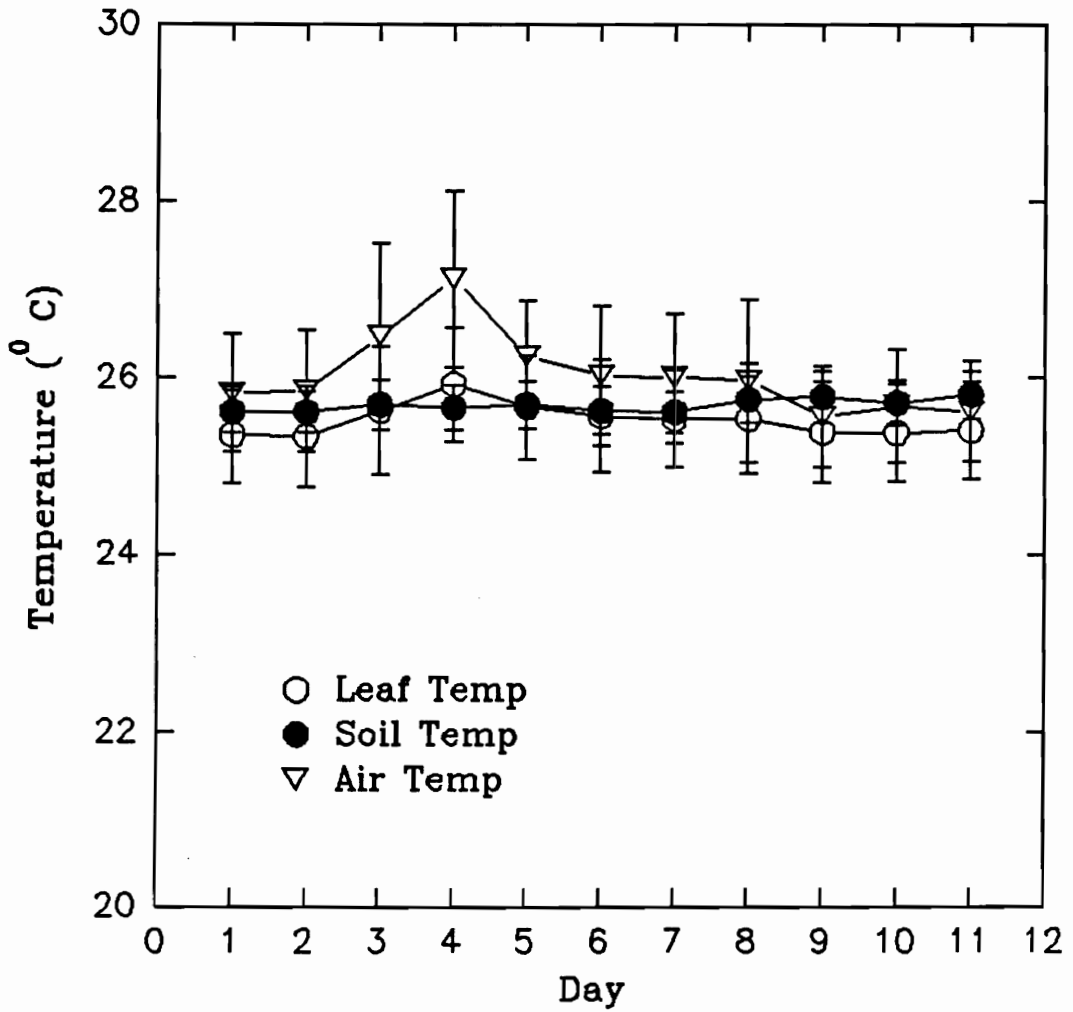


Figure 7: Average daytime air, soil and leaf temperatures in the control growth chamber.

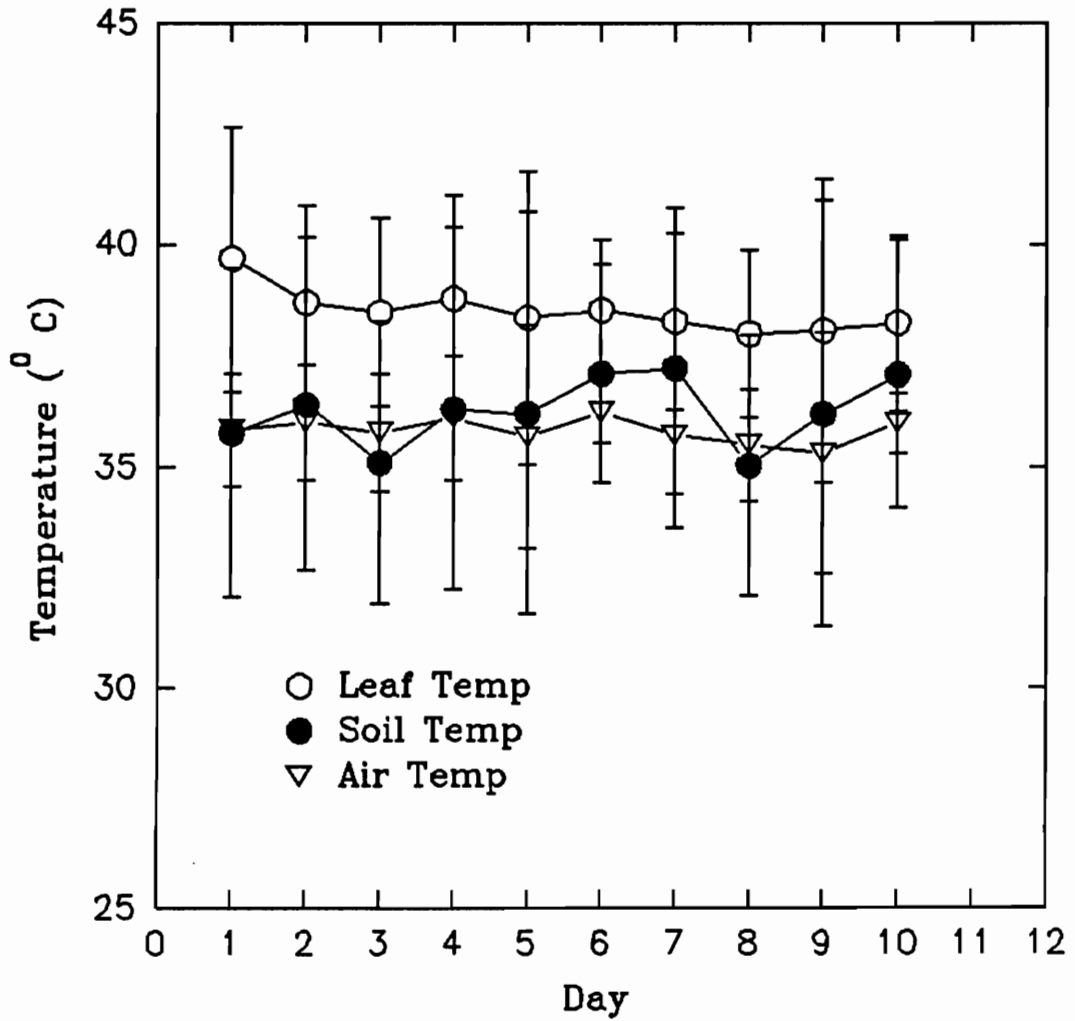


Figure 8: Average daytime air, soil and leaf temperature of the elevated growth chamber.

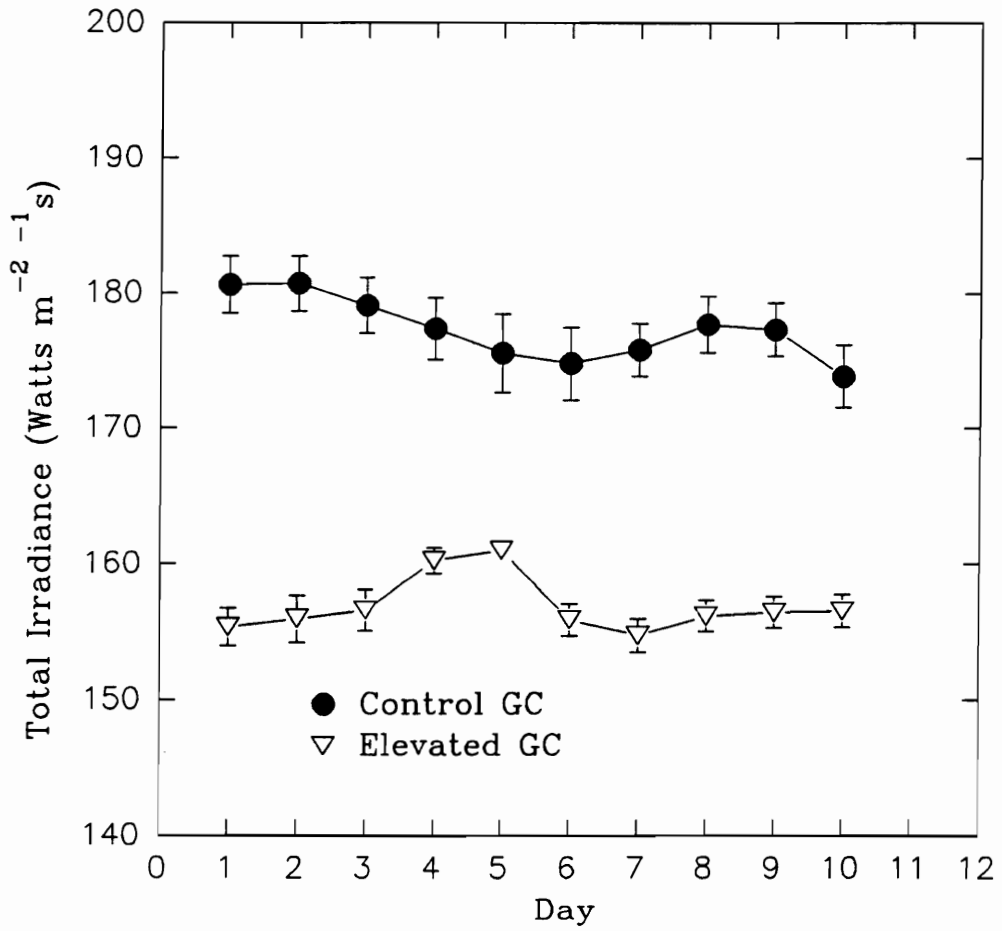
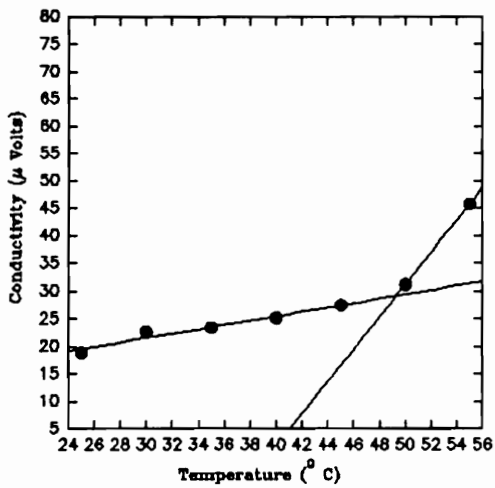
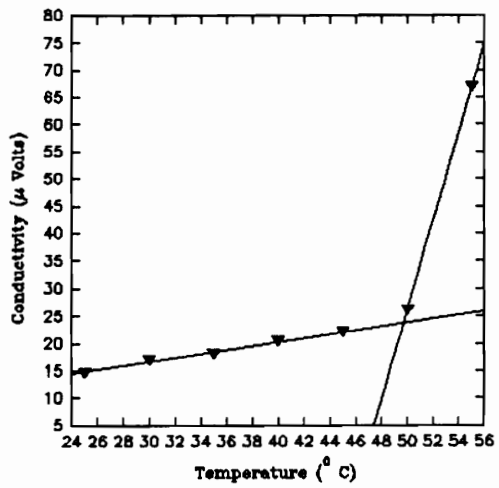


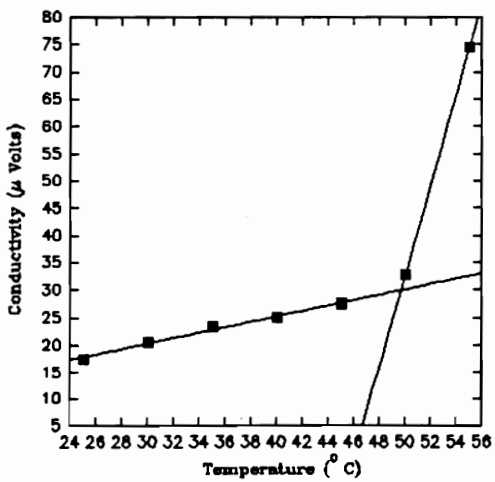
Figure 9: Average total daily irradiance in control and elevated temperature growth chambers.



a:

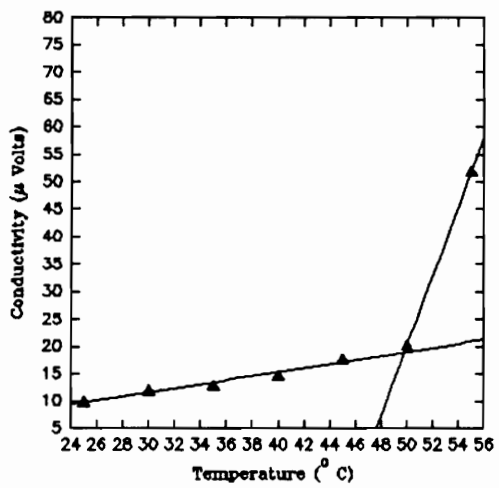


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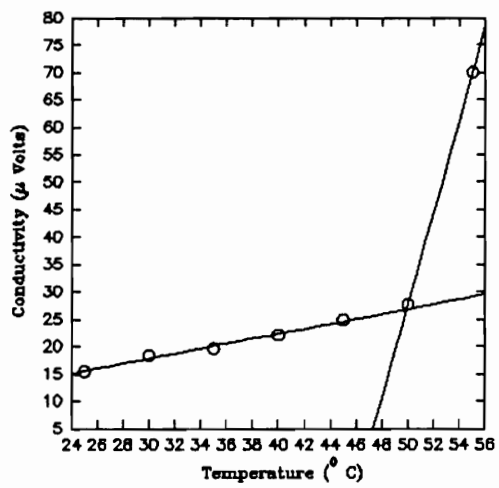


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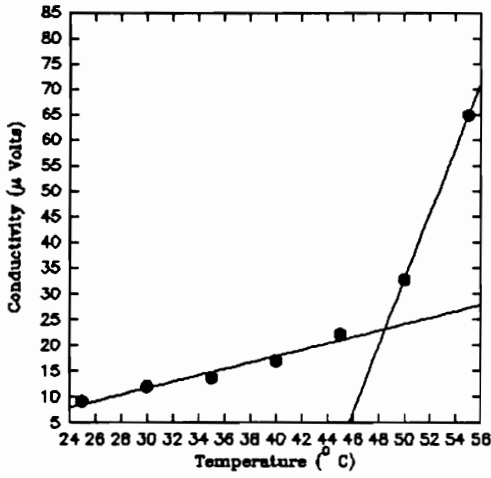
Figure 10: Electrolyte leakage measured at broad intervals, for *E. alleni* maintained at control temperatures. Figure continues onto next page.



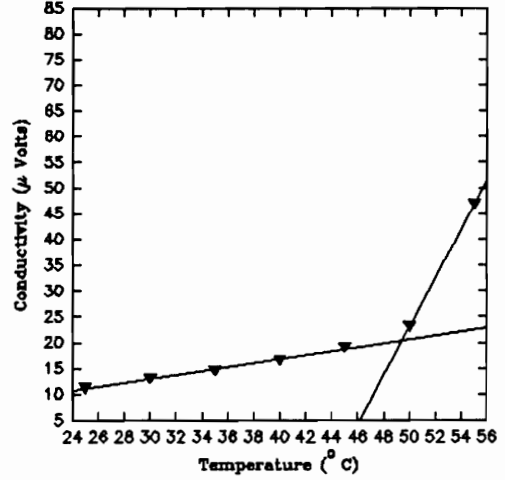
d:



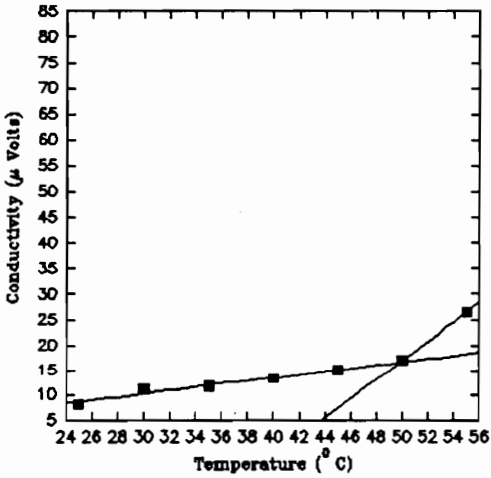
e:



a:

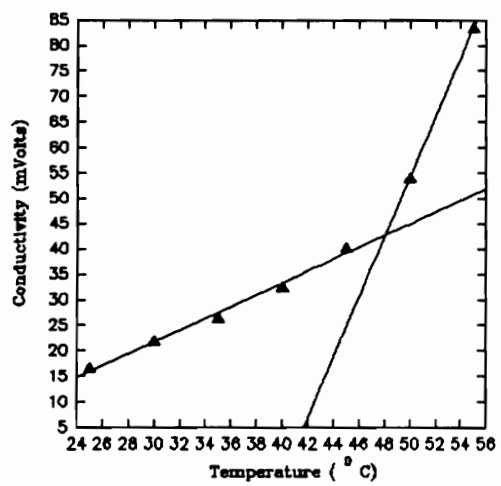


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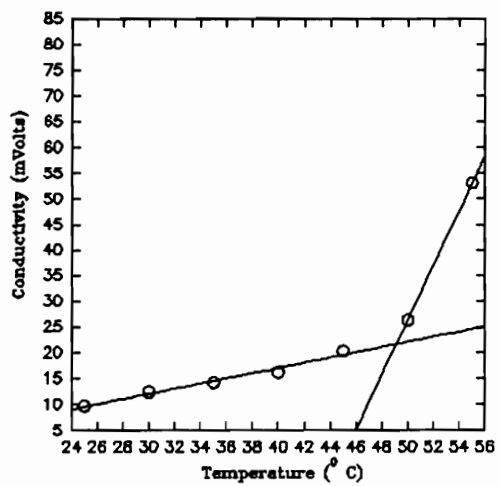


c:

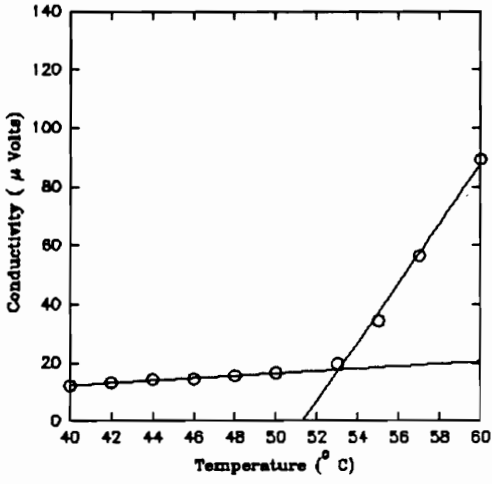
Figure 11: Electrolyte leakage measured at broad intervals for *E. alleni* maintained at elevated temperatures. Figure continues on next page.



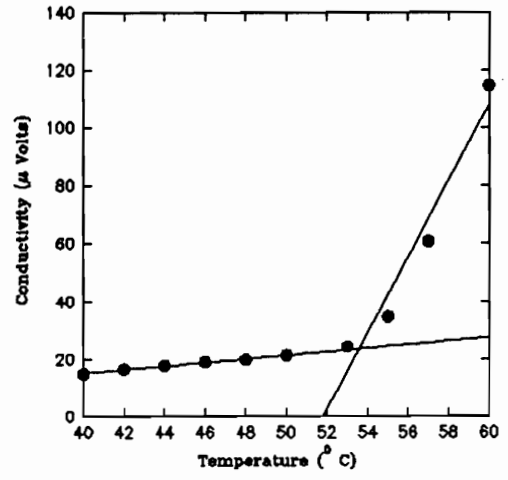
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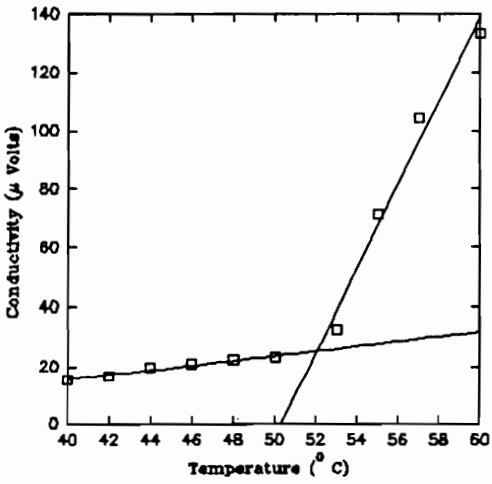
e:



a:

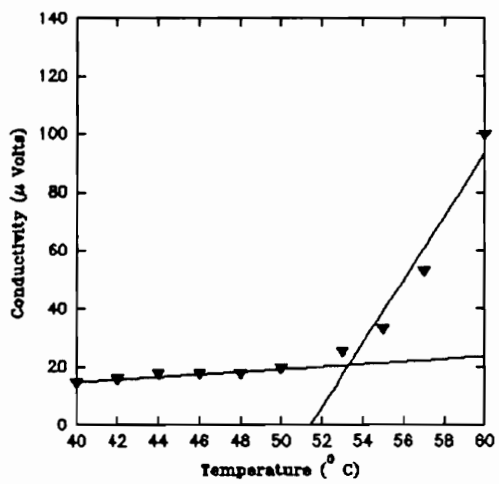


b:

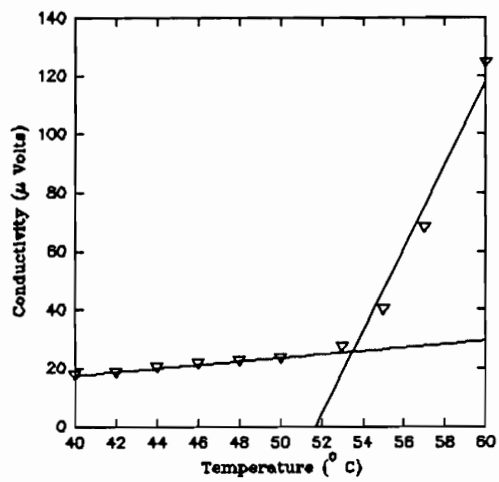


c:

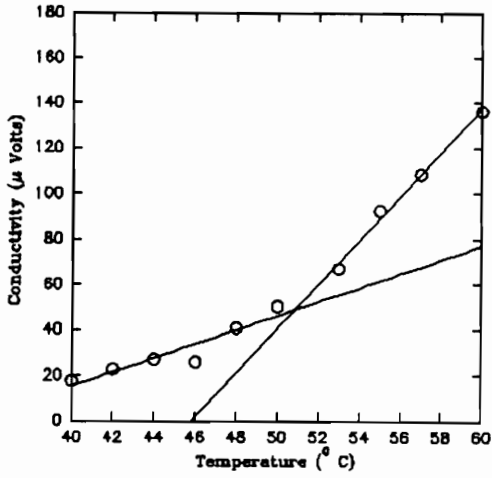
Figure 12: Electrolyte leakage measured at narrow intervals for *E. alleni* maintained at control temperatures. Figure continues on next page.



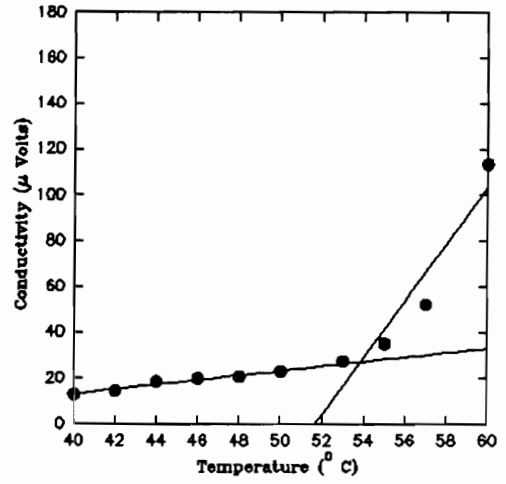
d:



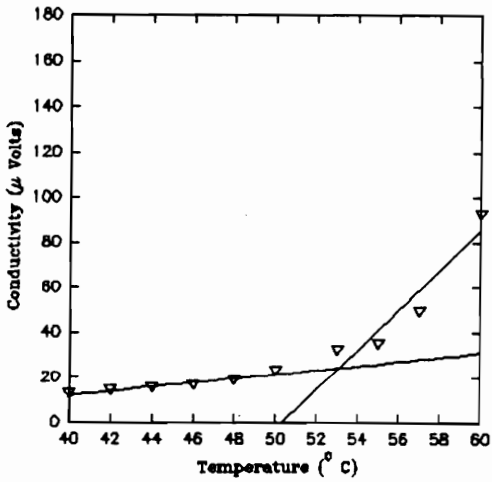
e:



a:

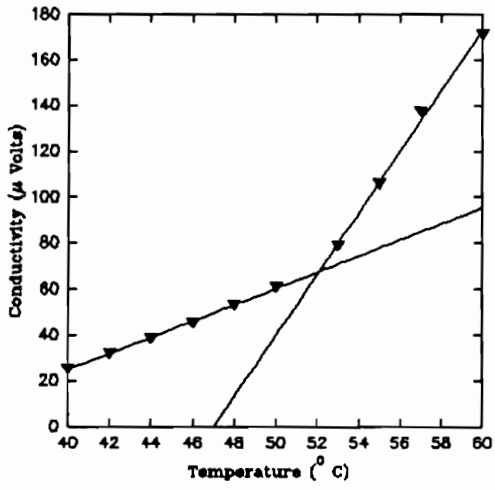


b:

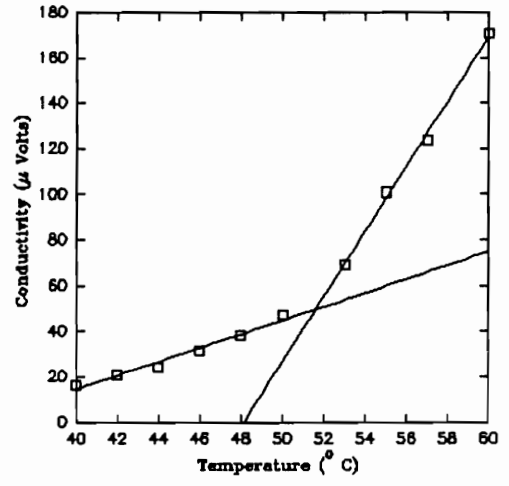


c:

Figure 13: Electrolyte leakage measured at narrow intervals for *E. alleni* maintained at elevated temperatures. Figure continues on next page.



d:



e:

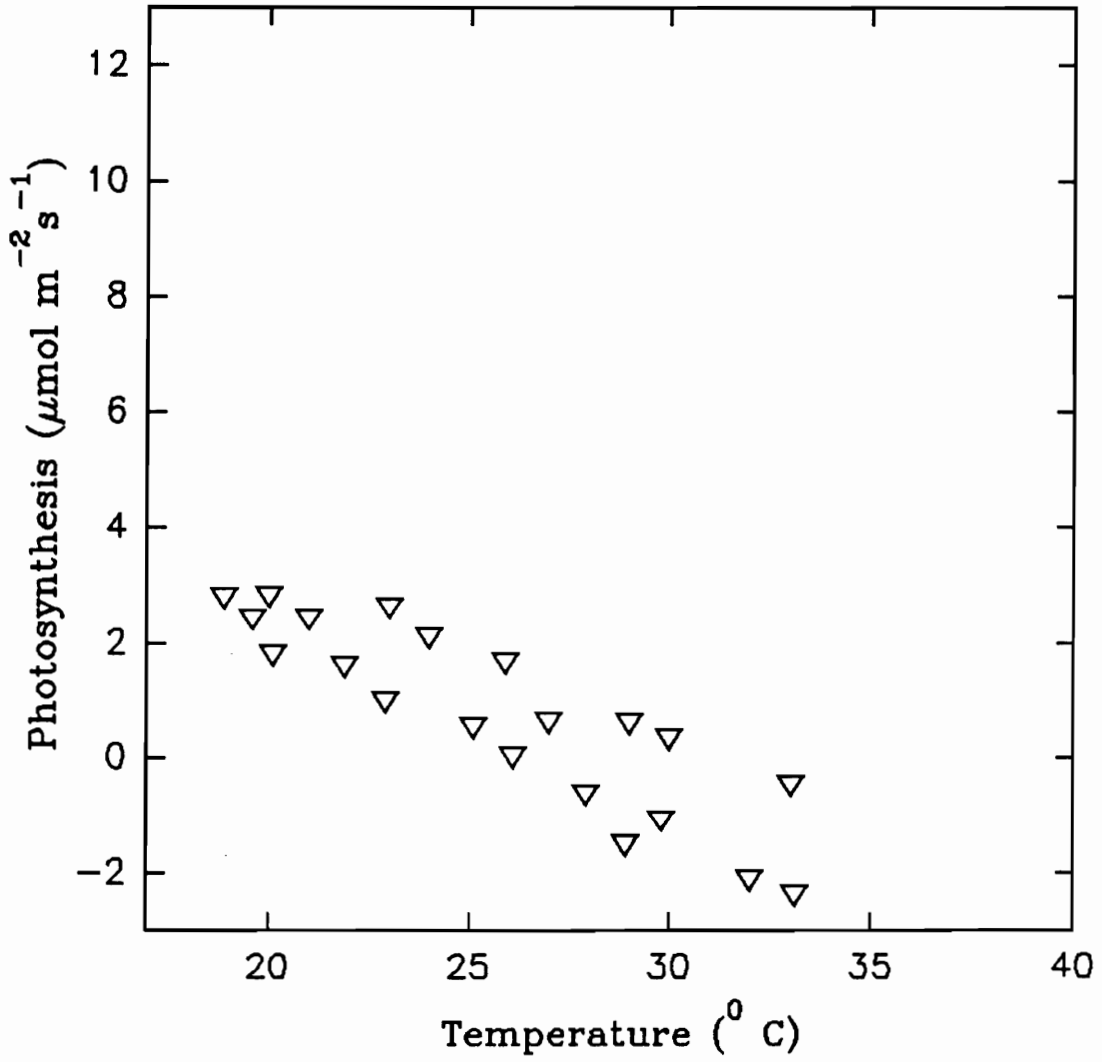


Figure 14: Photosynthetic response of *E. alleni* maintained at elevated temperatures.

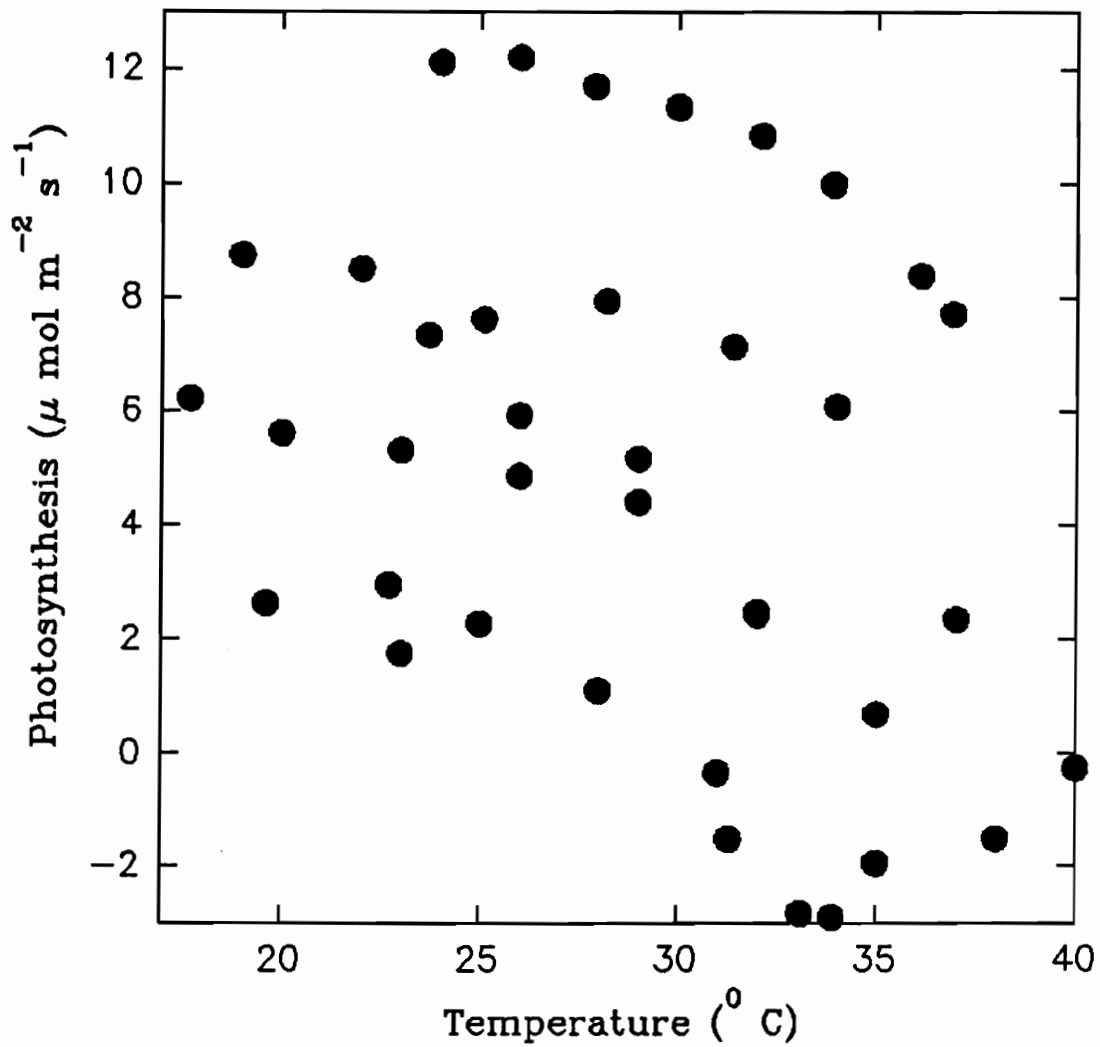


Figure 15: Photosynthetic response of *E. alleni* maintained at control temperatures.

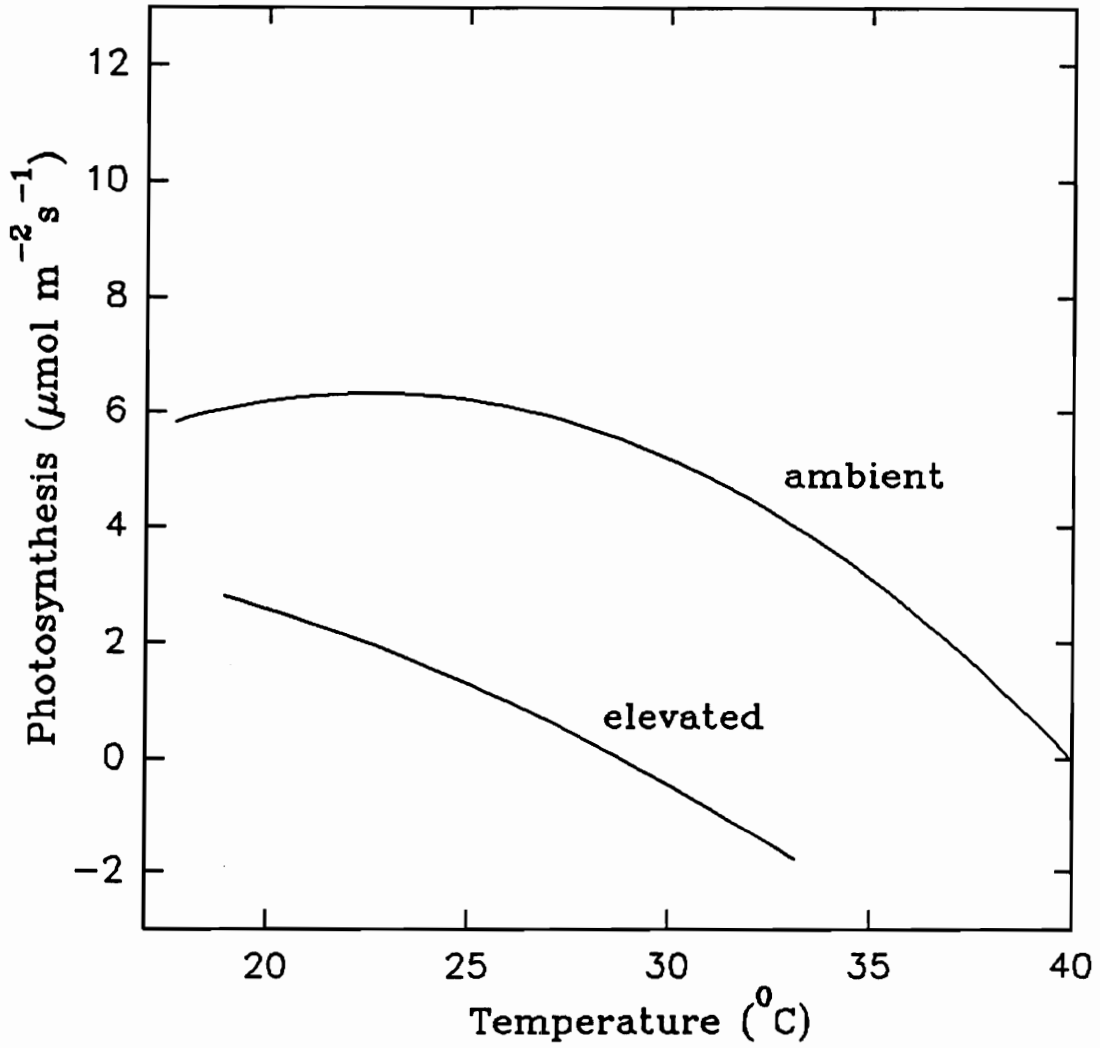
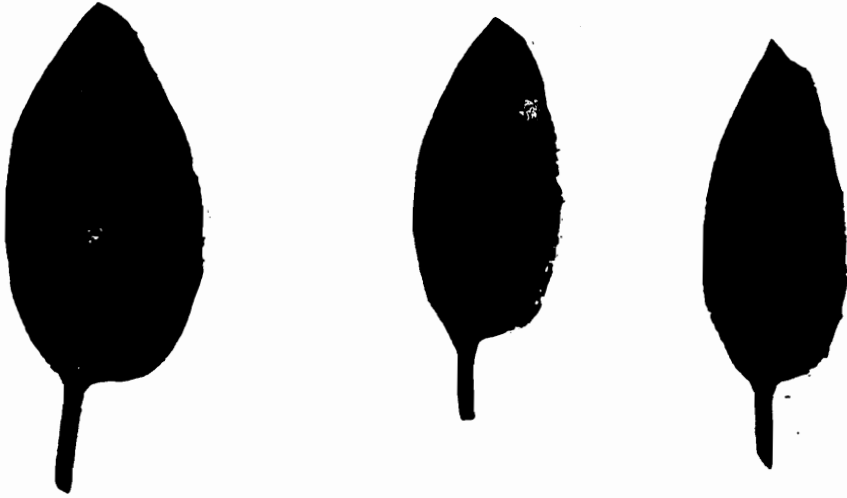


Figure 16: Summary of photosynthetic response of *E. alleni* maintained at control or elevated temperatures. Each line represents all plants in a treatment.

a.



b.

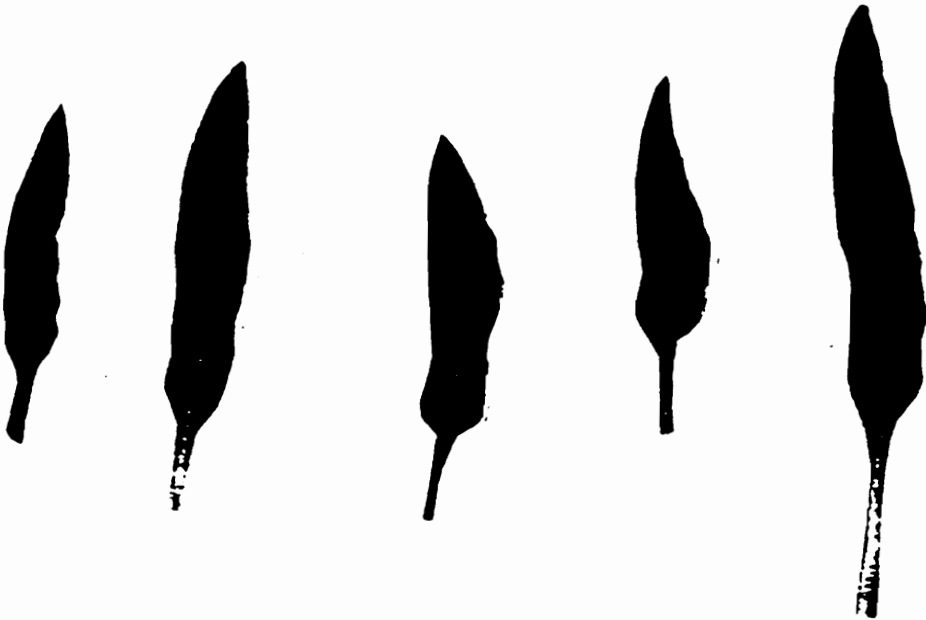


Figure 17: Leaf morphology of *E. alleni* maintained at control (a) or elevated (b) temperatures.

SUMMARY

The environment of the shale barrens is generally harsher than that of the eastern deciduous forest. They are exposed, steep rocky outcrops with a poorly developed soil. The barrens receive considerably more light than do wooded sites, and usually have a higher air temperature as well as a markedly higher soil surface temperature.

Shale barrens support a vegetation that is considerably different from that of the eastern deciduous forest. They are dominated by species such as Quercus illicifolia, Pinus virginiana, Junniperus virginiana, and Q. prinus. Although shale barrens are south facing, their vegetation differs from that of other non barren south facing slopes, potentially as a result of geologic differences.

This dissertation supports the hypothesis that Eriogonum alleni is an obligate heliophyte. Its intolerance to shaded conditions precludes its occurrence as an understory herb in the eastern deciduous forest. E. alleni would not be able to accumulate enough resources to survive the shade of a closed canopy.

Although high light requiring, E. alleni does not occur in high light environments such as open fields or canopy gaps. It may not be able to compete with the weeds, grasses and seedlings that usually occupy these sites, however it, like other rock outcrop species (Baskin and Baskin, 1989) can

thrive off the shale barren in cultivation. Studies with transplants of E. alleni into non shale barren sites would be helpful in assessing its competitive ability.

E. alleni does produce a large number of seeds each year, however, there are no obvious animal vectors of dispersal and the seeds are not adapted for wind dispersal. The distribution of E. alleni within a shale barren is patchy. Seeds may simply fall at the base of the parent plant or be washed down the slope and lost. A study of E. alleni's distribution and dispersal habits would be helpful in answering the question of its restriction to the shale barren.

E. alleni cannot tolerate prolonged exposure to elevated temperatures. In the field, plants are able to maintain leaf temperatures close to that of ambient air temperature. Soil surface temperature, however, reaches temperatures well above physiological tolerance. Seedlings of E. alleni are unable to withstand these high temperatures (Platt, 1951; Kaltenbach, unpubl.; pers. obs.). Unless the seedlings are well established by early summer, they will not survive. Information on shale barren microhabitat would be helpful on determining favorable sites for seedling establishment. This could be particularly useful when considering endangered shale barren endemic species.

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APPENDIX

Species Code:

Species are listed in the order they appear in tables 1 and 2.

PIVA: Pinus virginiana
JUVA: Junniperus virginiana
QUPR: Quercus prinus
QUIL: Quercus ilicifolia
QURU: Quercus rubra
QUAL: Quercus alba
CARYA: Carya species
OSVA: Ostrya virginiana
AMAR: Amelanchier arborea
QUVE: Quercus velutina
SAAL: Sassafras albidum
COFL: Cornus florida
HAVA: Hamamelis virginiana
ACRU: Acer rubrum
FRAM: Fraxinus americanum
QUMA: Quercus marilandica
RHUS: Rhus species
CECA: Cercis canadensis
VITIS: Vitis species
CEOC: Celtis occidentalis
BELE: Betula lenta
CADE: Castanea dentata
MAAC: Magnolia accuminata
NYSY: Nyssa sylvatica
QUCO: Quercus coccinea
ROPS: Robinia pseudoaccacia
PIPU: Pinus pungens
PIRI: Pinus rigida
PIST: Pinus strobus
KALA: Kalmia latifolia
MEPI: Menzesia pilosa
VAC: Vaccinium species
PRSE: Prunus serotina
RHODO: Rhododendron species
ACPE: Acer pensylvanicum
CARCO: Carpinus caroliniana
LITU: Liriodendron tulipifera
CORYLUS: Corylus species
GAYBA: Gaylusaccia baccata
LEUC: Leucothoe species
VIBAC: Viburnum accuminata
QUERC: Quercus species
UNK: Unknown species

Table 1: Eigen values generated by NTSYS vegetation community analysis using species importance values as character states.

	1	2	3
PIVA	0.562	-0.284	0.051
JUVA	0.625	-0.251	-0.510
QUPR	-0.183	0.807	0.260
QUIL	0.769	-0.409	-0.286
QURU	0.808	-0.566	-0.052
QUAL	-0.208	-0.421	0.744
CARYA	0.498	0.333	0.506
OSVA	0.208	-0.171	0.841
AMAR	0.193	-0.381	0.858
QUVE	-0.182	0.499	-0.371
SAAL	-0.336	0.872	-0.008
COFL	-0.212	0.644	0.279
HAVA	-0.696	-0.593	0.304
ACRU	-0.244	0.674	0.217
FRAM	0.609	-0.242	-0.524
QUMA	0.000	-0.000	-0.000
RHUS	0.788	-0.341	-0.454
CECA	0.787	-0.339	-0.460
VITIS	0.741	-0.310	-0.508
CEOC	0.609	-0.242	-0.524
BELE	-0.427	-0.245	-0.134
CADE	-0.908	0.308	-0.246
MAAC	-0.686	-0.410	-0.169
NYSY	-0.304	0.858	-0.261
QUCC	-0.823	-0.503	-0.173
ROPS	-0.809	-0.493	-0.175
PIPU	-0.172	0.506	-0.372
PIRI	-0.779	-0.472	-0.176
PIST	-0.826	-0.505	-0.172
KALA	-0.735	0.153	-0.354
MEPI	-0.753	0.151	0.019
VAC	-0.235	0.927	-0.186
PRSE	0.208	-0.171	0.841
RHODO	-0.637	-0.387	-0.085
ACPE	-0.653	-0.102	-0.006
CARCO	-0.092	0.845	0.130
LITU	-0.633	-0.403	-0.090
CORYLUS	-0.633	-0.403	-0.090
GAYEA	-0.383	0.379	-0.418
LEUC	-0.633	-0.403	-0.090
VIBAC	-0.831	-0.512	-0.163
QUERC	-0.547	-0.727	0.245
UNK	0.478	-0.276	0.428

Table 2: Eigen values generated by NTSYS vegetation community analysis using species presence/absence as character states.

	1	2	3
PIVA	0.587	0.672	0.422
JUVA	0.587	0.672	0.422
QUPR	0.520	-0.175	0.761
QUIL	0.616	0.490	0.522
QURU	0.636	0.136	0.630
QUAL	0.844	-0.156	0.062
CARYA	0.554	-0.402	0.567
OSVA	0.753	0.225	-0.150
AMAR	0.669	-0.151	0.486
QUVE	0.822	-0.320	-0.066
SAAL	0.589	-0.462	0.414
COFL	0.687	-0.622	0.189
HAVA	0.833	-0.156	-0.046
ACRU	0.728	-0.467	0.193
FRAM	0.756	0.514	-0.209
QUMA	0.724	0.299	-0.055
RHUS	0.622	0.673	0.219
CECA	0.622	0.673	0.219
VITIS	0.698	0.601	0.029
CEOC	0.756	0.514	-0.209
BELE	0.859	0.198	-0.249
CADE	0.722	-0.621	-0.015
MAAC	0.910	-0.001	-0.245
NYSY	0.706	-0.380	0.228
QUCO	0.838	-0.309	-0.146
ROPS	0.880	-0.155	-0.141
PIPU	0.780	-0.474	-0.071
PIRI	0.880	-0.155	-0.141
PIST	0.910	-0.001	-0.245
KALA	0.717	-0.468	0.085
MEPI	0.852	-0.148	-0.190
VAC	0.642	-0.396	0.275
PRSE	0.795	0.380	-0.146
RHODO	0.782	-0.120	-0.294
ACPE	0.751	-0.274	-0.190
CARCO	0.714	0.069	-0.218
LITU	0.881	0.181	-0.345
CORYLUS	0.881	0.181	-0.345
GAYBA	0.811	-0.320	-0.175
LEUC	0.881	0.181	-0.345
VIBAC	0.869	-0.155	-0.250
QUERC	0.817	0.085	0.196
UNK	0.736	0.467	0.092

VITA

Suzanne Hill Braunschweig entered Towson State University in 1984 intending to become a marine biologist, but became interested in botany instead. She spent two summers as an intern at the Smithsonian Environmental Research Center in Edgewater, MD during the summers of 1986 and 1987. She graduated from Towson State magna cum laude in 1988, spent the summer at the Mountain Lake Biological Station in Giles County Virginia, and started graduate school as a doctoral candidate in biology at Virginia Tech that fall. Her career interests are towards teaching at the college level.

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