

THESIS

NET PHOTOSYNTHESIS OF SELECTED FOLIAGE PLANTS
UNDER LOW IRRADIATION

Submitted by
Robert Glen Pass

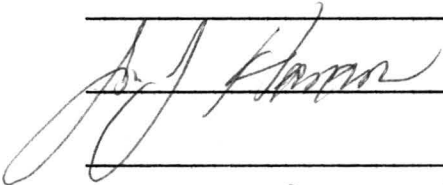
In partial fulfillment of the requirements
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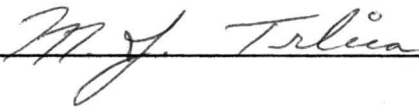
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED
UNDER OUR SUPERVISION BY ROBERT GLEN PASS ENTITLED
NET PHOTOSYNTHESIS OF SELECTED FOLIAGE PLANTS UNDER
LOW IRRADIANCES BE ACCEPTED AS FULFILLING IN PART
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Committee on Graduate Work



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ABSTRACT OF THESIS

NET PHOTOSYNTHESIS OF SELECTED FOLIAGE PLANTS UNDER LOW IRRADIATION

Net CO₂ exchange, dark respiration, light compensation points, and light acclimation rates were determined for Brassaia actinophylla, Nephrolepis exaltata 'Bostoniensis,' and Scindapsis aureus under four irradiation levels. These three species exhibited increased rates of net CO₂ uptake and decreased rates of dark respiration at the lowest irradiances, indicating an increase in photosynthetic efficiency. They demonstrated a 1.4 to 5.0 fold reduction in light compensation points over a seven week period of acclimation. Brassaia actinophylla reached its minimum light compensation point in 5 weeks, Scindapsis aureus in 3 weeks, and Nephrolepis exaltata 'Bostoniensis' never reached a minimum light compensation point.

The plants were re-acclimated to lower irradiation levels for 3 weeks to determine if there was a change in photosynthetic activity. Brassaia actinophylla was capable of re-acclimating by showing increased photosynthetic efficiency at all irradiation levels within this period. Nephrolepis exaltata 'Bostoniensis' and Scindapsis aureus only approached the point of no net CO₂ evolution.

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INTRODUCTION

The use of foliage plants is increasing rapidly as an important interior design feature in airports, apartments, business offices, homes, hotels, shopping malls, and other public buildings. In 1974, wholesale foliage plant sales increased \$43 million, seven times the combined sales increase for carnations, chrysanthemums, gladiolas, and roses (40). Sales continued to increase from \$185 million in 1975 to \$236 million in 1976 (2). In the past five years, the basic crop value increase throughout the United States has been over 300% (44).

The popular use of foliage plants for interiors has initiated concern for proper acclimation of these plants to enhance their survival in new environments. Acclimation refers to the climatic adaptation of an organism (plant) to a new environment; specifically, moving a foliage plant from the optimum conditions of greenhouse production to the limiting conditions of an interior environment. Research has shown that acclimation prior to placement indoors is beneficial to most foliage plants. The length of acclimation as well as type of acclimation varies for specific foliage plants (21, 22).

Light is the most important factor in plant acclimation (33). Interior environments have low light intensities which put limitations on plants, both physiologically and metabolically. In order to survive these limitations, plants must adapt to these low light intensities.

Plants respond differently to light, depending upon species and previous history. Literature going back to the turn of the century has shown that many species: (1) are damaged at too high light intensities, (2) actually perform better at less than maximum available solar radiation, and (3) will respond more efficiently to high or low light intensities if they have been preconditioned to those high or low light intensities. The observation has been made in commercial production that rapid changes in environmental conditions of the greenhouse generally affect plants adversely.

Previous work at Colorado State University (DePauw and DePauw, 1975) has shown that there is marked variation among plants within a species which can be attributed to the previous history of the plants. Secondly, plants grown under high light intensities will have higher light compensation points than plants grown under low light intensities. And thirdly, if plants are moved from a high light intensity to a low light intensity, there is a period of time required for acclimation before a new and lower light compensation point is reached. The light compensation point is the light intensity at which there is no net exchange of CO_2 , or the point at which photosynthesis and respiration are essentially equal (60). If the interior light intensity is below the light compensation point, the plant will respire away carbohydrate reserves and limit chances for long term survival (33). This implies that the light compensation point is the point at which the plant does not grow.

The cultural requirements for producing a salable plant are different from those conditions for maximum customer satisfaction. Once produced, the plant should undergo a period of acclimation before sale. Studies of plant acclimation have been mostly empirical. This research is an attempt to place acclimation requirements on a sound basis, applicable to a wide range of plant conditions. In order to accomplish this goal, a system was designed and built for measuring net CO₂ exchange rates for whole plants. It was important to measure the net CO₂ exchange rates under relatively low light intensities to reproduce light conditions typical to most interior environments. Utilizing the results from these measurements, the approximate time required for plants to acclimate to their minimum light compensation point was determined.

REVIEW OF LITERATURE

Acclimation of foliage plants is primarily aimed at converting sun grown plants to shade plants adaptable to interior low light environments (24). Conklin (18) developed a system for "preacclimatizing" plants grown for interior landscapes. He observed that plants held for two months or more in heavily shaded greenhouses on reduced watering schedules showed a minimum loss of quality when moved to low light interiors. The factors responsible for these results have not been clearly determined, but it is felt that reductions in light are primarily responsible for the improved plant quality.

One means of measuring and monitoring the light acclimation rate of plants is measurement of the photosynthetic rate. One method involves the use of an infrared gas analyzer (4, 15, 33, 55, 59, 61). This method of analysis takes advantage of the ability of CO_2 to absorb certain wavelengths of infrared radiation. As the CO_2 concentration increases, absorption of infrared radiation increases so that the intensity of the radiation on the analyzer sensor decreases. Infrared gas analysis has the advantage of giving instantaneous readings of the CO_2 concentration in a stream of air passing over a plant in a closed system (60).

Factors Influencing Photosynthesis

The rate of photosynthesis in any plant is determined by the most limiting factor. Liebig, in 1843, expressed this concept in its simplest form as his "Law of the Minimum" (6, 29). The possible limiting factors of photosynthesis include irradiation, respiration, temperature, carbon dioxide, moisture, leaf age and morphology, and nutrition. There has been some question as to the study of these factors independently since the adaptation of a plant depends on all these factors collectively (7, 11). However, it seems logical, for research purposes, to hold as many variables constant as possible when establishing the minimum, optimum, and maximum limits of any one factor (64). When a plant produced under optimum conditions is acclimated to the limitations of interior landscapes, one must realize the total aspect of the plant responses.

Irradiation and Photosynthetic Efficiency

Plants which occupy shaded habitats are incapable of high photosynthetic rates. They grow best at low light intensities. Plants that grow under high light intensities in their native habitats have a high capacity for photosynthesis at saturating light intensities. However, they show lower rates of photosynthesis than shade grown plants at low light intensities (11, 12). These differences in photosynthetic efficiencies can be induced by the particular light intensity at which a species is grown. Leaves of sun species grown under low light

intensities show light saturation curves which resemble those of shaded plants. The classification of plants into sun and shade plants cannot be made entirely on the basis of light saturation curves or light compensation points, their adaptability to a selected light intensity must also be considered (7, 8, 11). Bjorkman and Holmgren (7) suggest that this adaptability is determined from genetic adaptation to the light environment prevailing in their native habitat. Genetic adaptation may help explain why some tropical foliage plants will acclimate to extremely low light intensities, while others will not.

Bohning and Burnside (12) have examined a representative selection of sun and shade species. Photosynthesis by the sun species was saturated at a light intensity of 2,000 to 3,000 foot-candles (ft-c) while the shade species were saturated at a light intensity of 300 to 1,000 ft-c. The light compensation point for the sun species ranged from 100 to 150 ft-c while it was 50 ft-c for the shade species. Ludlow (48) reported similar results for sun and shade ferns. Bjorkman (9) transferred native whole plants to the laboratory to measure their photosynthetic abilities. The shade species exhibited low dark respiration rates (0.06 to 0.16 micromoles $\text{CO}_2 \text{ dm}^{-2} \text{ min}^{-1}$) and low compensation points. The sun species showed higher light compensation points with dark respiration rates of 0.40 to 0.80 micromoles $\text{CO}_2 \text{ dm}^{-2} \text{ min}^{-1}$. The light saturation points for the shade species were in the range of 2.1 to 3.1 mg $\text{CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ and 21 to 36 mg CO_2

$\text{dm}^{-2}\text{hr}^{-1}$ for the sun species. Patterson (57) reported a similar pattern of photosynthetic response of Celastrus orbiculatus Thunb.

Bjorkman and Holmgren (7) growing sun and shade ecotypes of Solidago virgaurea L. under two different light levels, found that shade ecotypes had more efficient photosynthetic responses at low light intensities and that the sun ecotypes were more tolerant and efficient at higher light intensities. Bjorkman demonstrated that under ideal conditions, acclimation of the low efficiency, high light intensity plant to the higher efficiency of the low light intensity required only one week. This short period of acclimation is probably an exceptional case since other plant species have been shown to require much longer acclimation periods (66).

Leaf Morphology

Plants grown at high light intensities have a different leaf morphology than those grown at low light intensities (10, 26, 49, 56, 58). Higher light intensities initiate stronger development of palisade and spongy mesophyll regions resulting in thicker leaves (7, 10, 49, 56). Zurzycki (70) reported that Funaria grown under low light intensities had their chloroplasts arranged along the upper and lower surfaces of the palisade cells, perpendicular to the light source for maximum absorption of energy. There were fewer chloroplasts across a leaf section in shade leaves, but the chloroplasts were larger and contain more chlorophyll (17, 26, 48, 67). Ballantine and Forde (3)

demonstrated that soybean chloroplasts contained well-formed grana when grown under low light intensities, but corresponding leaves developed under high light intensities had rudimentary grana. The volume of stroma for leaves grown under low light intensities relative to the chloroplast volume appeared smaller (10, 11).

Conover and Poole (20) have shown that Philodendron oxycardium Schott retain their sun-leaves and may partially convert them to shade-leaves, while the new growth produced under low light intensities is of the shade-leaf type. It has not been determined whether sun-leaves can be converted to shade-leaves, and if there are corresponding morphological and physiological changes. Several reports (22, 38, 40, 63, 70) have shown that under high light intensities, the plant produces smaller, thicker foliage, stacked chloroplasts in the cells, and vertical orientation of grana within chloroplasts. These are protective mechanisms to prevent injury to cell components because of photo-oxidation. However, this does reduce photosynthetic efficiency of the plant. Under low light intensities, the chloroplasts are oriented in a single layer horizontal to the leaf surface, thereby improving the plants photosynthetic efficiency by intercepting more light energy. Ficus benjamina L. dropped its inefficient sun-leaves and produced more shade tolerant growth (19).

Respiration

Fonteno (33) reported a significant reduction in dark respiration for Brassaia actinophylla and Raphidophora aurea during 15 weeks of low light acclimation (11, 47, 68). This reduction in apparent respiration can be examined by separating respiration into growth and maintenance components (50, 51). Respiration has been generally termed the undesirable loss of CO₂ from the plant. However, McCree (16, 50) suggested that respiration is the process by which compounds needed for essential metabolic reactions were produced from carbohydrates. A high rate of dark respiration is correlated with high light intensities where rapid production of new compounds is required for increased growth. However, under reduced light intensities, the growth component of respiration becomes negligible, while the apparent low rate of respiration may result from the more efficient use of substrates derived from a lower maintenance component (33).

Pachysandra and Hedera are shade-tolerant species which have thick leaves and leaf arrangements which permit considerable self-shading. This indicates that the carbohydrate solvency of shade plants may depend more on the conservation of energy rather than the efficiency of its capture (36, 54). Grime (36) demonstrated that shade-tolerant species respiration rates in darkness were consistently lower than those measured in sun-tolerant species. This would indicate that shade-tolerant species have lower respiration rates.

Zelitch (69) stated that the rate of dark respiration was frequently affected by the previous intensity of illumination, and respiration usually increased following periods of increasing light intensity. The maximum rate of dark respiration was quantitatively related to the irradiance during the illumination period. Holmgren and Jarvis (42) proposed that increasing the irradiance for leaves of Rumex acetosa subsequently produced a higher rate of CO₂ efflux in darkness.

McCree and Troughton (51) concluded that respiration might account for a plant's ability to adapt to changes in light intensity. They exposed white clover (Trifolium repens) to different levels of light and found that the respiration rate adapted so as to maintain a constant proportion (about 20%) of the photosynthetic rate. Consequently, even when the light level dropped below the light compensation point, this adaptation occurred within 24 hours. The light compensation point dropped and the plants were able to resume efficient photosynthesis.

Photorespiration

Photorespiration is sometimes defined as light stimulated respiration. Photorespiration differs biochemically from dark respiration and is specifically associated with the oxidation of intermediate photosynthetic products (13, 44). Hatch's (37) recognition of different metabolic pathways in plants was caused by the photorespiration observed in C₃ plants and the lack of photorespiration in C₄ plants.

According to Zelitch (69) photorespiration rates can be three to five times greater than dark respiration rates.

Downton and Tregunna (30) found that C_4 plants have photosynthetic rates that are approximately double those of C_3 plants at optimum temperatures. Oxidation of glycolate does not occur in C_4 plants, preventing photorespiration. By inhibiting the oxidation of glycolate, Zelitch (69) found that tobacco (C_3) would behave like corn (C_4), with negligible photorespiration occurring. A reduction in photorespiration should increase net photosynthesis.

C_3 and C_4 Pathways

Fonteno (33) suggested that Raphidophora aurea might utilize the C_4 pathway. Calvin and Benson (29, 60) determined the basic cycle of CO_2 fixation by plants. In the Calvin-Benson cycle or C_3 pathway, ribulose-1,5-diphosphate is reacted with CO_2 , forming 2 molecules of 3-phosphoglyceric acid. The C_3 pathway can be thought of as the common denominator of all photosynthetic pathways.

The C_4 pathway, termed the C_4 -dicarboxylic acid cycle by Hatch and Slack (16, 37) enhances the C_3 pathway. The initial reaction is the reaction of phosphoenolpyruvate with CO_2 . This intermediate 4-carbon compound, oxaloacetate, immediately goes to either malate or aspartate for CO_2 in subsequent reactions in the thick-walled bundle sheath cells of C_4 plants. This CO_2 is not lost because of the thick walls that act as a physical barrier to CO_2 diffusion. Therefore,

CO₂ is concentrated for the initial reaction of the C₃ pathway. This results in high rates of CO₂ fixation at high light intensities and temperatures. In addition, reductions in the detrimental effects of high plant water stress are observed in C₄ plants (16, 30).

Temperature

Within the range of 15 to 35°C, temperature is usually not a limiting factor to photosynthesis (28, 46, 60). General optimum temperatures for C₃ and C₄ plants are 10 to 25°C and 30 to 40°C, respectively. Hew, Krotkov, and Calvin (41) concluded that while apparent photosynthesis increased with an increase in temperature from 20 to 40°C, net photosynthesis did not increase because of increased respiration.

Temperature extremes result in a depression of photosynthetic rates and can shift the point of optimal photosynthetic temperatures (66). A shift from 15 to 5°C in some mosses can result in lower light compensation and light saturation points (29). El-Sharkawy and Hesketh (31) showed that at 60°C and at 0°C the rate of photosynthesis for sunflower approached zero. A rise in temperature of growing conditions as seen in 'Grand Rapids' lettuce (Lactuca sativa) was correlated to an increase in the light compensation point (1). Other studies indicate similar results where a rise in temperature was correlated with a rise in the light compensation point for a variety of plant species (36, 52, 64).

Carbon Dioxide

The rate of photosynthesis will usually increase as the level of CO_2 is increased, until other factors become limiting. This saturation point differs depending upon the species and other factors. Gaastra (34) using cucumbers (Cucumis sativus), obtained CO_2 saturation at relatively low concentrations, approximately 1,000 ppm CO_2 . Once CO_2 saturation is reached, there is no appreciable increase in photosynthesis. Salisbury and Ross (60) showed that a tenfold increase in CO_2 concentration caused harmful effects on the growth of tomato plants (Lycopersicum esculentum) in approximately two weeks.

When the CO_2 level drops to the CO_2 compensation point, photosynthesis is limited and plants stop growing. Moss (53) determined that various species differ in the level to which they reduce the CO_2 concentration under limiting conditions. Hatch and Slack (37) demonstrated the reason for differing CO_2 compensation points between species. Sugarcane (Saacharum officinarum) and corn (Zea mays) fix CO_2 by way of the C_4 dicarboxylic acid pathway, while some small grains and grasses fix CO_2 by the C_3 carbon reduction pathway. Downton and Tregunna (30) proposed that C_4 plants have low CO_2 compensation points, and C_3 plants have high CO_2 compensation points.

Water Stress

El-Sharkawy and Hasketh (31) have indicated that water stress reduces the rate of photosynthesis. Boyer (14) showed that as water

stress increased, the leaf enlargement of sunflower was inhibited and stem elongation was decreased. He found that photosynthesis in plant species is differentially influenced by water stress, depending upon the stomatal behavior.

The rate of photosynthesis is determined by the rate of diffusion of CO_2 from the external air into the leaf. Gaastra (34) has shown that the stomatal diffusion resistance is a possible inhibitor of photosynthesis. He formulated three types of resistance: resistance caused by the external air, resistance due to stomata, and that due to the mesophyll cells. Fonteno (33) reported that Brassaia actinophylla and Raphidophora aurea showed the lowest leaf diffusive resistances of ten foliage plants examined, and showed that that resistance to water loss diminishes under low light intensities.

Leaf Age

Research has shown that photosynthetic rates of young leaves are relatively low, but increase up to a maximum at the apparent time of maturity, then decrease with increasing age. Salisbury and Ross (60) proposed that the decline in CO_2 uptake with increasing maturity results from changes in the chloroplasts. Older leaves become yellow, because of breakdown of the chlorophyll and chloroplasts become non-functional. Fonteno (33) determined that in general, older leaves of Brassaia actinophylla and Raphidophora aurea showed less CO_2 uptake than younger leaves.

Nutrition

Nutrition levels do affect the photosynthetic rates of plants. Devlin (29) explained that nutrient deficiencies result in incomplete development of some necessary components for the Hill reaction, possibly from the incomplete formation of chloroplast ultrastructure. Collard et al (17) reported that as fertilizer application rates increased, the light compensation point for Ficus benamina L. increased. High rates of nitrogen and potassium increased chlorophyll content of leaves, but may have sufficiently increased respiration rates to overcome the beneficial effects of increased chlorophyll and caused a rise in the light compensation point.

Light Acclimation Rates and Light Compensation Points

There has been considerable interest from commercial producers and universities to improve the quality of foliage plants by enhancing their ability to survive low light environments. Practical research has been aimed at acclimating sun grown plants to shade plants by placing them under high levels of shade prior to placement in low light environments (19, 23, 65). Systems have been developed for "pre-acclimatizing" foliage plants which demonstrated that plants grown under shade for at least two months showed improved quality when moved indoors (18). Several experiments conducted in Florida indicated that not only was light acclimation possible in the production area, but that the reduced light intensities would produce quality

plants with minimal investment costs and changes in production systems (21, 22, 23, 25).

Conover and Poole (23) utilized this acclimation procedure by placing Ficus benjamina L. under 80% shade for 5 weeks, which reduced leaf drop by 50% when plants were later placed in a low light environment. Further work by Conover and Poole (19) showed that by decreasing the light intensity from 12,000 ft-c to 2,500 ft-c for twelve weeks of acclimation, decreased leaf drop of Ficus benjamina L. when moved to 540 ft-c for eight hours per day for ten weeks. Reports by Vlahos and Boodley (65) showed no difference in leaf drop of Ficus nitida and Brassaia actinophylla when acclimated for nine weeks under 3,700 ft-c or 1,850 ft-c and then held indoors at 50 ft-c to 100 ft-c for eight to ten hours per day. More recently Conover and Poole (23) demonstrated that container-grown Ficus benjamina and Brassaia actinophylla acclimated under 40 to 80% shade for five weeks or more, then moved to an interior environment, had improved quality over plants grown in full sun. These plants had improved foliage retention as the light intensity of the interior environment was increased from 0.3 to 0.8 to 1.3 klux when supplied twelve hours daily. This work with Ficus benjamina by Conover and Poole showed that good quality plants, larger than those plants grown in full sun, can be produced under 80% shade, with reduced watering and nutritional practices (24). They have suggested that light acclimation with a minimum of 150 ft-c

for ten to twelve hours duration for seven days a week should be satisfactory for most species of foliage plants.

There are many possible lighting regimes which depend primarily on the light compensation point for the individual species. There are very few reports in the literature on light compensation points for foliage plants. Bohning and Burnside (12) reported the light compensation point for Nephrolepis exaltata bostoniensis to approximate 50 ft-c. Ludlow (49) determined the light compensation points for three native ferns from shade habitats to be 50 ft-c at 18°C (75 to 100 ft-c at 30°C). DePauw and DePauw (Unpublished data, Colorado State University, 1975) found that Dracaena marginata, acclimated under 400 ft-c for thirty days, lowered its light compensation point by 17%, 11% in the first week. Further studies showed the light compensation point for Ficus nekbuda, Dieffenbachia picta, and Dracaena dermensis 'Warneckii' to vary from less than 100 ft-c to more than 200 ft-c, indicating the degree of variability that can exist between plants of the same species. Collard et al (17) found that the light compensation point of Ficus benjamina decreased 300% when plants were grown under 80% shade (2,500 ft-c) rather than full sun (12,000 ft-c). Fonteno (32, 33) reported that the light compensation point for six foliage plants acclimated at $27 \mu\text{E m}^{-2} \text{sec}^{-1}$ decreased as much as 600% between weeks one and fifteen. Brassaia actinophylla had an initial light compensation point of $14 \mu\text{E m}^{-2} \text{sec}^{-1}$ and $4 \mu\text{E m}^{-2} \text{sec}^{-1}$ for week fifteen. Raphidophora aurea had an initial light compensation

point of $38 \mu\text{E m}^{-2} \text{sec}^{-1}$ and $6 \mu\text{E m}^{-2} \text{sec}^{-1}$ for week fifteen (33).

Vlahos and Boodley (65) suggested that Brassaia actinophylla could be maintained at 100 ft-c indoors, which may be interpreted as the light compensation point (23). Work by Kofranek (45) indicated similar results when Brassaia actinophylla was held under 430 to 860 lux indoors with cool white fluorescent lighting for sixteen hours per day for four months.

There are several texts and articles available giving information on the light requirements for foliage plants (27, 35). However, these recommendations are excessively broad and sometimes conflicting (33). For example, Brassaia actinophylla has been reported by DeWerth (27) to require 1,000 to 5,000 ft-c for optimum growth, but will tolerate 500 to 1,000 ft-c, and will survive at a minimum of 30 to 50 ft-c. Graf (35) shortened the optimum growth range to 1,000 to 3,000 ft-c lengthened the tolerant range to 100 to 1,000 ft-c, and listed survival at a minimum of 50 ft-c. This uncertainty is ample evidence for a need to determine the actual light requirements for foliage plants utilizing available research techniques.

MATERIALS AND METHODS

A system to measure the rate of net CO₂ exchange for whole plants was designed to determine the light compensation points and acclimation rates of selected foliage plants. The system consisted of two distinct parts: 1) the light acclimation chambers which contained the foliage plants and their replicates, and sample chambers, and 2) the infrared gas analysis system (Fig. 1).

Light Acclimation Chambers

The light acclimation chambers were built to create an isolated, fixed irradiation level, and to accommodate nine whole plants (three replications of three species) and the sample chamber (Fig. 2). The chambers measured eight feet cubed and were constructed of $\frac{1}{4}$ " x 4' x 8' masonite on a 2" x 4" frame. The interior was painted with a flat white latex base paint. The irradiation source consisted of four double tubed 40 Watt, Sylvania, cool white, fluorescent fixtures and one 250 Watt, Sylvania, high pressure sodium fixture. Different irradiation levels in the four chambers were accomplished by raising and lowering the fixtures and covering the fixtures with cheesecloth screens. Irradiation levels were measured and monitored weekly, utilizing a Lambda meter, Model LI-185,¹ with a quantum sensor

¹ Lambda Instruments Corp., Inc., Lincoln, Nebraska 68508.

Figure 1. A schematic illustration of a light chamber and the infrared gas analysis system.

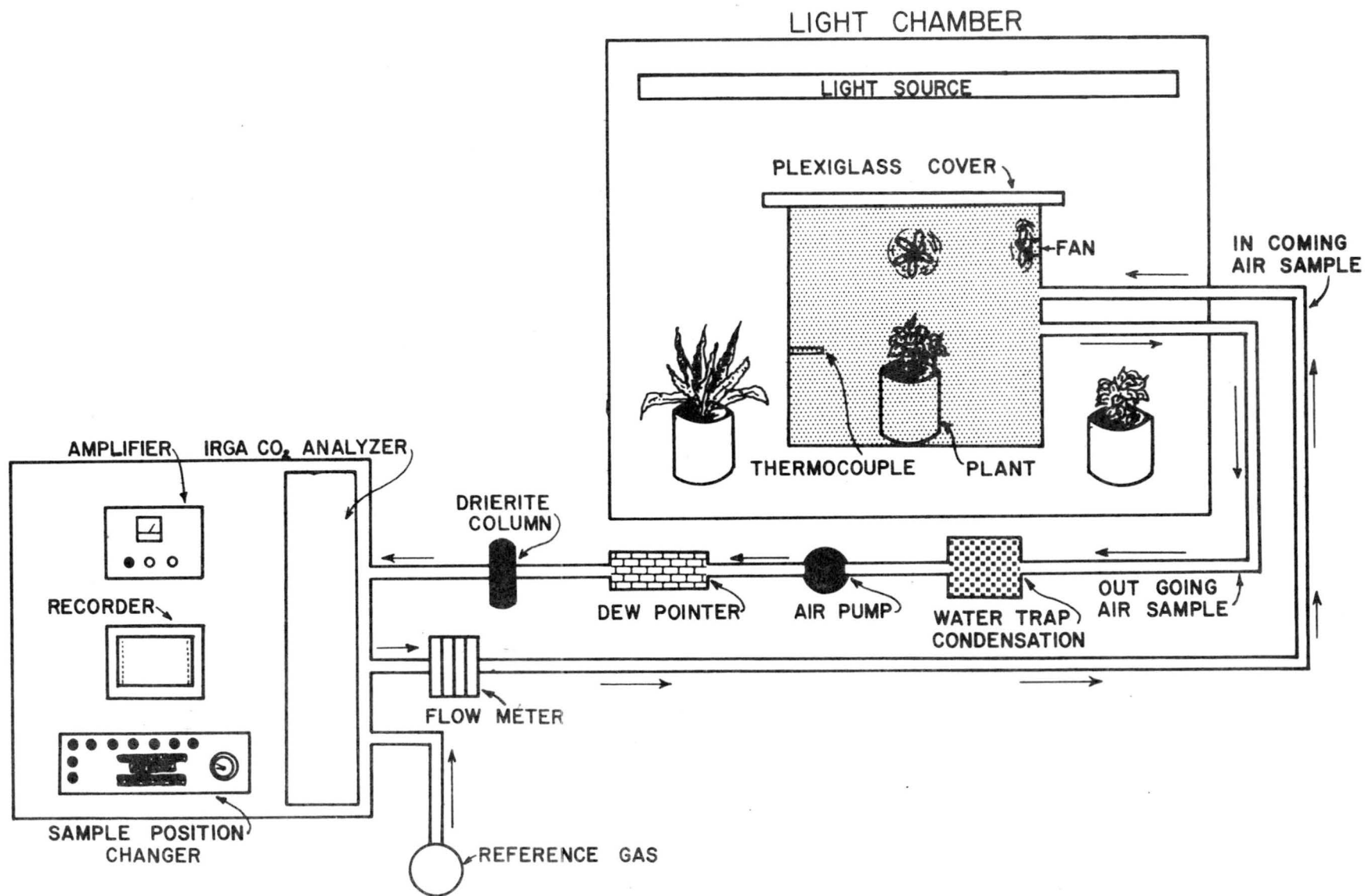


Figure 2. The greenhouse where plant material was held prior to the experiments, and the light acclimation chambers.

Figure 3. A sample chamber with plexiglass top and circulating fan (top of photograph).



($\mu\text{E m}^{-2} \text{s}^{-1}$) and a photometric sensor (lux). Each irradiation source was measured for photosynthetically active radiation utilizing an I. S. C. O. Spectroradiometer, Model SR.² Measurements are graphically compared in Figure 4. The environmental parameters of each light chamber are listed in Table 1. The duration of irradiation was controlled by a series of 24-hour time clocks set for 14 hours per day. The temperature was controlled through the modification of the greenhouse evaporative pad cooling and unit heater systems. Temperatures were monitored constantly with copper-constantan thermocouples (26 gauge) in conjunction with a 12-position Bristol Dynamaster Recorder.³

Sample Chambers

The closed system sample chambers were constructed to allow for the measurement of net CO_2 exchange rates for whole plants. The chambers were built of 3/4" plywood sides and bottom (32" x 32" x 48"). The chambers were spray painted with a white polyurethane base paint⁴ to minimize gas diffusion. The top of the sample chamber was a 36" square sheet of 3/8" clear plexiglass placed on a rubber gasket covered with a thermoseal grease to complete the chamber seal (Fig. 3). The sample air inlet and outlet were positioned on different

²Instrument Specialties Co., Inc., Lincoln, Nebraska 68507.

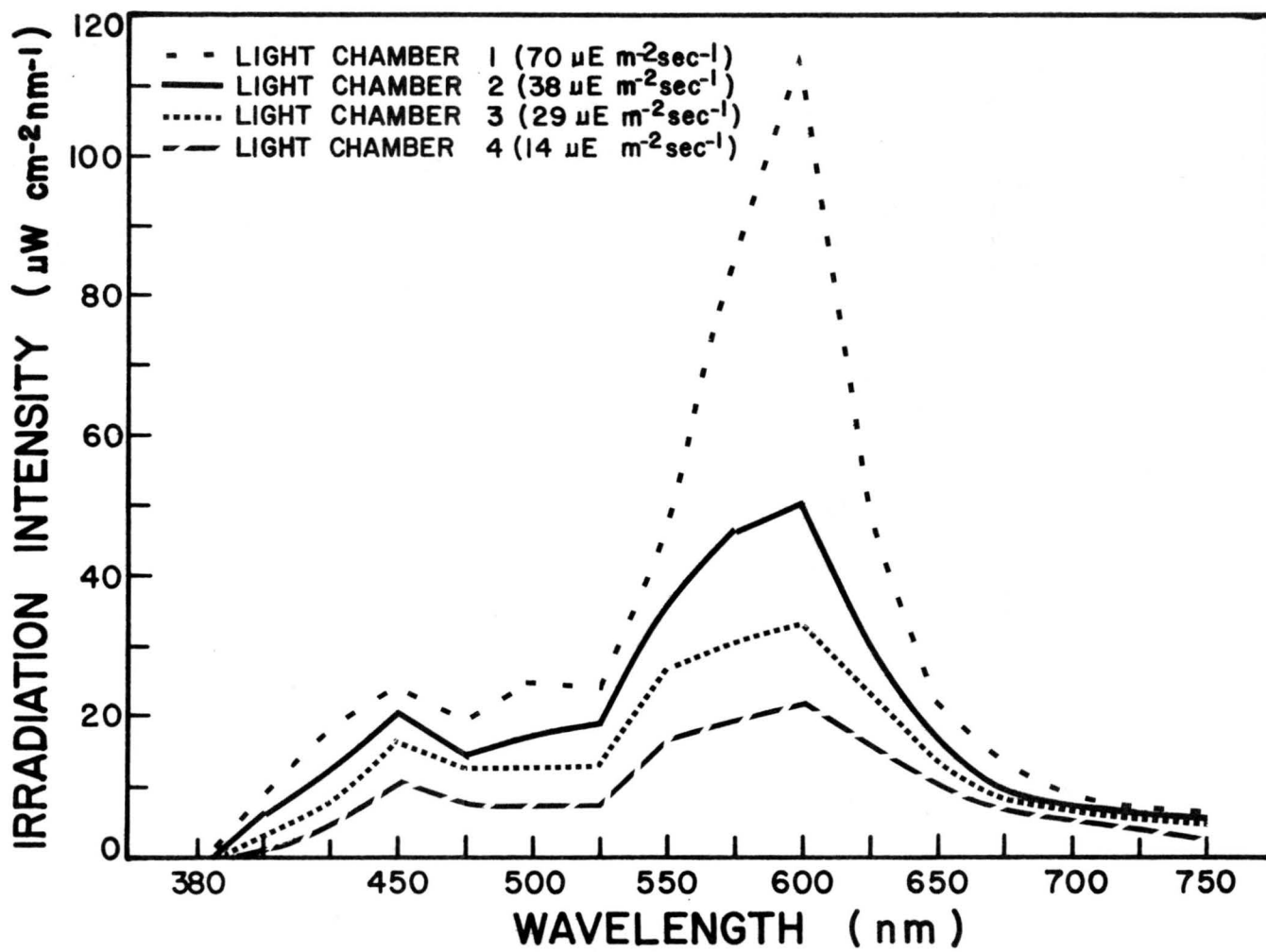
³The Bristol Company, Waterbury, Connecticut 06720.

⁴Polane Polyurethane, Sherwin-Williams Paints, Dallas, Texas

Table 1. Environmental parameters within the light acclimation chambers.

	Light Chambers			
	1	2	3	4
<u>Temperature</u>				
Interval:	22-28°C	22-28°C	20-26°C	20-26°C
Mean:	25°C	25°C	24°C	24°C
<u>Irradiation</u>				
$\mu\text{E m}^{-2} \text{s}^{-1}$:	70 E	38 E	29 E	14 E
fc:	400 fc	223 fc	173 fc	81 fc
Duration:	14 hrs	14 hrs	14 hrs	14 hrs
<u>Humidity</u>				
Relative %:	70-100%	70-100%	70-100%	70-100%

Figure 4. Spectroradiometric measurements for each light chamber.



planes of the same side of the chamber to allow for adequate mixing of incoming air. Two small fans (1/100 hp, 1550 cfm) were mounted on different planes on adjacent sides to create a homogeneous CO₂ concentration within each sample chamber, and to provide adequate wind velocity to reduce boundary layer resistances. Ambient air temperatures of the light chambers were responsible for the temperature control of the sample chambers. Copper-constantan thermocouples were mounted in each sample chamber to monitor air and leaf temperatures and were recorded on the Bristol recorder.

Carbon Dioxide Analysis

A Beckman Infrared Gas Analyzer, Model 315B Differential,⁵ was used for all measurements of CO₂ exchange in these experiments (Fig. 5). The analyzer was calibrated using two standard gases (Matheson, 335 and 570 ppm CO₂) so that the deflection of one recorder unit represented a change in differential of 3.0 ppm CO₂. Calibration checks were made at regular intervals and the gain control was altered if an apparent drift of more than one percent was observed. Pre-purified nitrogen was used for the zero gas in the reference cell of the analyzer. A continuous record of the CO₂ differential was kept, utilizing a Hewlett Packard, Model 680, Strip Chart Recorder.⁶ A

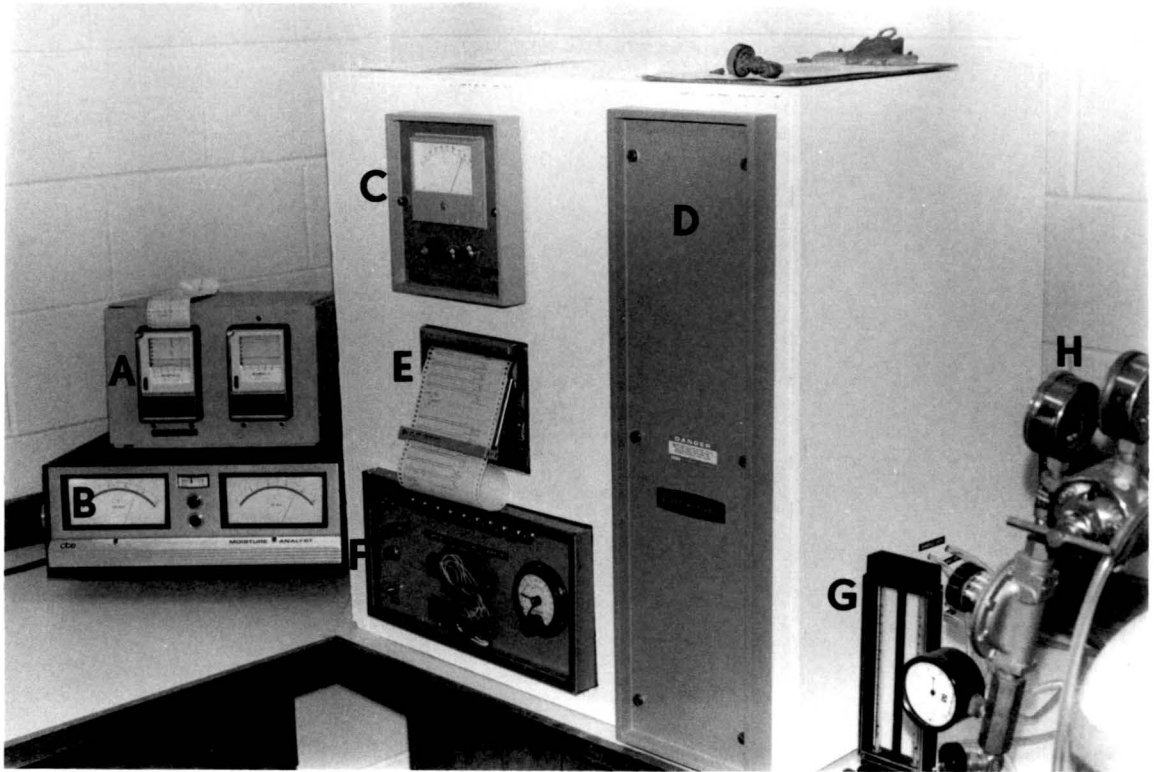
⁵Beckman Instruments, Inc., Fullerton, California 92634.

⁶Hewlett Packard, Inc., Fullerton, California 92634.

Figure 5. The infrared gas analysis system.

- A - Recorders
- B - Moisture Analyzer
- C - IRGA amplifier
- D - IRGA analyzer
- E - CO₂ recorder
- F - Sample Changer
- G - Flow meter
- H - Calibration gases

Figure 6. Plant material used in Experiments I and II.
The squares in the grid pattern behind the
plants represent one square dm.



Scindapsus aureus

Brassaia actinophylla

*Nephrolepis exaltata
bostoniensis*



flow rate of 420 ml/min was maintained for the sample gas. Once the gas left the sample chamber via $\frac{1}{4}$ " tygon tubing, it passed through a water trap to collect any water condensation. An air pump, Neptune, Dyna-Pump, Model 3,⁷ pulled the sample air to the pump, then pushed the sample through a dew point sensor, Moisture Analyst, Model 84M,⁸ where the humidity measurements were continually recorded on a Rustrak Recorder, Model 288.⁹ All moisture was removed from the air sample in the passage through a Drierite column. The air sample passed through the infrared gas analyzer, back through a flow meter, and returned to the appropriate sample chamber.

A time-saving feature of the sample gas system was the Hanan Sample Position Changer.¹⁰ Each sample chamber was connected to a separate solenoid pair allowing sample gas from the appropriate sample chamber to be removed and returned on a time basis. The switching system was set on a six minute time interval so that each sample chamber was sampled for six minutes in sequence, then sampling was repeated.

⁷Neptune Products, Inc., Dover, New Jersey 07801.

⁸C.T.E., Inc., Sunnyvale, California 94088.

⁹Gulton Industries, Inc., East Greenwich, Rhode Island 02818.

¹⁰Dr. J. Hanan, CSU, Fort Collins, Colorado 80523.

Plant Material

Three species of foliage plants, Brassaia actinophylla Endl., Nephrolepis exaltata 'Bostoniensis' (L.) Schott, and Scindapsis aureus Schott (43), were selected for their economic importance and taxonomic diversity.

Commercially salable plants in six inch pots were received in March, 1977 (Fig. 6). Vegetatively propagated Nephrolepis exaltata 'Bostoniensis' and seed propagated Brassaia actinophylla were obtained from Tagawa Greenhouses Inc., Brighton, Colorado. Plants of Scindapsis aureus were vegetatively propagated from plants obtained from Yoder's Inc., Fort Myers, Florida. The potting media consisted of one part peat to one part perlite. Each plant received a top dress application of 14-14-14 osmocote fertilizer upon arrival. All plants were grown in a Fiberglass Reinforced Plastic (FRP) covered, air cooled greenhouse until the start of the light acclimation experiments on July 7, 1977. Environmental parameters within the greenhouse one month prior to the experiments are listed in Table 2.

Twelve plants of each species were selected for uniformity at the start of the experiments. All remnants of the osmocote fertilizer were removed, the pots were leached thoroughly and received no additional source of fertilizer through the duration of the experiments.

Table 2. Greenhouse environmental parameters from 6/1 to 7/6/77.

<u>Temperature</u>	
Day:	Heat to 21°C
	Cool to 24°C
Night:	Heat to 18°C
<u>Irradiation</u>	
Mean Max:	931 $\mu\text{E m}^{-2} \text{s}^{-1}$
	5200 ft-c
	0.83 $\text{cal cm}^{-2} \text{min}^{-1}$
<u>Humidity</u>	
Interval:	35 to 95%

Experiment I

Rates of net CO_2 exchange were measured by placing the replicated species in the sample chamber within each of the light chambers. The rate of CO_2 exchange was determined by the change of CO_2 concentration in each sample chamber with time. A plant was measured for net CO_2 exchange differential for six minute intervals, six times within a three hour period to establish a steady state of CO_2 flux. This period of time allowed four plants to be sampled during one 14 hour day, followed by one plant sampled in the dark, to establish the dark respiration rates. Net CO_2 measurements were made on each plant three times a week for the seven week duration of the

experiment. These three CO_2 measurements were averaged to give a mean net CO_2 exchange rate for one week.

Experiment II

The procedure remained the same for Experiment II. The objective of Experiment II was to observe the time and rate for a plant to re-acclimate to a change in irradiation. Plants acclimated under the highest irradiation level ($70 \mu\text{E m}^{-2} \text{s}^{-1}$) were moved to the next highest irradiation level ($38 \mu\text{E m}^{-2} \text{s}^{-1}$). Plants from $38 \mu\text{E m}^{-2} \text{s}^{-1}$ were moved to $29 \mu\text{E m}^{-2} \text{s}^{-1}$, and plants from $29 \mu\text{E m}^{-2} \text{s}^{-1}$ were moved to the lowest irradiation level, $14 \mu\text{E m}^{-2} \text{s}^{-1}$. Plants at the lowest irradiation level were moved to the highest irradiation level. The experiment was terminated after three weeks.

Root and Soil Respiration

Considerations were made for removing the effects of root and soil respiration. At the time of the experiments it was felt that plastic bags to isolate the pot and soil were permeable to CO_2 and could not be utilized. However, Fonteno (33) showed that the plastic bags he used to isolate the pot and soil allowed no interference by root zone respiration with the CO_2 measurements. Another method was suggested and tried on a pre-experimental basis, utilizing paraffin wax and mineral oil at a ratio of 1:1 (5, 15) to seal the soil surface. Over 2 to 3 weeks period of time there appeared to be restricted soil

aeration and water movement, resulting in a detrimental influence to the plants CO_2 exchange rate. Both methods were therefore abandoned. However, an attempt to measure the root and soil respiration was made. Three replications of each species, with all the photosynthetic area removed, were utilized for the measurements. The mean rate of belowground respiration for the three species was approximately $0.03 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. A Tukey HSD mean separation test for the means of these three species showed no significant differences at the 5% level.

Leaf Area

The leaf area was determined for each plant in both experiments with the use of a Li-Cor Portable Leaf Area Meter, Model LI-3000.¹¹ The portable leaf area meter permitted non-destructive, intact leaf area measurements.

Calculations of Net CO_2 Exchange

All photosynthetic and respiratory rates determined for Experiments I and II were computed by the equation (5, 15, 59):

$$P_n \text{ or } R_d = ((MVT_1 P / LTP_1) (\Delta \text{ppm/hr} \times 10^{-6})) / LA$$

where: P_n = net photosynthesis ($\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$)

R_d = dark respiration ($\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$)

¹¹ Lambda Instruments Corp., Inc., Lincoln, Nebraska 68508.

M = mole weight of CO₂ (44,010 mg)

V = volume of closed system (804.2 l)

T₁ = 273°K

P = average barometric pressure (635 mm Hg)

L = mole volume of CO₂ (22.414 l)

T = 298°K

P₁ = standard barometric pressure (760 mm Hg)

Δppm/hr = CO₂ exchange rate in parts per million per hour converted to the volume fraction of CO₂ by multiplying by 10⁻⁶

LA = leaf area of one side (dm²)

The computed net CO₂ exchange rates at the four irradiation levels were subjected to linear regression analysis for each species and an equation for each resulting line was obtained using the formula:

$$y = B_1 x + B_0, \text{ where (33):}$$

y = net CO₂ exchange rate

x = irradiance

B₁ = slope

B₀ = y-intercept

Light compensation points were computed by substituting y = 0 into the equation and solving for x, the resulting formula for light compensation points being $x = -B_0 / B_1$.

All corrections applied to the raw data and calculated rates of CO₂ exchange and light compensation points were achieved by the use of a computer. The program listed all the observations in an orderly

fashion, calculated the rates of net CO_2 exchange, light compensation points, and plotted the relationships of net CO_2 exchange with irradiation for each plant species.

The two experiments were treated as split plots in design, with the species being the mainplot and the acclimation time as the subplots. Analysis of variance (Repeated Measures Program Design) was performed on the net CO_2 exchange rates in each experiment (62). Significant mean separations were made using Tukey's HSD test at the 5% level of probability.

RESULTS AND DISCUSSION

Experiment I

Results of Experiment I are shown in Tables 3 and 4, and Figures 7, 8, and 9. General observations and statements can be made for the three plant species. Net CO₂ exchange rates decreased with decreasing irradiation levels. At 70 $\mu\text{E m}^{-2} \text{s}^{-1}$ there was always net CO₂ uptake over the seven week period. However, the net amount of CO₂ fixed consistently decreased over the seven weeks. At the lowest irradiation level, 14 $\mu\text{E m}^{-2} \text{s}^{-1}$, the CO₂ evolution diminished over the duration of the experiment. The CO₂ fixation, CO₂ evolution, and dark respiration rates were usually significantly greater during the first week of acclimation.

Brassaia actinophylla. Net CO₂ uptake occurred at all irradiation levels except for week one at 14 $\mu\text{E m}^{-2} \text{s}^{-1}$. Although CO₂ uptake decreased over the course of the experiment, the rates of decrease were only significantly greater for week one versus the other weeks of the experiment (Table 3 or Fig. 7). Dark respiration and consequential CO₂ evolution also diminished through time for all irradiation levels during the experiment. Dark CO₂ evolution decreased significantly during weeks 1, 3, and 5, but thereafter, there was no further reduction during the seventh week (Table 4 or Fig. 7).

Table 3. Mean net CO₂ uptake (+) and evolution (-) in mg CO₂ dm⁻² hr⁻¹ at four irradiation levels for plants acclimated after 1, 3, 5, and 7 weeks. Means in a column for a species with similar letters are not significantly different (P = 5%).

Species	Weeks	Irradiation Levels ($\mu\text{E m}^{-2} \text{sec}^{-1}$)			
		14	29	38	70
<u>Brassaia actinophylla</u>	1	-0.851a	1.113a	1.798a	8.113a
	3	0.151b	0.448b	0.946b	2.696b
	5	0.196b	0.476b	0.819b	1.965b
	7	0.149b	0.381b	0.650b	1.398b
<u>Nephrolepis exaltata</u> 'Bostoniensis'	1	-3.003a	-2.282a	-1.703a	0.818a
	3	-2.012a	-1.212a	-1.034a	0.672a
	5	-0.640b	-0.570b	-0.316b	0.105b
	7	-0.130b	-0.070b	0.028b	0.097b
<u>Scindapsis aureus</u>	1	-1.271a	0.618a	1.558a	4.815a
	3	-0.172b	0.582b	1.241b	3.261b
	5	-0.148b	0.442b	0.983b	1.022b
	7	-0.042b	0.128b	0.191b	0.788b

Table 4. Mean dark respiration rates which represent CO₂ evolution in mg CO₂ dm⁻² hr⁻¹ following four irradiation levels for plants acclimated after 1, 3, 5, and 7 weeks. Means in a column for a species with similar letters are not significantly different (p = 5%).

Species	Weeks	Irradiation Levels ($\mu\text{E m}^{-2} \text{sec}^{-1}$)			
		14	29	38	70
<u>Brassaia actinophylla</u>	1	-5.608a	-6.241a	-6.465a	-5.998a
	3	-1.975b	-2.775b	-2.931b	-3.831b
	5	-1.249c	-1.163c	-1.308c	-1.736c
	7	-1.199c	-0.981c	-1.175c	-0.865c
<u>Nephrolepis exaltata</u> 'Bostoniensis'	1	-5.467a	-5.302a	-5.604a	-5.739a
	3	-1.953b	-2.198b	-2.216b	-2.108b
	5	-1.299b	-1.472b	-1.385b	-1.792b
	7	-1.176b	-1.187b	-1.031b	-1.135b
<u>Scindapsis aureus</u>	1	-3.189a	-3.211a	-3.996a	-4.425a
	3	-2.901b	-2.393b	-2.411b	-3.516b
	5	-1.121c	-1.146c	-1.744c	-2.594c
	7	-1.091c	-1.044c	-1.135c	-1.444c

Figure 7. Upper: Net CO₂ exchange rates for Brassaia actinophylla. Fixed irradiation levels were 14, 29, 38, and 70 $\mu\text{E m}^{-2}\text{s}^{-1}$. CO₂ fixation is represented by all points above and CO₂ evolution by all the points below the zero axis. Light compensation points were interpreted as the point where the regression lines intersected the zero axis.

Lower: Dark respiration rates for Brassaia actinophylla as affected by irradiation environment.

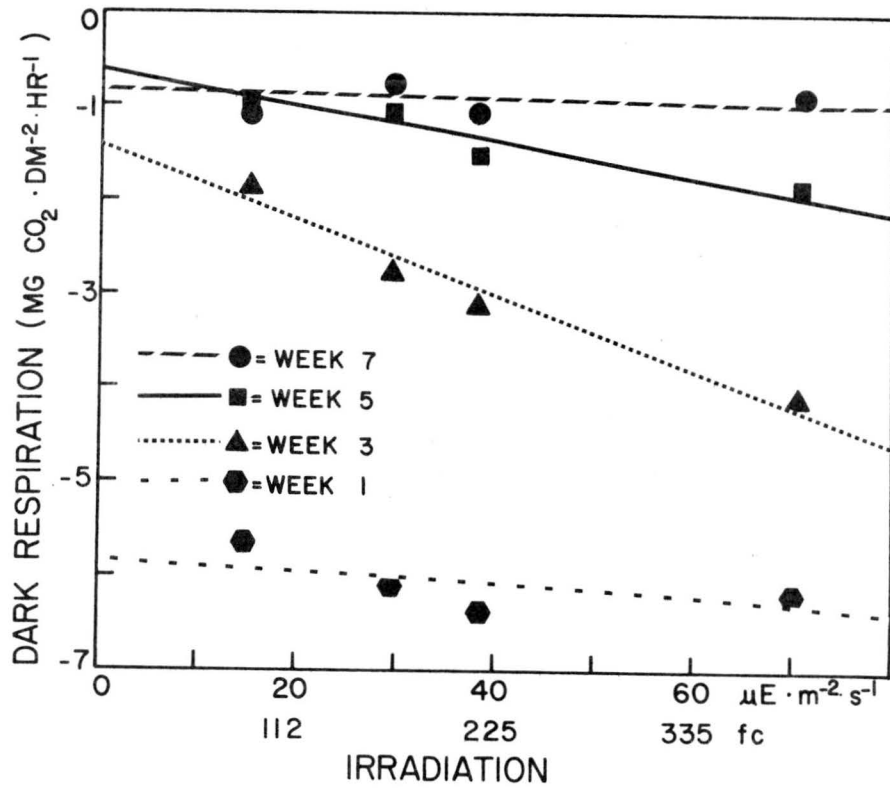
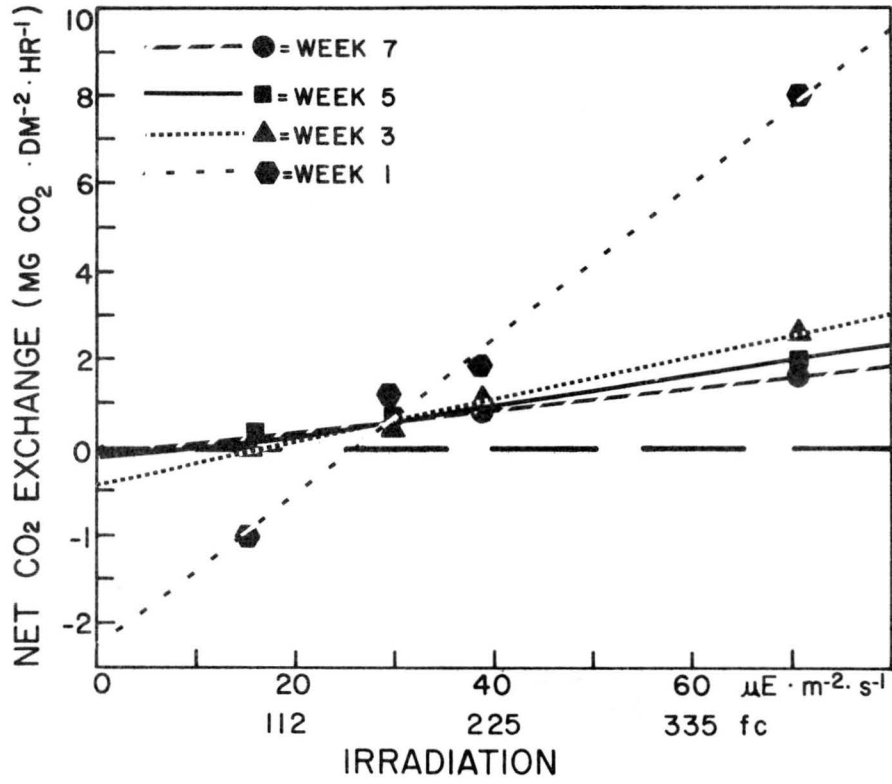


Figure 8. Upper: Net CO₂ exchange rates for Nephrolepis exaltata 'Bostoniensis.' Fixed irradiation levels were 14, 29, 38, and 70 $\mu\text{E m}^{-2}\text{s}^{-1}$. CO₂ fixation is represented by all points above and CO₂ evolution by all points below the zero axis. Light compensation points were interpreted as the point where the regression lines intersected the zero axis.

Lower: Dark respiration rates for Nephrolepis exaltata 'Bostoniensis' as affected by irradiation environment.

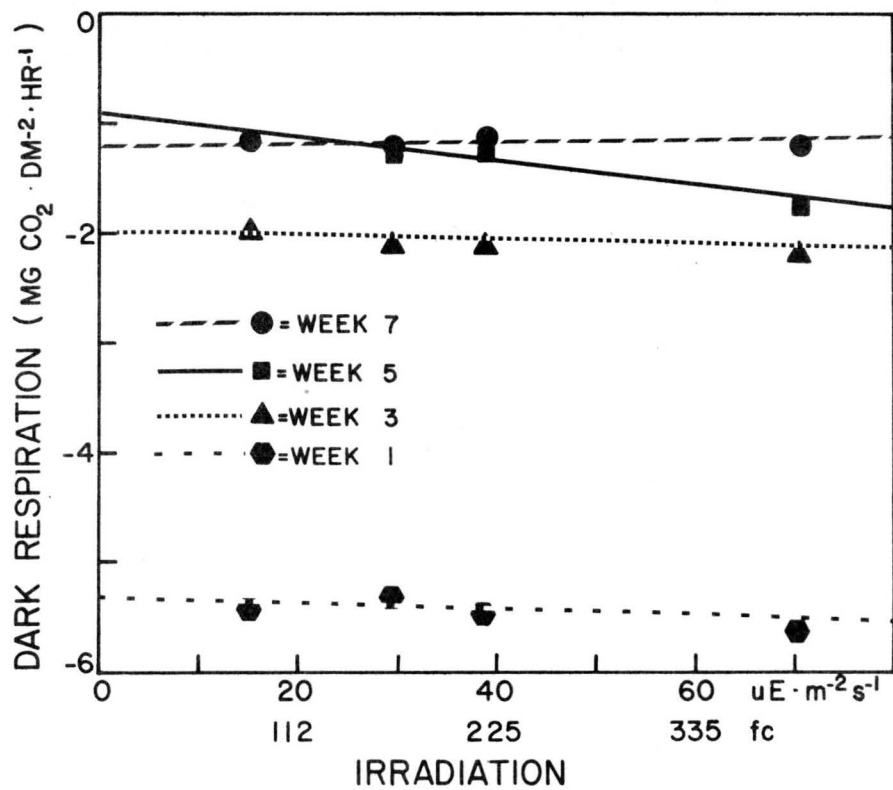
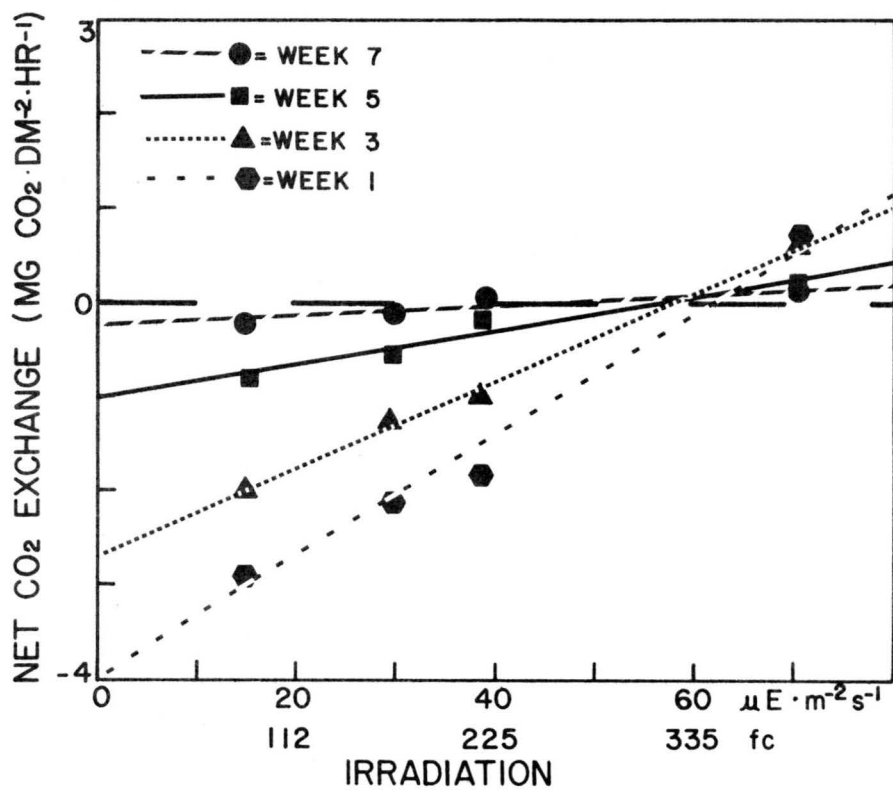
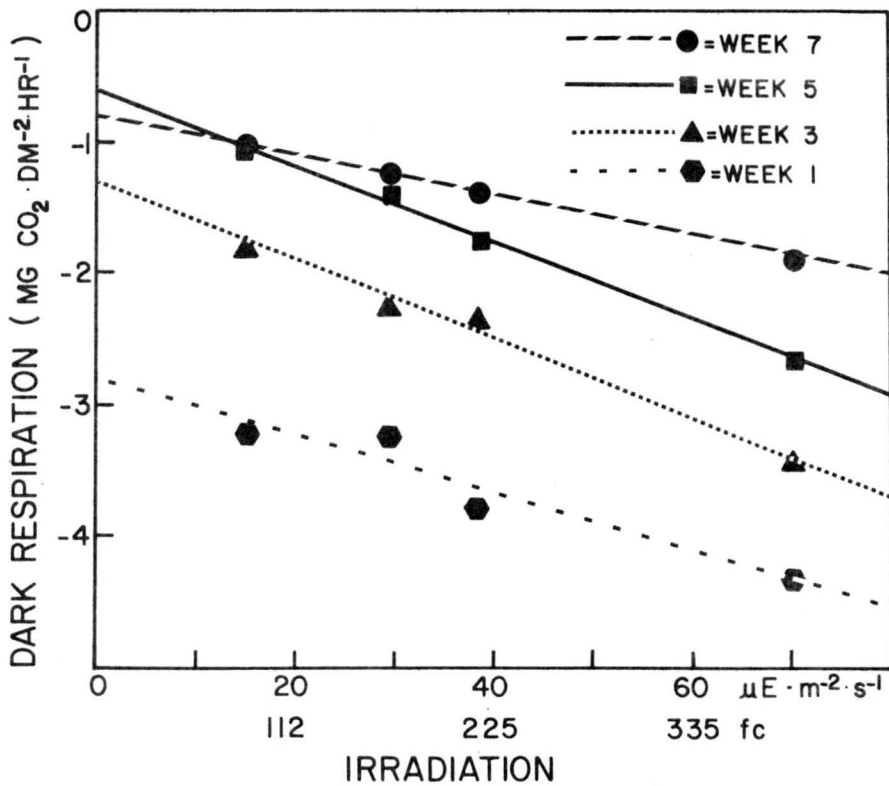
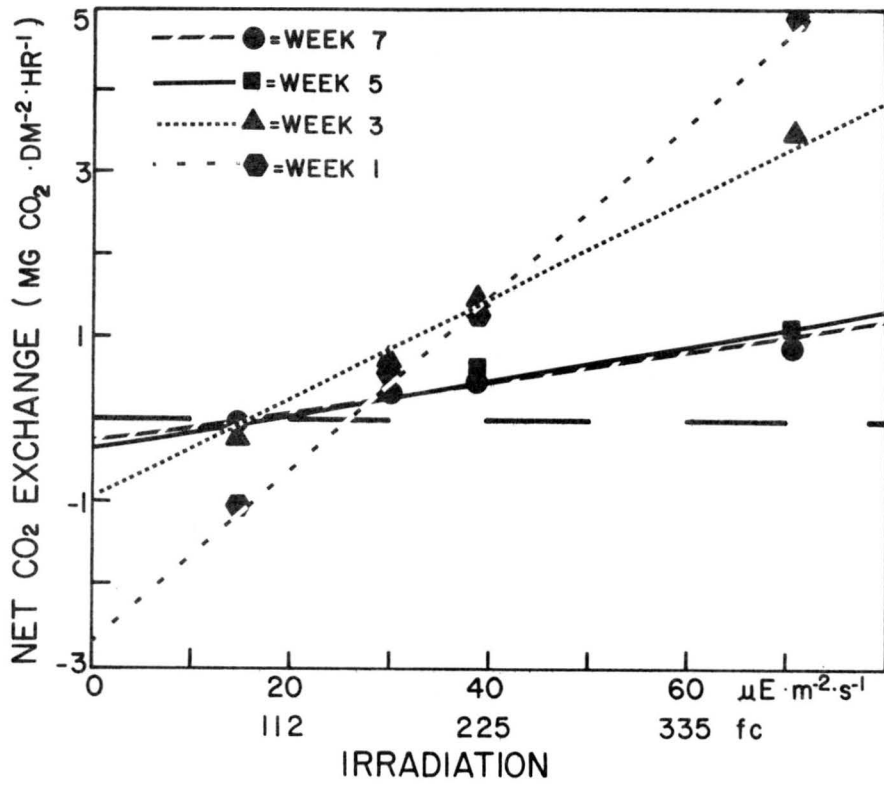


Figure 9. Upper: Net CO₂ exchange rates for Scindapsis aureus. Fixed irradiation levels were 14, 29, 38, and 70 $\mu\text{E m}^{-2}\text{s}^{-1}$. CO₂ fixation is represented by all points above and CO₂ evolution by all points below the zero axis. Light compensation points were interpreted as the point where the regression lines intersected the zero axis.

Lower: Dark respiration rates for Scindapsis aureus as affected by irradiation environment.



Nephrolepis exaltata 'Bostoniensis'. Net CO₂ uptake only occurred at 70 $\mu\text{E m}^{-2} \text{s}^{-1}$ for the duration of the experiment. CO₂ evolution took place at all the lower irradiation levels and was significantly greater for weeks one and three. CO₂ evolution decreased until week five and then leveled off (Table 3 or Fig. 8). A significant reduction in dark respiration occurred between weeks one and three and did not change significantly for the extent of the experiment (Table 4 or Fig. 8).

Scindapsis aureus. CO₂ fixation took place at a diminishing rate for irradiation levels 70, 38, and 29 $\mu\text{E m}^{-2} \text{s}^{-1}$, respectively. CO₂ evolution resulted only at the lowest irradiation level, 14 $\mu\text{E m}^{-2} \text{s}^{-1}$. Less CO₂ was evolved during weeks 3, 5, and 7 than during week one (Table 3 or Fig. 9). The dark respiration rates were lower for this species during week one, but like the other species, decreased during weeks three and five at all irradiation levels (Table 4 or Fig. 9).

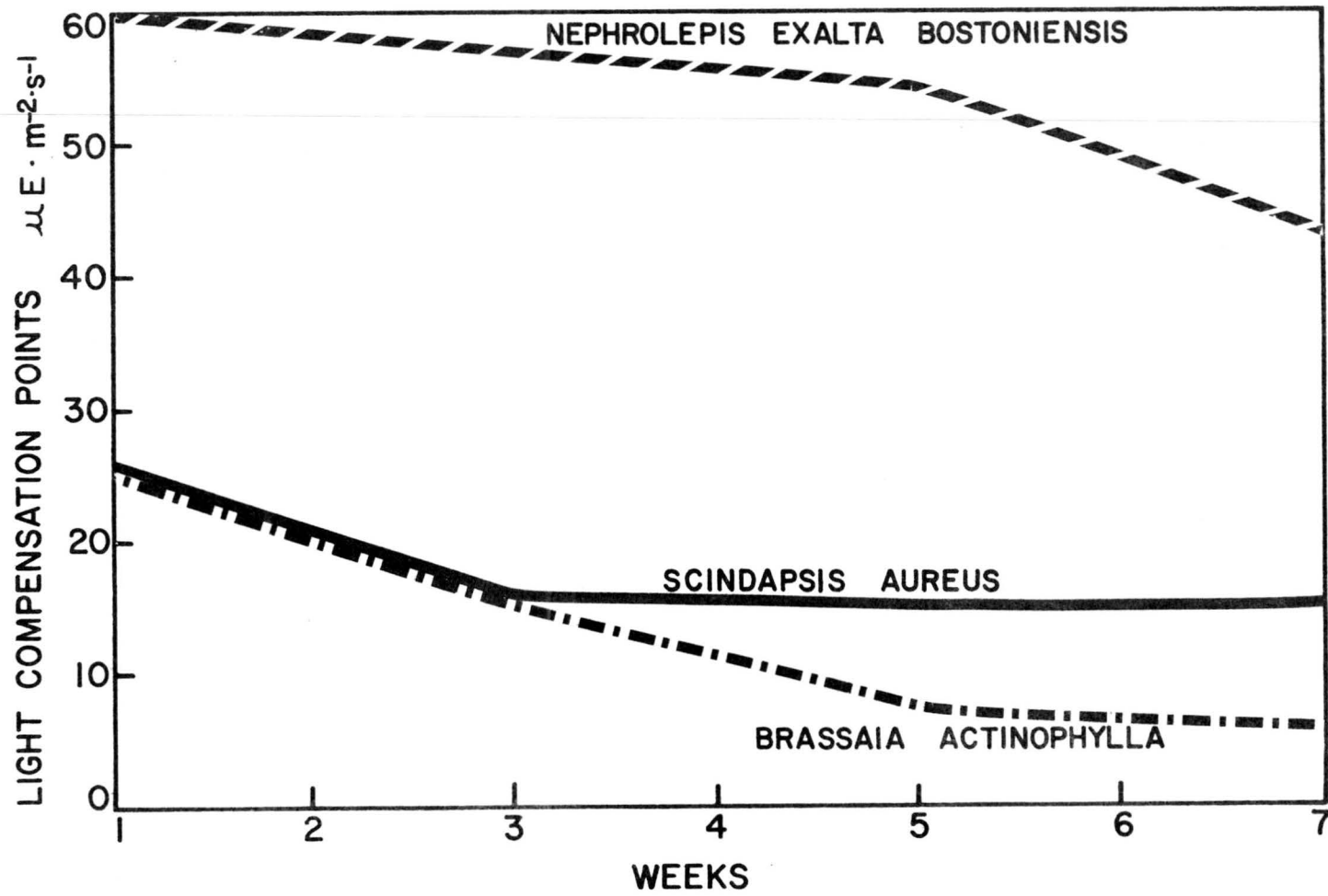
Light Compensation Points

Brassaia actinophylla exhibited the most dramatic reduction in light compensation points of the three plant species (Table 5 or Fig. 10). There was a five-fold reduction in the light compensation point from week one to week seven. Nephrolepis exaltata 'Bostoniensis' exhibited the highest light compensation points and the slowest rate of acclimation with a 1.4 fold reduction from week one to week seven. Scindapsis aureus was intermediate in acclimation rate with a 1.7

Table 5. Light compensation points for three plants acclimated to irradiance environment after 1, 3, 5, and 7 weeks.

	Weeks	$\mu\text{E m}^{-2} \text{sec}^{-1}$	foot-candles	lux
<u>Brassaia actinophylla</u>	1	25	145	1566
	3	15	87	940
	5	7	41	443
	7	5	27	313
<u>Nephrolepis exaltata</u> 'Bostoniensis'	1	60	338	3650
	3	58	347	3748
	5	54	312	3370
	7	44	255	2754
<u>Scindapsis aureus</u>	1	26	150	1620
	3	16	93	1004
	5	15	87	940
	7	14	81	875

Figure 10. Rates of acclimation for Brassaia actinophylla,
Nephrolepis exaltata 'Bostoniensis,' and
Scindapsis aureus.



fold reduction in light compensation points from week one to week seven.

Experiment II

Results of Experiment II are shown in Tables 6 and 7, and Figures 11, 12, and 13. Net CO₂ exchange rates diminished with decreasing irradiation levels. At 70 μE m⁻² s⁻¹ there was always net CO₂ uptake for the three week period of re-acclimation. CO₂ evolution in the dark was always lowest for all treatments for the third week of re-acclimation.

Brassaia actinophylla. Net CO₂ fixation took place at all irradiation levels except for week one at 14, 29, and 38 μE m⁻² sec⁻¹. Dramatic increases in net CO₂ uptake for irradiation levels 14, 29, and 38 μE m⁻² sec⁻¹ and dark respiration rates at all irradiation levels occurred during the second week (Tables 6 and 7, Fig. 11). Minimum net CO₂ exchange and dark respiration rates took place during the third week of re-acclimation.

Nephrolepis exaltata 'Bostoniensis'. Net CO₂ fixation occurred only at 70 μE m⁻² sec⁻¹ for the three week period (Tables 6 and 7 or Fig. 12). CO₂ evolution occurred at all lower irradiation levels. The amount of CO₂ fixed or evolved consistently decreased over the three week period. A significant reduction in dark respiration took place between weeks one and two and did not change appreciably for the third week of re-acclimation.

Table 6. Mean net CO₂ uptake (+) and evolution (-) in mg CO₂ dm⁻²hr⁻¹ at four irradiation levels for plants re-acclimating after weeks 8, 9, and 10.

Species	Weeks	Irradiation Levels ($\mu\text{E m}^{-2}\text{sec}^{-1}$)			
		14	29	38	70
<u>Brassaia actinophylla</u>	1	-1.13	-0.60	-0.64	2.94
	2	0.38	1.17	1.33	2.04
	3	0.14	0.15	0.23	0.60
<u>Nephrolepis exaltata</u> 'Bostoniensis'	1	-0.87	-1.01	-1.48	2.40
	2	-0.44	-0.41	-0.27	0.70
	3	-0.06	-0.08	-0.11	0.42
<u>Scindapsis aureus</u>	1	-1.08	-0.97	-1.65	0.98
	2	-0.27	-0.36	-0.66	0.82
	3	-0.05	-0.06	-0.11	0.11

Table 7. Mean dark respiration rates which represent CO_2 evolution in $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ following four irradiation levels for plants re-acclimating after weeks 8, 9, and 10.

Species	Weeks	Irradiation Levels ($\mu\text{E m}^{-2} \text{ sec}^{-1}$)			
		14	29	38	70
<u>Brassaia actinophylla</u>	1	-0.63	-0.53	-0.56	-0.50
	2	-2.42	-3.07	-4.04	-3.38
	3	-0.26	-0.20	-0.30	-0.26
<u>Nephrolepis exaltata</u> 'Bostoniensis'	1	-3.19	-3.14	-2.77	-3.93
	2	-0.42	-0.20	-0.21	-0.29
	3	-0.28	-0.20	-0.17	-0.29
<u>Scindapsis aureus</u>	1	-1.58	-1.82	-2.33	-2.39
	2	-0.14	-0.19	-0.23	-0.25
	3	-0.13	-0.13	-0.15	-0.19

Figure 11. Upper: Net CO₂ exchange rates for Brassaia actinophylla during the three weeks of re-acclimation.

Plants moved from: (irradiation level)

Light chamber 1: 14 to 70 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 2: 70 to 38 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 3: 38 to 29 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 4: 29 to 14 $\mu\text{E m}^{-2}\text{sec}^{-1}$

Lower: Dark respiration rates for Brassaia actinophylla during the three weeks of re-acclimation as affected by irradiation environment.

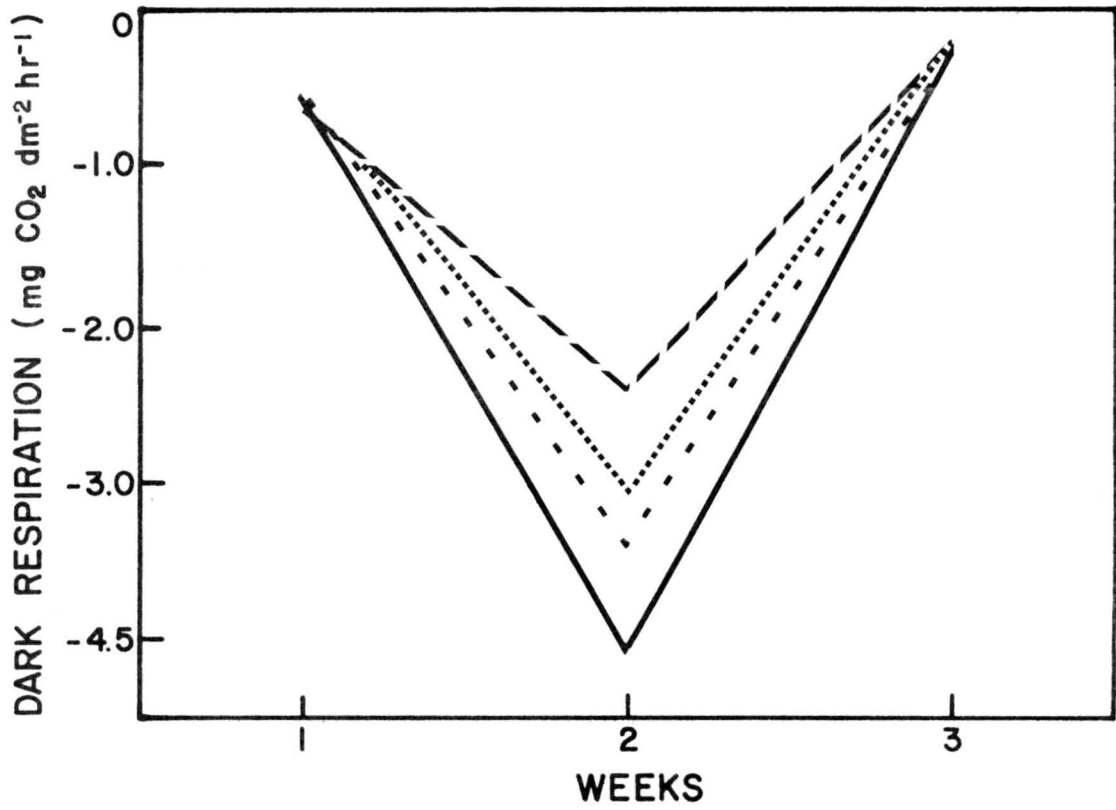
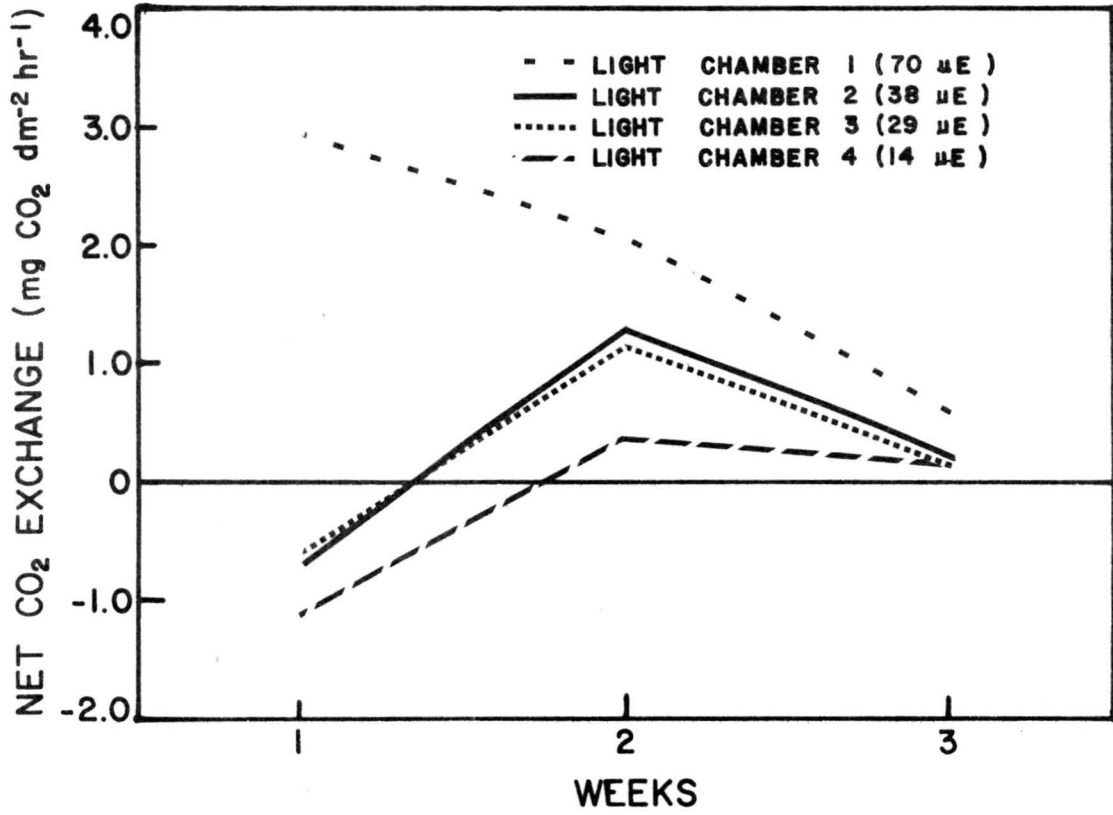


Figure 12. Upper: Net CO₂ exchange rates for Nephrolepis exaltata 'Bostoniensis' during three weeks of re-acclimation.

Plants moved from: (irradiation level)

Light chamber 1: 14 to 70 $\mu\text{E m}^{-2} \text{sec}^{-1}$
Light chamber 2: 70 to 38 $\mu\text{E m}^{-2} \text{sec}^{-1}$
Light chamber 3: 38 to 29 $\mu\text{E m}^{-2} \text{sec}^{-1}$
Light chamber 4: 29 to 14 $\mu\text{E m}^{-2} \text{sec}^{-1}$

Lower: Dark respiration rates for Nephrolepis exaltata 'Bostoniensis' during three weeks of re-acclimation as affected by irradiation environment.

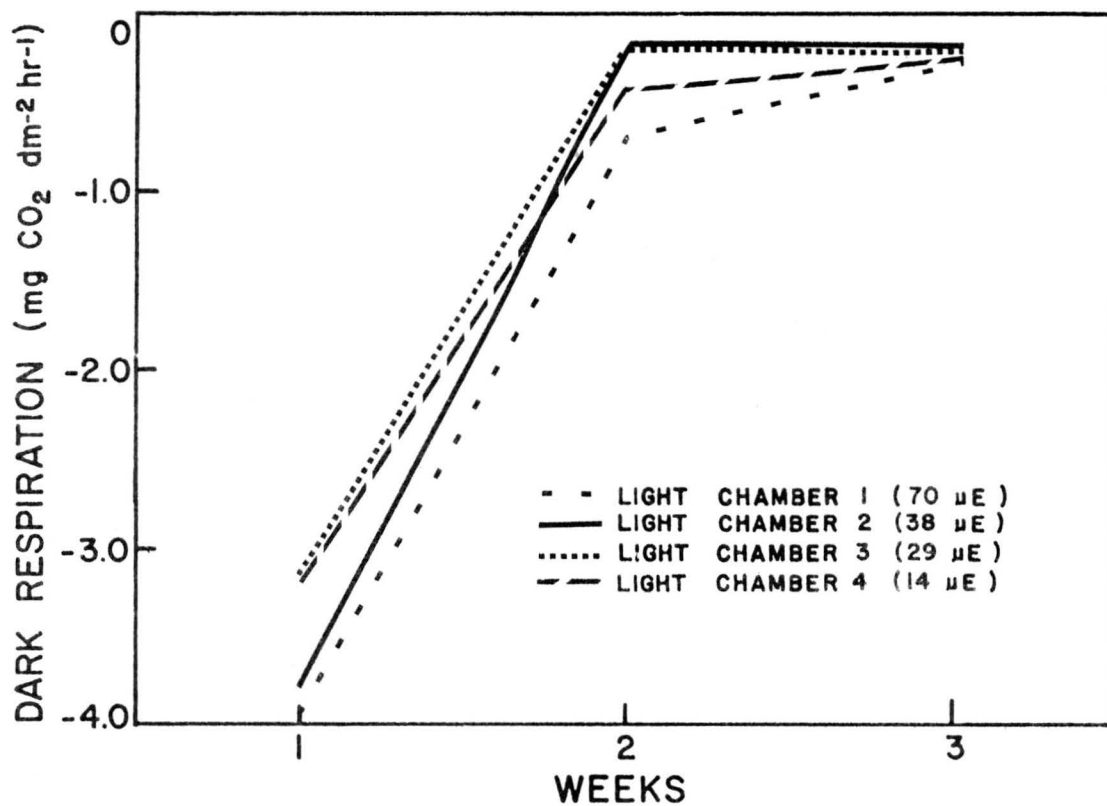
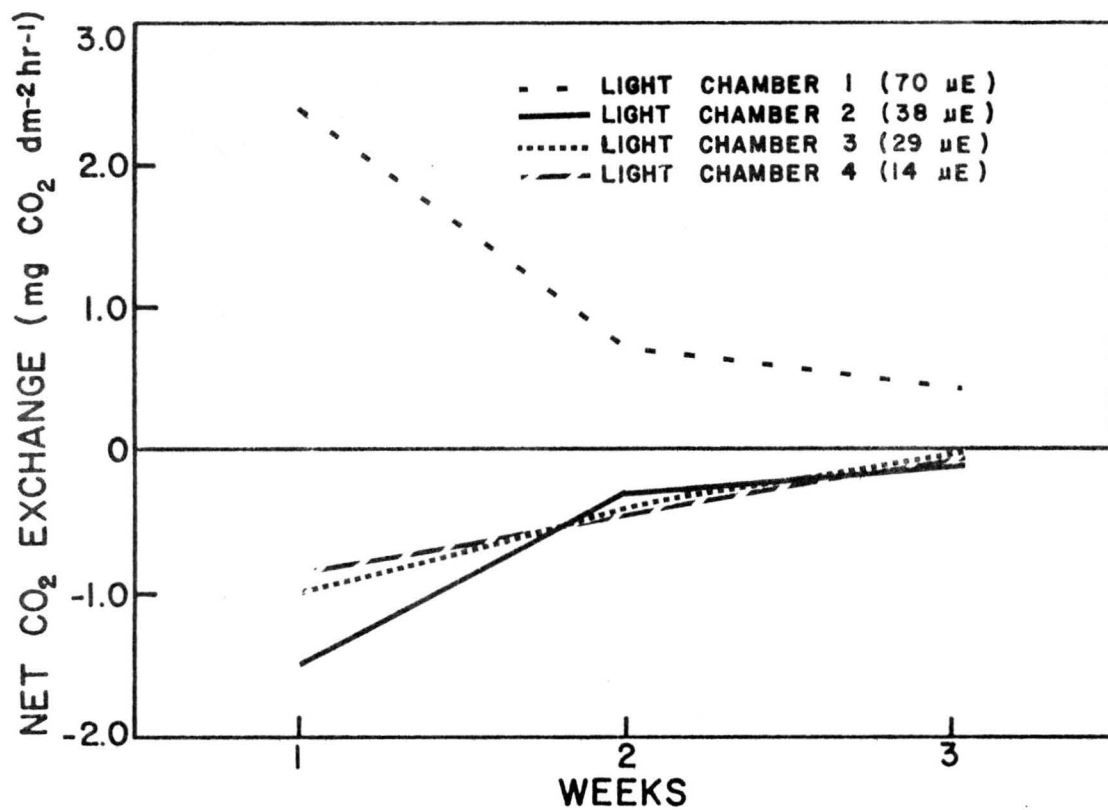
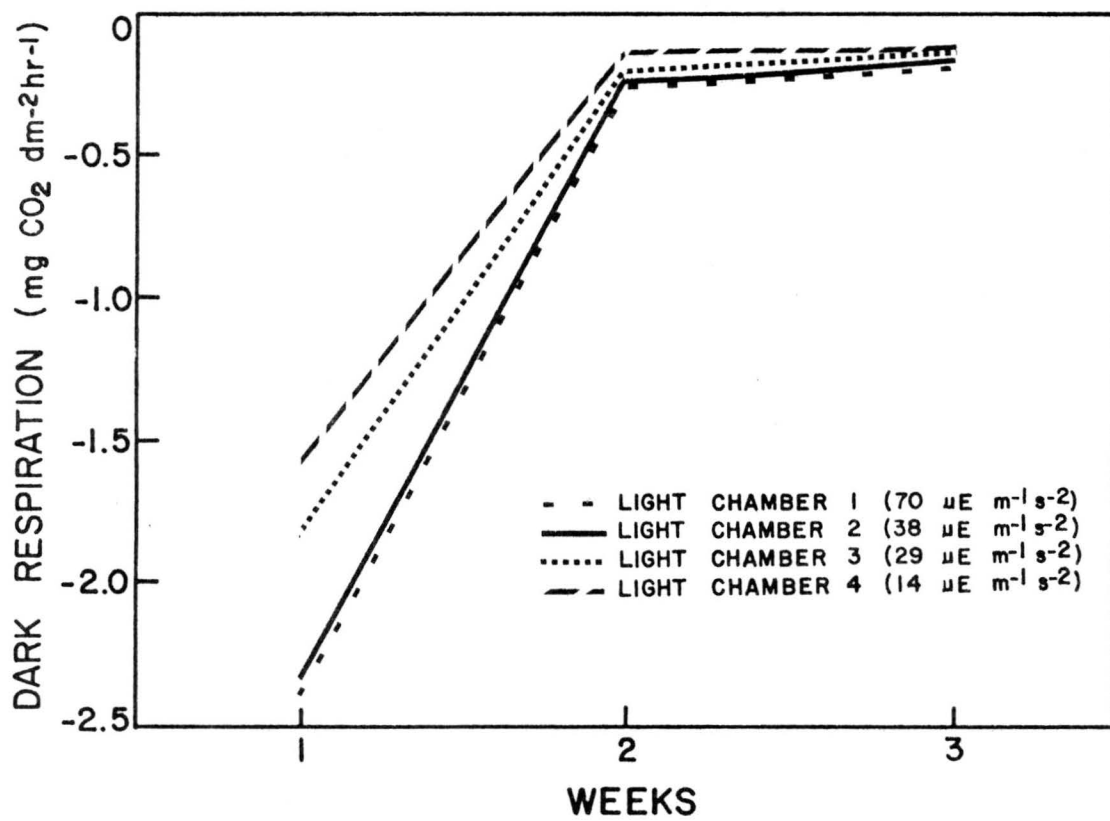
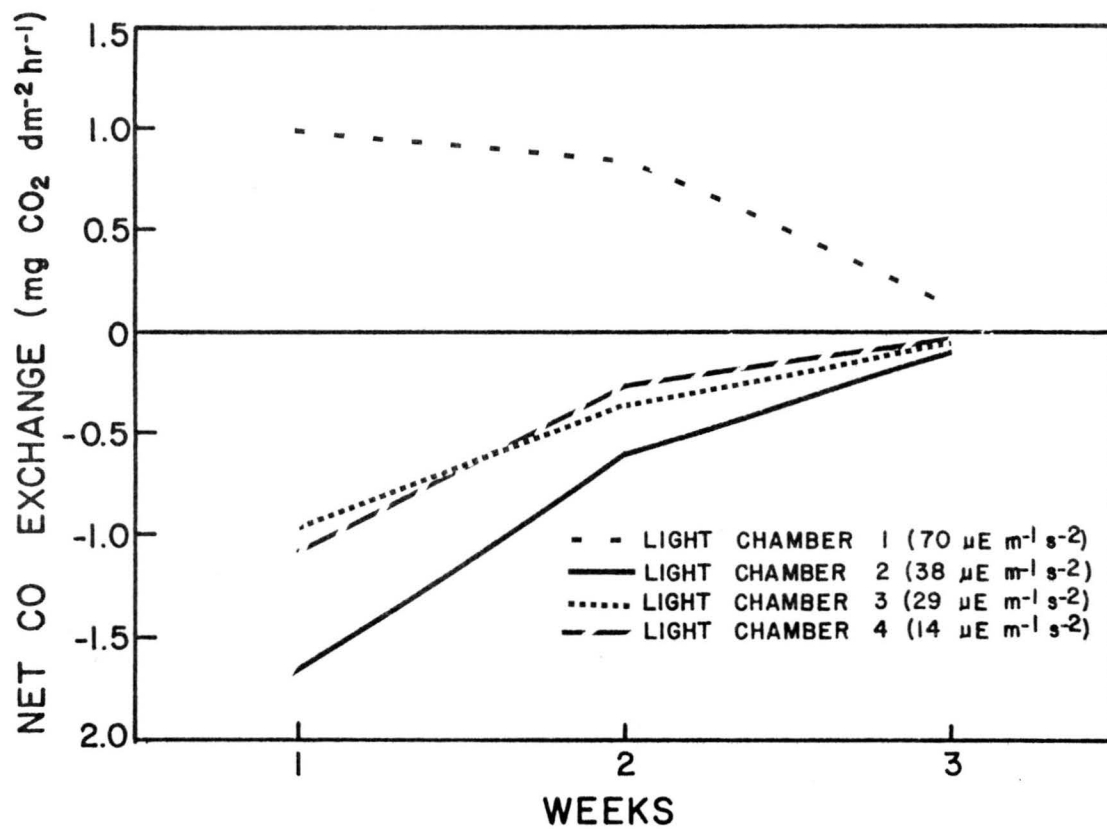


Figure 13. Upper: Net CO₂ exchange rates for Scindapsis aureus during the three weeks of re-acclimation.

Plants moved from: (irradiation level)

Light chamber 1: 14 to 70 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 2: 70 to 38 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 3: 38 to 29 $\mu\text{E m}^{-2}\text{sec}^{-1}$
Light chamber 4: 29 to 14 $\mu\text{E m}^{-2}\text{sec}^{-1}$

Lower: Dark respiration rates for Scindapsis aureus during the three weeks of re-acclimation as affected by irradiation environment.



Scindapsis aureus. Net CO₂ uptake only took place at 70 μE m⁻² sec⁻¹ for the three weeks of re-acclimation (Tables 6 and 7 or Fig. 13). The amount of CO₂ fixed or evolved consistently diminished over the three week period. Significant reduction in dark respiration occurred between weeks one and two and did not appreciably change for week three.

Discussion

Results from the first experiment showed that each species differs in rates of net CO₂ exchange, dark respiration, and time needed for acclimation. The three species showed decreased rates of net CO₂ uptake through time at the higher irradiation levels, with increased rates of net CO₂ uptake at the lower irradiation levels. All species exhibited significant decreases in dark respiration rates with the length of time for acclimation. Results indicated that photosynthetic efficiency increased at low irradiation levels as a result of acclimation.

Results of net CO₂ exchange and dark respiration rates showed that Brassaia actinophylla was capable of the greatest photosynthetic efficiency at low irradiation levels; Scindapsis aureus was intermediate, and Nephrolepis exaltata 'Bostoniensis' had the lowest photosynthetic efficiency. The changes that occurred during the process of acclimation appeared to result from the plants' ability to photosynthesize more efficiently, with a reduction in respiration rates.

Increased photosynthetic efficiency may in part be due to changes in leaf morphology. Older leaves of some species produced under high irradiation may improve photosynthetic efficiency at low irradiation by: 1) increasing chlorophyll production, and 2) re-orientation of chloroplasts. There is evidence that irradiation available to plant leaves influences chloroplast positioning (70). Under high irradiation, chloroplasts arrange themselves in a vertical position to minimize light interception. However, under low irradiation, chloroplasts arrange themselves in a horizontal position, perpendicular to the irradiation source to maximize photon interception. New leaves grown under low irradiation will usually be larger, providing more surface area for energy interception. Chloroplasts will develop in the orientation for maximum energy capture. These chloroplasts contain well-formed grana which enhances their ability to capture and make more efficient use of photon energy.

CO₂ evolution in the dark for the three species was significantly reduced during the seven weeks of acclimation. Several reports in the literature conclude that plants grown in shade have lower respiration rates than those grown in exposed habitats (33, 36, 48, 50, 51, 54). McCree (50, 51) suggested that dark respiration could be characterized as having both maintenance and growth components. Greenhouses that provide plants with an ideal environment for maximum photosynthesis and respiration result in increased plant growth. The growth component of respiration would be great in order to provide a

rapid supply of new materials for increased growth (33). Because of the high growth component, maintenance would also be high to sustain high levels of substrates and enzymes to enhance rapid growth (33, 51). However, under low irradiation, photosynthesis is reduced, limiting the rate of CO_2 fixed as carbohydrates. McCree (50, 51) explained that the growth component is reduced because the carbohydrate supply was limiting, resulting in reduced plant growth. This lower growth component required less substrate and enzymes, and thereby reduced the maintenance component (33). During acclimation, the evident reduction in dark respiration may result from the change in the relative importance of the two components, where the lower maintenance component is responsible for greater efficiency at the lower irradiation levels.

Photorespiration is an important consideration in photosynthesis. Fonteno (33), in some preliminary research, proposed that Raphidophora aurea exhibited some C_4 plant characteristics, not reaching a light saturation point typical to most foliage plants. Photorespiration is not measurable in C_4 plants. Zelitch (69) characterized photorespiration as being three to five times greater than dark respiration in C_3 plants. Unfortunately, photorespiration was not accounted for in these experiments, and cannot be used to account for differences in plant behavior.

Irradiation history in production has been shown to influence the plant's rate of acclimation and minimum light compensation point.

Often, plants are produced under irradiation levels beyond their light saturation point where maximum photosynthesis occurs. It has been proposed that if plants were grown at, rather than beyond the light saturation point, acclimation to a minimum light compensation point could be accomplished more quickly and economically. This reasoning could be used to explain why Nephrolepis exaltata 'Bostoni-ensis' did not acclimate to its anticipated minimum light compensation point within the seven weeks. Graf (35) estimated 100 ft-c as an expected survival light intensity, whereas the results of Experiment I showed the minimum light intensity to be 250 ft-c after seven weeks of acclimation.

Results from the first experiment showed that each species had a light compensation point differing in intensity and rate of change over the seven week period. The light compensation point could be used as an index of minimum light requirements. Brassaia actinophylla showed the lowest, Scindapsis aureus the intermediate, and Nephrolepis exaltata 'Bostoni-ensis' the greatest minimum light requirement. In terms of rates of acclimation, Brassaia actinophylla reached its minimum light compensation point in 5 weeks, Scindapsis aureus took 3 weeks, and Nephrolepis exaltata 'Bostoni-ensis' appeared never to reach its expected light compensation point during the seven weeks of the experiment.

In an effort to explain these differences in light compensation points, McCree (51) gave evidence that the maintenance component

of respiration dominated at low irradiation levels, and lowered with the lowering of the irradiation to a minimum point. The light compensation point is a function of the photosynthesis to respiration ratio. By lowering the acclimation irradiance, the maintenance respiration component is lowered thus allowing for efficient photosynthetic fixation of CO_2 at that new low irradiation level. However, plants will reach a minimum irradiation level which is dependent on species and production history.

For practical application, acclimation of Brassaia actinophylla and Scindapsis aureus can be achieved in approximately 3 to 5 weeks. However, Nephrolepis exaltata 'Bostoniensis' may require production under lower irradiation levels to improve acclimation rates and lower minimum light compensation points.

Experiment II was designed to determine if there was any change in photosynthetic efficiency when plants were re-acclimated to lower irradiation levels. Each species differed in rate of net CO_2 exchange, dark respiration, and re-acclimation. The plants being re-acclimated at $70 \mu\text{E m}^{-2} \text{s}^{-1}$ did not follow the photosynthetic and respiratory patterns of the other irradiation levels because they were acclimated for seven weeks at $14 \mu\text{E m}^{-2} \text{s}^{-1}$. All species showed net CO_2 fixation at $70 \mu\text{E m}^{-2} \text{s}^{-1}$.

Brassaia actinophylla exhibited increased photosynthetic efficiency and reduced respiration rates at all irradiation levels for week three. Net CO_2 fixation did not occur for Nephrolepis exaltata

'Bostoniensis' and Scindapsis aureus at the three lowest irradiation levels for the three weeks. However, dark respiration rates for both species decreased significantly over the three weeks. These results would indicate that Brassaia actinophylla was capable of re-acclimating by increased photosynthetic efficiency at all irradiation levels within three weeks. Nephrolepis exaltata 'Bostoniensis' and Scindapsis aureus only approached the point of no CO₂ evolution or fixation during the three week period. This may indicate they require longer periods of time to re-acclimate to new and lower irradiation levels, or that they were already near their minimum light compensation point.

SUMMARY AND CONCLUSIONS

Whole plant net CO₂ exchange and dark respiration rates were determined for three foliage plant species under irradiation levels approximating interior environments. Results illustrated that each species differed in rates of net CO₂ exchange, dark respiration, and acclimation. The three species showed decreased rates of net CO₂ uptake at higher irradiation levels, with increased rates of net CO₂ uptake at lower irradiation levels during a seven week period of acclimation. All species exhibited significant decreases in dark respiration rates. These results showed that photosynthetic efficiency increased at low irradiation levels as a result of acclimation. During acclimation, the reduction in dark respiration appeared to play an important role in greater photosynthetic efficiency at low irradiation levels. Brassaia actinophylla was capable of the greatest photosynthetic efficiency; Scindapsis aureus was intermediate, and Nephrolepis exaltata 'Bostoniensis' had the lowest photosynthetic efficiency.

Light compensation points were determined utilizing linear regression analysis. Results showed that each species had a light compensation point differing in intensity and rate of change for the duration of the experiment. The three species exhibited a 1.4 to 5.0 fold reduction in light compensation points over the seven weeks of

acclimation. Using the light compensation point as an index of minimum light requirements, Brassaia actinophylla showed the lowest minimum light requirement; Scindapsis aureus was intermediate, and Nephrolepis exaltata 'Bostoniensis' had the greatest minimum light requirement. The light compensation point was a function of the photosynthesis-to-respiration ratio. By lowering the acclimation irradiance, respiration was lowered, allowing for efficient photosynthetic fixation of CO₂. The minimum light requirement was dependent on plant species and production history. Irradiation history in production has been shown to influence the plant's rate of acclimation and minimum light compensation point. Plants are often produced under irradiation levels beyond their light saturation point where maximum photosynthesis occurs. If plants were produced at their light saturation point rather than beyond, acclimation to a minimum light compensation point could be done more quickly and economically. Results for the acclimation of Nephrolepis exaltata 'Bostoniensis' may give some evidence to this theory, because it did not acclimate to its expected minimum light compensation point within the seven week period.

In terms of acclimation rates, Brassaia actinophylla reached its minimum light compensation point in 5 weeks, Scindapsis aureus took 3 weeks, and Nephrolepis exaltata 'Bostoniensis' never appeared to reach its anticipated minimum light compensation point during the 7 weeks. Utilizing this information collectively for practical

applications, acclimation of Brassaia actinophylla and Scindapsis aureus can be achieved in approximately 3 to 5 weeks. However, Nephrolepis exaltata 'Bostoniensis' may require some change in production irradiation to improve acclimation rates and lower minimum light compensation points.

The three species were re-acclimated to lower irradiation levels for three weeks to determine if there was a change in photosynthetic efficiency. Results indicated that Brassaia actinophylla was capable of re-acclimating by exhibiting increased photosynthetic efficiency at all irradiation levels within the three weeks. Nephrolepis exaltata 'Bostoniensis' and Scindapsis aureus only approached the point of no net CO₂ evolution during the 3 weeks. This might indicate that they required longer periods of time to re-acclimate to new and lower irradiation levels or that they were already near their minimum light compensation point before being moved to lower irradiation levels.

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APPENDIX

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Table 1. AOV table for Brassaia actinophylla (Experiment I).

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	0.0638	1.792	3	0.00076	0.00256
R/I	8	0.0356	--	8	0.28956	--
W	6	0.0262	4.597**	6	0.39776	96.31**
WxI	18	0.0547	9.597**	18	0.01054	2.552**
E(b)	48	0.0057	--	48	0.00413	--

** Indicates significant difference at 1% level.

¹I = irradiance, R/I = replications/irradiance, W = weeks.

Table 2. AOV table for Nephrolepis exaltata 'Bostoniensis' (Experiment I).

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	0.00269	0.812	3	0.0575	0.2163
R/I	8	0.00331	--	8	0.2659	--
W	6	0.0499	20.97**	6	0.3354	86.00**
WxI	18	0.01176	4.94**	18	0.00383	0.9821
E(b)	48	0.00238	--	48	0.00390	--

** Indicates significant difference at 1% level.

¹I = irradiance, R/I = replications/irradiance, W = weeks.

Table 3. AOV table for Scindapsis aureus (Experiment I)

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	0.0076	0.0976	3	0.0616	0.890
R/I	8	0.0779	--	8	0.0692	--
W	6	0.1013	27.013**	6	0.0717	6.289**
WxI	18	0.0260	6.933**	18	0.00461	0.404
E(b)	48	0.00375	--	48	0.01141	--

** Indicates significant difference at 1% level.

¹I = irradiance, R/I = replications/irradiance, W = weeks.

Table 4. AOV table for Brassaia actinophylla (Experiment II).

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	6.9727	2.8533	3	44.6692	0.0532
R/I	8	2.4437	--	8	839.1961	--
W	2	0.8922	1.9775	6	1.2053	0.0638
WxI	6	0.2743	0.6080	6	8.0697	0.4273
E(b)	16	0.4512	--	16	18.8857	--

** Indicates significant difference at the 1% level.

¹I = irradiance, R/I = replications/irradiance, W = weeks.

Table 5. AOV table for Nephrolepis exaltata 'Bostoniensis' (Experiment II).

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	3.1572	3.2509	3	31.6830	0.1110
R/I	8	0.9712	--	8	285.4367	--
W	2	0.4048	5.0813**	2	32.3686	0.5860
WxI	6	0.0507	0.6364	6	2.2971	0.0416
E(b)	16	--	--	16	55.2338	--

** Indicates significant difference at the 1% level.

¹I = irradiance, R/I = replication/irradiance, W = weeks.

Table 6. AOV table for Scindapsis aureus (Experiment II).

	<u>Photosynthesis</u>			<u>Dark Respiration</u>		
	df	MS	F	df	MS	F
I ¹	3	6.5778	4.1918**	3	32.6262	0.0298
R/I	8	1.5696	--	8	1096.0661	--
W	2	0.2628	1.6093	2	37.3758	1.7330
WxI	6	0.2521	1.5433	6	20.9362	0.9615
E(b)	16	0.1633	--	16	21.7744	--

** Indicates significant difference at the 1% level.

¹I = irradiance, R/I = replication/irradiance, W = weeks.

Figure 1. Spectroradiometric measurements comparing total solar radiation with that which was transmitted through the FRP greenhouse utilized to hold foliage plants from March to July 1977. Measurements were taken November 6, 1977 (1200 hrs, cloudless).

