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Light intensity relations and the growth the ostrich fern /

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LIGHT INTENSITY RELATIONS
AND THE GROWTH THE OSTRICH FERN

A Thesis Presented

By

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CHAPTER 1

INTRODUCTION

1.1 Botanical Description

The ostrich fern, Matteuccia struthiopteris L. Todaro, is distributed throughout northern temperate regions of the world. Commonly referred to as the fiddlehead fern, this plant is a member of a sub family of Onocleoid ferns common to northern latitudes (Dykeman, 1984). The ostrich fern consists of a vertical underground rhizome located just below the soil surface called a crown. Leaves, referred to as fronds, are produced by individual apical meristem cells located in this crown.

In the sporophytic stage of development, the ostrich fern produces three types of fronds: vegetative fronds whose primary function is photosynthesis, reproductive fronds or sporophyll whose function is to produce spores for reproduction, and fronds which form as protective scales and food storage organs located around the crown (fig. 1.1). Due to single meristematic cells, rather than meristematic regions, organ development is much slower in the fern than in higher plants. To produce a fully developed frond may take a period from three to five years (Bower, 1923).

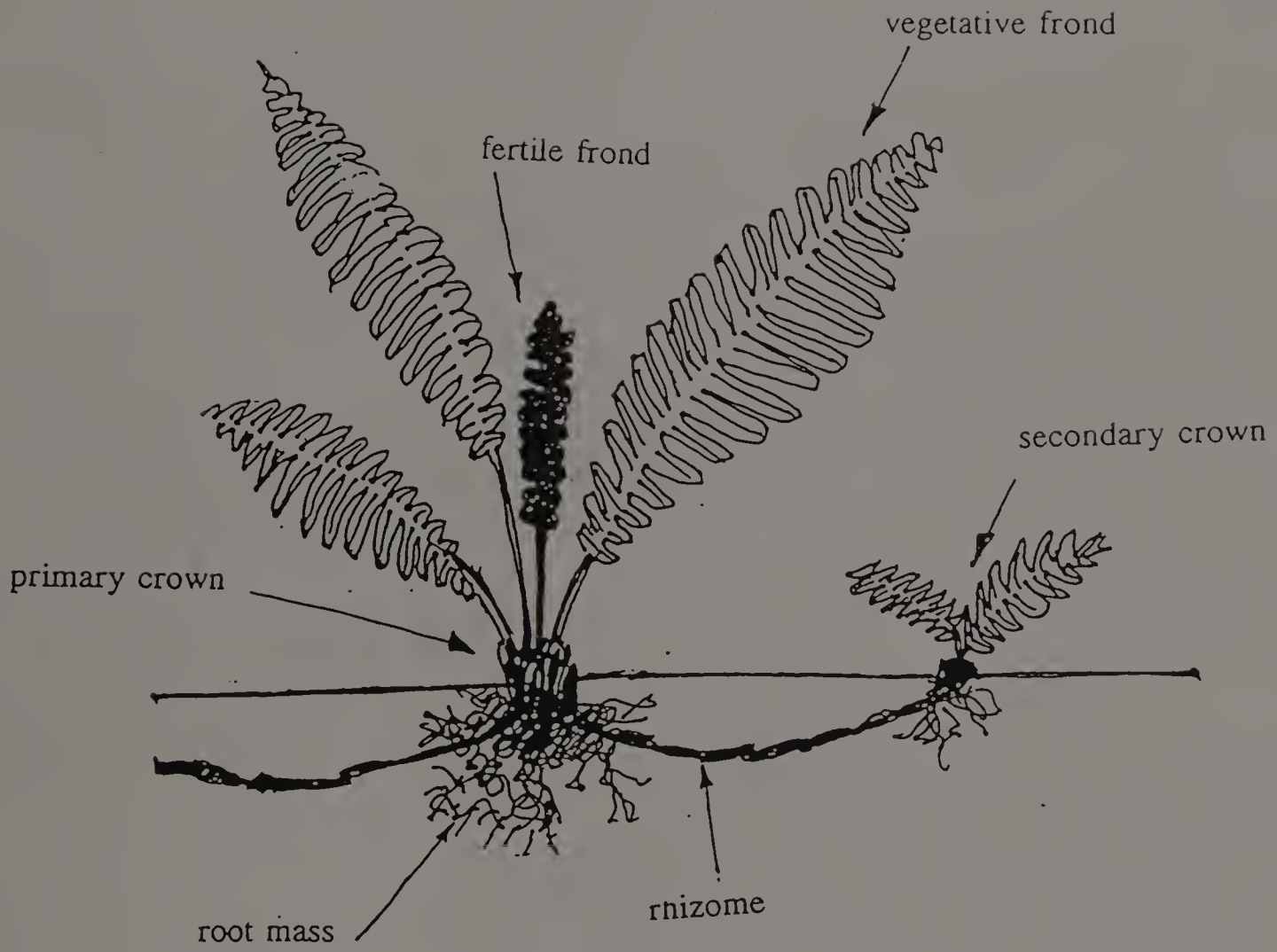

Figure 1.1 Botanical description of the Ostrich fern, Mattueccía struthiopteris L. Todaro.

Rhizomes located at the base of the crown produce a system of fibrous roots. All roots are adventitious and primary. Like most Pteridophytes, the ostrich fern produces a shallow root system. By spreading from mature plants and producing secondary crowns at a distance from the initial, or primary crown, rhizomes also serve as the principle mode of reproduction for the ostrich fern. Stands of ostrich ferns are in reality a population of clones connected by subterranean networks of rhizomes. Local clonal ecotypes have evolved which are suited to varying regional conditions (Dykeman, 1981a).

The physiology of ferns is quite different from that of higher plants. In addition to lacking a highly developed root system and having slow organ development, fern vascular tissues are less specialized than those observed in higher plants. The xylem of ferns consists only of tracheid cells with no vessels. Tracheid and sieve tube cells do not elongate, but remain short, not long and cylindrical as those observed in higher plants. Also, frond epidermis tissue lacks the ability to produce a cuticle, important for limiting evapo-transpiration from leaves. Many of these physiological characteristics make ferns susceptible to drought conditions. Although not an obligatory wetland species, the ostrich fern favors wet environments, but not saturated soil conditions (Goldoftas, 1981). Stands of ostrich ferns are located primarily in transition zones

between wetland and upland regions, particularly in riparian zones adjacent to streams and rivers.

1.2 Horticultural History

Emerging crosiers of the ostrich fern, also called fiddleheads, and named for the resemblance to a bishop's crook or pastoral staff called a crosier, have been used as a food source by Native Americans since before the arrival of the first European settlers to North America (von Aderkas, 1983). Today, in the northeastern regions of North America croziers are still harvested for commercial markets in the early spring from native stands located under the canopies of the northern hardwood forests (Von Aderkas, 1984; Goldoftas, 1981).

Many people consider the crosiers a delicacy and networks of transportation have developed to ensure rapid distribution to markets throughout Canada and the United States. Crosiers are regarded as best when eaten immediately after harvest. High respiration and transpiration rates quickly reduce marketable quality, although crosiers may be stored at 0 to 2 C° in a water bath, or at cold room conditions of 100% relative humidity for as long as three weeks before loosing appreciable market value (Dykeman, 1980).

Harvesting of fiddleheads occurs during a short two to three week period in the spring when croziers are emerging from recently dormant crowns. Emergence occurs as early as March in southern ranges through to June in northern ranges. Traditional harvesting consists of groups of pickers traversing native stands gathering emerging crosiers. Harvested crosiers are then sold to local markets or to buyers for wider distribution. Harvesting of native stands has several limitations, including rapid stock depletion due to over-harvesting, difficulties in stand management, strict seasonal availability of crosiers, and a limited geographic area of production (Dykeman, 1984, Von Aderkas, 1984). If the ostrich fern could be grown successfully under field conditions, perhaps the crop would have a greater market potential and yields may be increased (Dykeman, 1984). One could imagine a crop grown and managed in a manner similar to asparagus. The first cluster of emerging crosiers in the spring would be harvested and marketed, while subsequent growth would be allowed to mature and "recharge" the crown, ensuring ample carbohydrate storage and crozier development for harvest the following year. Or, as in the case of the Belgian endive, entire crowns could be harvested in the fall and then hydroponically forced at any time following the completion of dormancy requirements, thereby expanding greatly the time in which the product could be marketed

(Corey and Tan, 1994). Harvesting of crosiers would not then be limited to a brief period in early spring.

Ostrich ferns were grown, under field conditions, for the production of fiddleheads, with considerable success, by R.G. White in the early nineteen sixties (von Aderkas, 1984). Yields of up to 334 kg/ha were achieved before the study was ended prematurely due to a lack of new plant material. Today, in vitro propagation techniques offer the potential of an unlimited source of planting material (Dykeman and Cumming, 1985).

Aspects of dormancy and the clonal selection of suitable cultivars for the field have been studied (Dykeman, 1977, 1981a, 1981b). Dykeman (1985) has also investigated the effects of different harvesting regimes on long term growth. The possibilities of off-season production of croziers has lead to hydroponic forcing investigations which resulted in near continuous crozier yields over a three week period, suggesting a 14 day harvesting program (Corey and Tan, 1994).

Dykeman (1980 and 1991), working with the New Bruswick Department of Agriculture, has developed guidelines for the production of fiddleheads under field conditions. Ostrich ferns grow well in sandy and sandy loam soil types. Production guidelines recommend that dormant crowns be planted directly below the soil surface with a distance of 1.0 m between crowns (10,000 crowns/ha). To facilitate

root development and to aid in soil moisture retention, a 3.0 cm layer of mulch should then be deposited above the crowns. Transplanted crowns should then be supplied with adequate irrigation to ensure 2.5-3.0 cm of water per week.

Plant populations may double from secondary crown development every year for the first 3 to 5 years after planting. After this period stand establishment is considered complete with crown densities approaching 300,000 plants/ha. From 6 to 12 crosiers may then be harvested per crown per year without fear of stand depletion. Dykeman (1980) notes that plants are initially sensitive to field conditions, but after stand establishment is complete mutual shading acts to improve plant health. Dykeman (1980) also cautions that there "remains many questions on the management requirements of this potential crop" and that "production technology is still in the preliminary state of development".

1.3 Research Directions

Initial research began with hydroponic forcing experiments focused on determining how different harvesting and crown "recharge" regimes would effect long term growth and development. Crowns were forced hydroponically and crosiers were then harvested for varying lengths of time.

Subsequently, crowns were placed in potting soil under greenhouse conditions and given varying "recharge" times to allow for tissue growth and carbohydrate accumulation for the next harvest. Under greenhouse conditions vegetative tissue became chlorotic and frond desiccation and die-back occurred within 3 weeks. This unexpected result suggested the ostrich fern may be more sensitive than expected to high light levels.

Both physiological characteristics and previous research (Dykeman 1981a and 1984) suggest the ostrich fern is sensitive to many conditions which differ from the plants native habitat. The most dramatic difference is between light levels in the field and those encountered in native stands. Located under hardwood canopies, native stands of ostrich ferns receive only 5 to 30% of ambient photosynthetically active radiation (PAR). This observation suggests conditions be modified with shade cloth to better suit the cultural requirements of the ostrich fern. After stand establishment has occurred, shade cloth protection may no longer be needed. Yet, stand establishment requirements of 3 to 5 years are very costly. Shorter stand establishment times and increasing crown productivity may be possible with better suited field production regimes.

The relationship of the ostrich fern to light conditions, particularly during the stand establishment period, needs to be better understood if fiddleheads are to

be grown successfully as a horticultural crop. This study was undertaken to understand the role of light on growth and development of ostrich ferns during the first year of stand establishment.

1.3.1 Shade Treatments, 1993

This experiment tested whether reduced light levels would decrease tissue damage caused by high light intensities. All cultural practices, excluding the use of shading treatments, were based on the recommendations of Dykeman (1980 and 1991). Four shading treatments were chosen to reduce light levels and to determine optimal light conditions. Shading treatments and a non-shaded control created light levels of roughly 22, 46, 73, and 100% of ambient light. Extraneous root tissue was removed for fresh weight purposes. Plant growth measurements were recorded over the season.

1.3.2 Shade Treatments, 1994

This experiment was developed to determine if other cultural practices, in conjunction with shading treatments, could be altered to improve stand establishment. Shading treatments identical to those in the above experiment were used. A fall planting schedule was used in the hope that this would allow for more adequate root establishment in the spring prior to frond emergence. This should potentially

reduce water stress problems. Crown fresh weights were not taken because the cutting of extraneous root tissue may also reduce the vitality of rhizome tissue, lowering the potential of a successful transplanting. A new cultivar native to the Connecticut River Valley was used to determine if a local ecotype would be better suited to regional climactic and soil conditions than those selected by Dykeman (1981a) from New Bruswick. Plant growth measurements were recorded over the season.

1.3.3 Planting Density

High density planting may offer a method of modifying field conditions to support stand establishment. It has been noted that after stand establishment has occurred and plant population densities are maximal plant health significantly improves due to mutual shading between individuals in the stand (Dykeman, 1980). Community interactions are supportive of individual plant health. Three planting densities, 20, 40 and 60 cm, were selected to determine if plant to plant interactions could assist in stand establishment. Plant growth measurements were recorded over the season.

1.3.4 Frond Tissue Response

Frond emergence occurs primarily in the spring. Few to no new fronds emerge, unless croziers are removed or fronds

are damaged (Dykeman, 1985). The health and photosynthetic activity of these initial fronds will largely determine growth patterns for the following year. Above investigations focus on how shade treatments, in conjunction with other field conditions, affect plant growth.

Isolating the specific causes of tissue damage observed in the field is difficult. Other factors, such as drought conditions and possibly heat stress, appear to be involved. To help isolate the specific effects of light levels on tissue health plants were grown under the four light level treatments employed in previous shade experiments. Crowns were forced in the fall to avoid high summer temperatures. Plants were grown in potting soil and watered daily to help prevent water problems from occurring. Tissue conductivity was measured as an index of any cellular damage occuring under any of the shade treatments. To determine the level of chlorosis, chlorophyll a and b contents were also measured.

1.3.5 Photosynthetic Response

To determine the natural affinity of the ostrich fern towards light levels and to indicate the upper range of light conditions to which the fern can acclimatize a photosynthetic response curve was generated. Photosynthesis and subsequent biomass accumulation over a growing season is the major determinant of crop yield and as such a comparison

with other commercially grown species would provide an index of potential growth (Lawlor, 1993). The rate of photosynthesis is also an excellent indicator of plant health (Bloom et al., 1986).

1.3.6 Crown Response to Shock Induced Dormancy

Crown tissue shock induced by high light intensities and other adverse conditions caused all frond tissue to die. Crowns entered into a state where no evidence of further growth was visible, taken to be a state of premature dormancy. This experiment was designed to see if cold-temperature vernalization was required to break this 'shock' induced dormancy and to determine the length of any vernalization requirements.

CHAPTER 2

MATERIALS AND METHODS

2.1 Shade Treatments, 1993

Crowns of the ostrich fern (Matteuccia struthiopteris cu. N.B.35) were obtained from Dr. Brian W. Dykeman at the New Brunswick Department of Agriculture. All cultural practices were based on the suggestions of Dykeman (1980 and 1991) and the experiments were done at the University of Massachusetts Research Farm, South Deerfield MA. Experimental plots were located on a Hadley fine sandy loam soil type (Typic Udifluvent, coarse silty, mixed, non-acidic, mesic), common of alluvial soils in the Connecticut River Valley. A randomized complete block design with four treatments and three replications of twelve individuals per plot was used (fig. 2.1). Plots covered an area of 14 ft^2.

Four light levels were created by using two types of meshed nylon shade cloth, a cotton shade cloth traditionally used in tobbacco cultivation, and a non-shaded treatment, creating light levels of roughly 22, 46, 73 and 100% of ambient light, respectively (fig. 2.2). Light levels in the PAR wavelengths were determined using a Decagon ceptometer. Shade cloth was suspended at a height of 5 ft above the soil surface and covered the top and three sides of each plot.

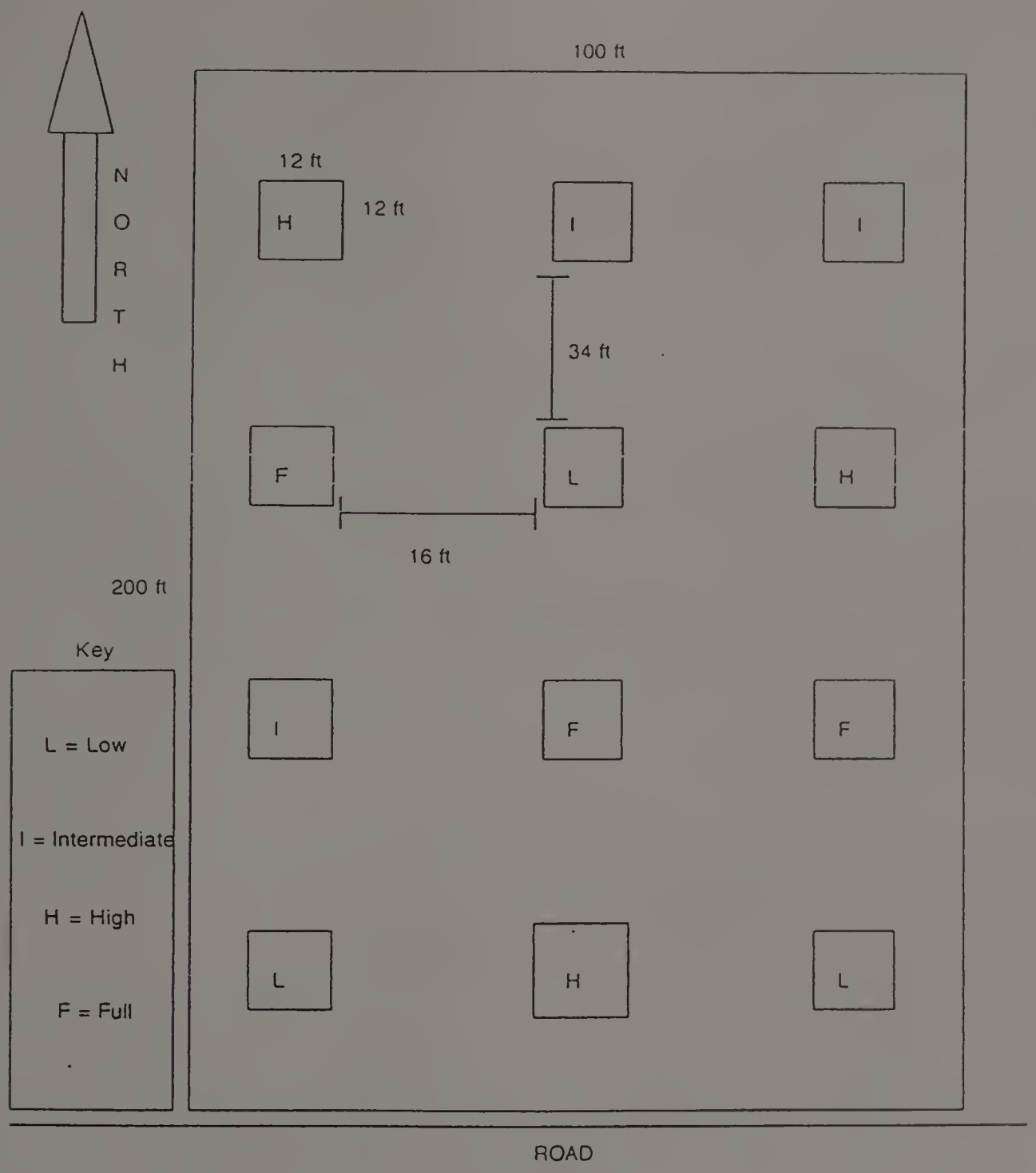

Figure 2.1 Experimental design for shading effects on growth and development, 1993 season.

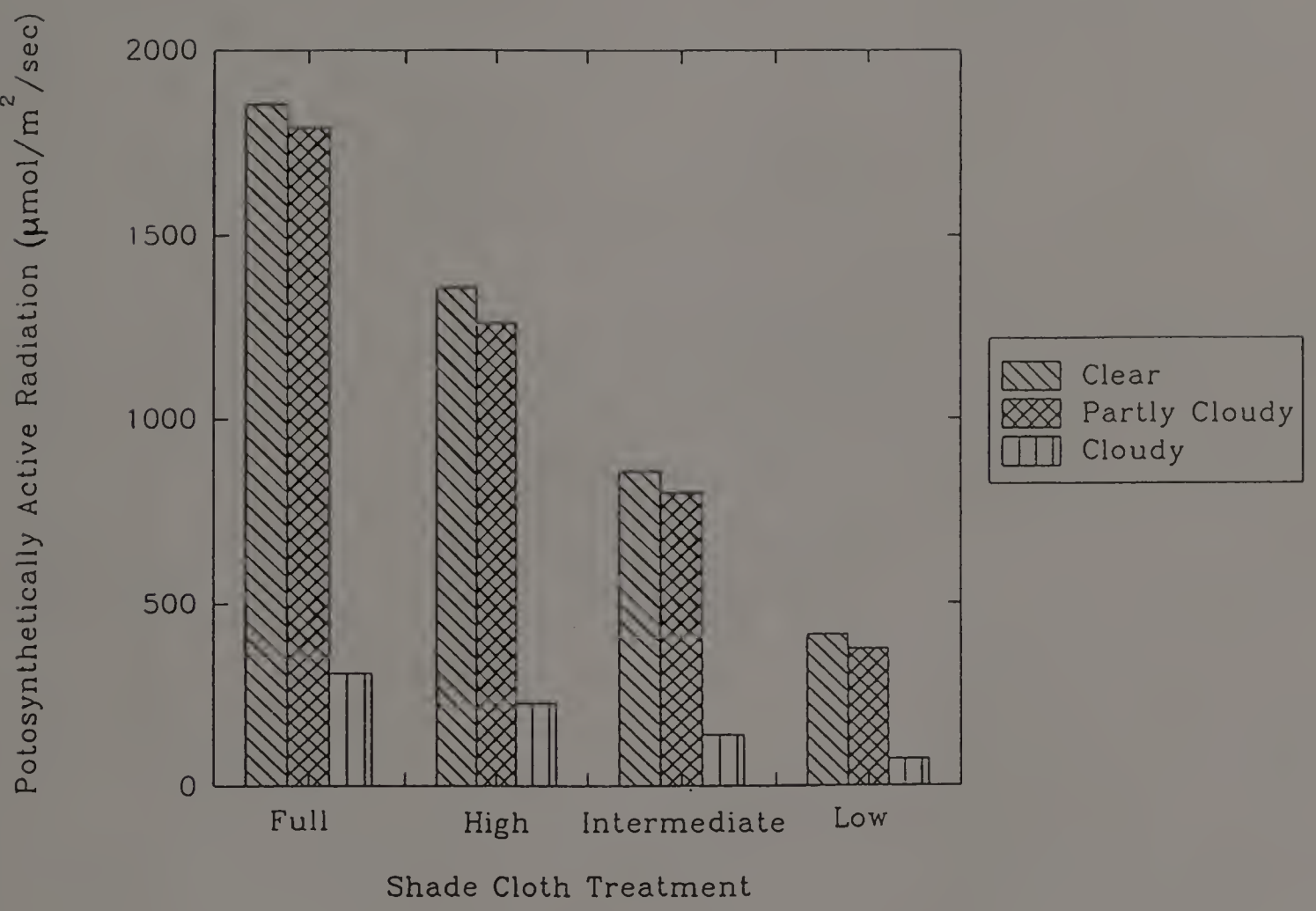

Figure 2.2 Transmittance of photosynthetically active radiation (PAR) through shade cloth under variable light conditions.

The north side of each plot remained unshaded to allow for plant care and sampling.

Before planting the field was plowed and disc harrowed. Fertilizer (5:20:20, N-P-K) was broadcast and incorporated at a rate of 1000 kg/ha prior to planting (cultivation practices were based on the suggestions of Dykeman, 1980). After washing, removing extraneous root tissue, and weighing, crowns were planted on June 14, 1993. The crowns were planted directly below the soil surface with 3 ft spacing between individual plants. Straw mulch was layered to a depth of 3 cm over each plot for weed control and to reduce evaporation from the soil. Plants were irrigated as needed throughout the growing season to insure 2.5 to 3.0 cm of water per week. Weed control was by hand cultivation.

At three times over the growing season (43, 85, and 120 days after frond emergence) crown activity, the number of fronds per plant, and the length of each frond from the soil surface to the top of the frond, was recorded. Crowns were harvested 170 days after frond emergence and crown fresh weights were determined.

2.2 Shade Treatments, 1994

A randomized complete block design with four treatments and three replications of 16 individuals per plot was used

(fig. 2.3). The experimental conditions were identical to those previously described for shade treatments in 1993. Cultural practices were based on the recommendations of Dykeman (1980 and 1991) with changes aimed at improving stand establishment. A fall, as opposed to a spring planting regime, was used. Plant material was changed with crowns of Matteuccia struthiopteris cu. U.M. 1, selected from plant material growing on the banks of the Connecticut River in South Deerfield, Massachusetts, being used in the trials. Extraneous root tissue was not removed from rhizomes prior to planting and the number of samples per plot was increased from 12 to 16 plants.

Crowns were planted on October 24, 1993. Crown activity, the number of fronds per crown, and frond lengths were recorded at four times during the growing season at 28, 53, 78, and 120 days after frond emergence on April 25, 1994.

2.3 Planting Density

Cultural practices were identical to those previously attributed to Dykeman (1980 and 1991). Treatments consisted of three planting densities of 20 cm, 40 cm, and 60 cm distances between individuals. The highest planting density was based on the "optimum" density of 300,000 plants per

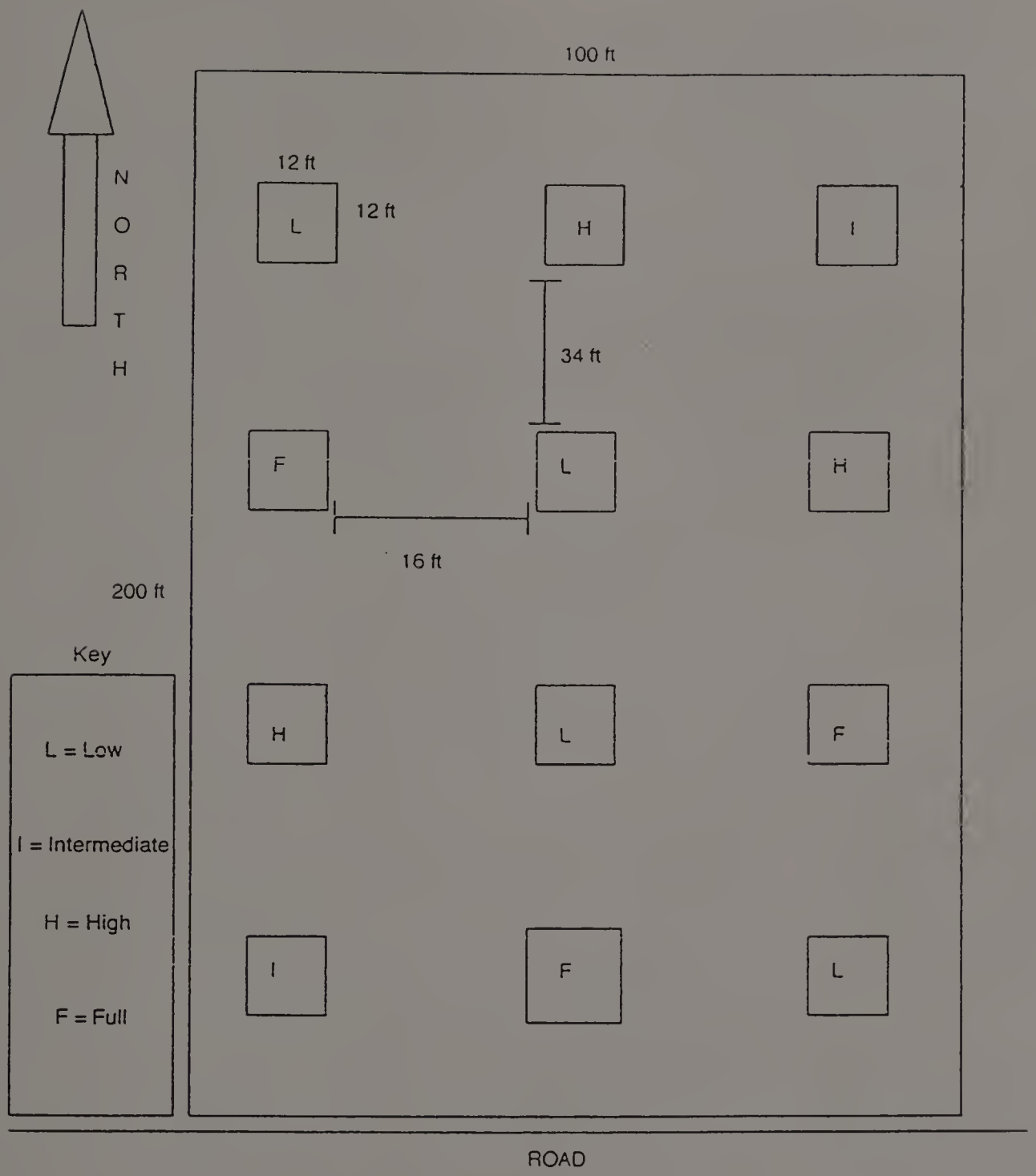

Figure 2.3 Experimental design for shading effects on growth and development, 1994 season.

hectare determined by Dykeman after five years of stand establishment in New Brunswick experiments (Dykeman, 1980). Extraneous root tissue was not removed from rhizomes. Crowns of the cultivar U.M.1 were transplanted on May 4, 1994. Frond emergence occurred during the week of May 8, 1994.

A randomized complete block design with three treatments and three replications of 36 individuals per plot was used (fig. 2.4). Records of crown activity and the number of fronds per crown were recorded from the central four plants in each plot at monthly intervals from May through October.

2.4 Frond Tissue Response

Shade cloth, of the same type previously described, was suspended above potted ostrich ferns creating light levels of 22, 46, 73 and 100% of ambient light. Shade cloth supporting structures, 4′ long, 3′ wide and 3′ tall, were covered with shade cloth on all exposed sides.

Crowns of the cultivar U.M. 1 were removed from cold storage and planted in 6″ pots with Pro-Mix BX potting soil on September 3, 1994, when high temperatures would not be

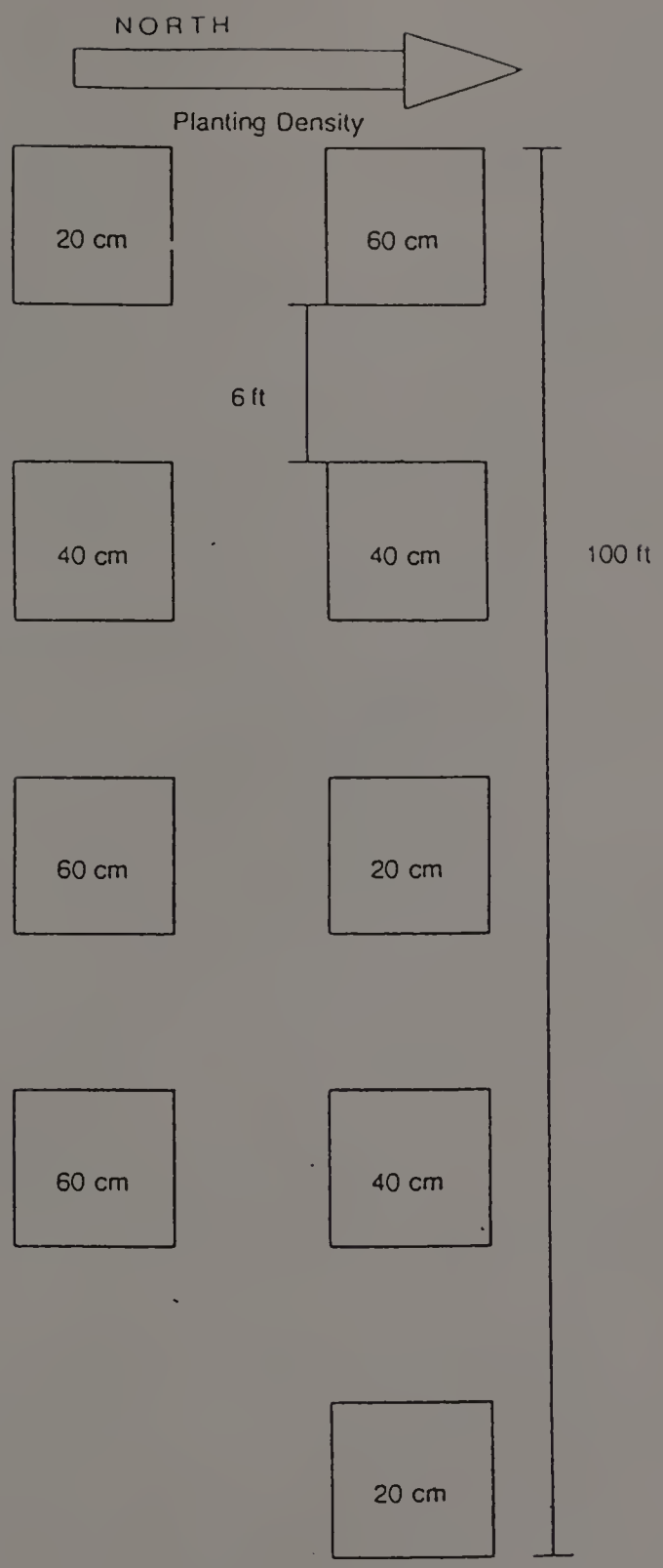

Figure 2.4 Experimental design for planting density effects on growth and development, 1994 season.

detrimental. Ten crowns were placed under each treatment and were watered daily.

Samples of three fronds were removed from separate individuals in each treatment beginning on September 16. Pinnae were subsequently removed from the central 15 cm section of each frond rachis. Tissue was weighed and then ground with a mortar and pestle. Chlorophyll extractions were made with 1 g of tissue in 10 ml of 80% acetone. Absorbances were determined by a Spec 21 Spectrophotometer and chlorophyll concentrations were determined from the following formulae (Witham et al., 1986):

$$\text{mg chlorophyll a/g tissue} = [12.7(D_{683}) - 2.69(D_{645})] \times V/1000 \div W$$

$$\text{mg chlorophyll b/g tissue} = [22.9(D_{645}) - 4.68(D_{663})] \times V/1000 \div W$$

where:
D=optical density reading of the chlorophyll extract at the indicated wavelength, V=final volume of the 80% acetone chlorophyll extract, and W=fresh weight, in grams, of extracted tissue.

Conductivity measurements were made by placing 1.0 g of plant tissue in 10 ml of deionized water. Conductivity

measurements were then recorded 1 hour after tissue submergence.

2.5 Photosynthetic Response

Due to the difficulty of attaching leaf clamp chambers to the frond structure of the ostrich fern a flow through gas exchange system was developed to measure the carbon dioxide exchange rates of whole plants at different light intensities (Field et al., 1991) (Fig. 2.5). PAR levels were measured using a Decagon ceptometer. Inlet and outlet gas samples were measured using a Varian 3400 gas chromatograph equipped with a methanizer to measure carbon dioxide concentrations.

Crowns of the cultivar U.M. 1 were removed from cold storage and potted in 6" pots filled with Pro-Mix BX potting soil two weeks prior to experimental use. Plant material was watered daily. Leaf area measurements were made using a Li-COR model 3100 area meter. Photosynthetic rates were calculated on a leaf area and weight basis and a photosynthetic light response curve was generated. A light compensation point (LCP) and a light saturation value (LSV) were estimated from the response curve (Beadle et al., 1985).

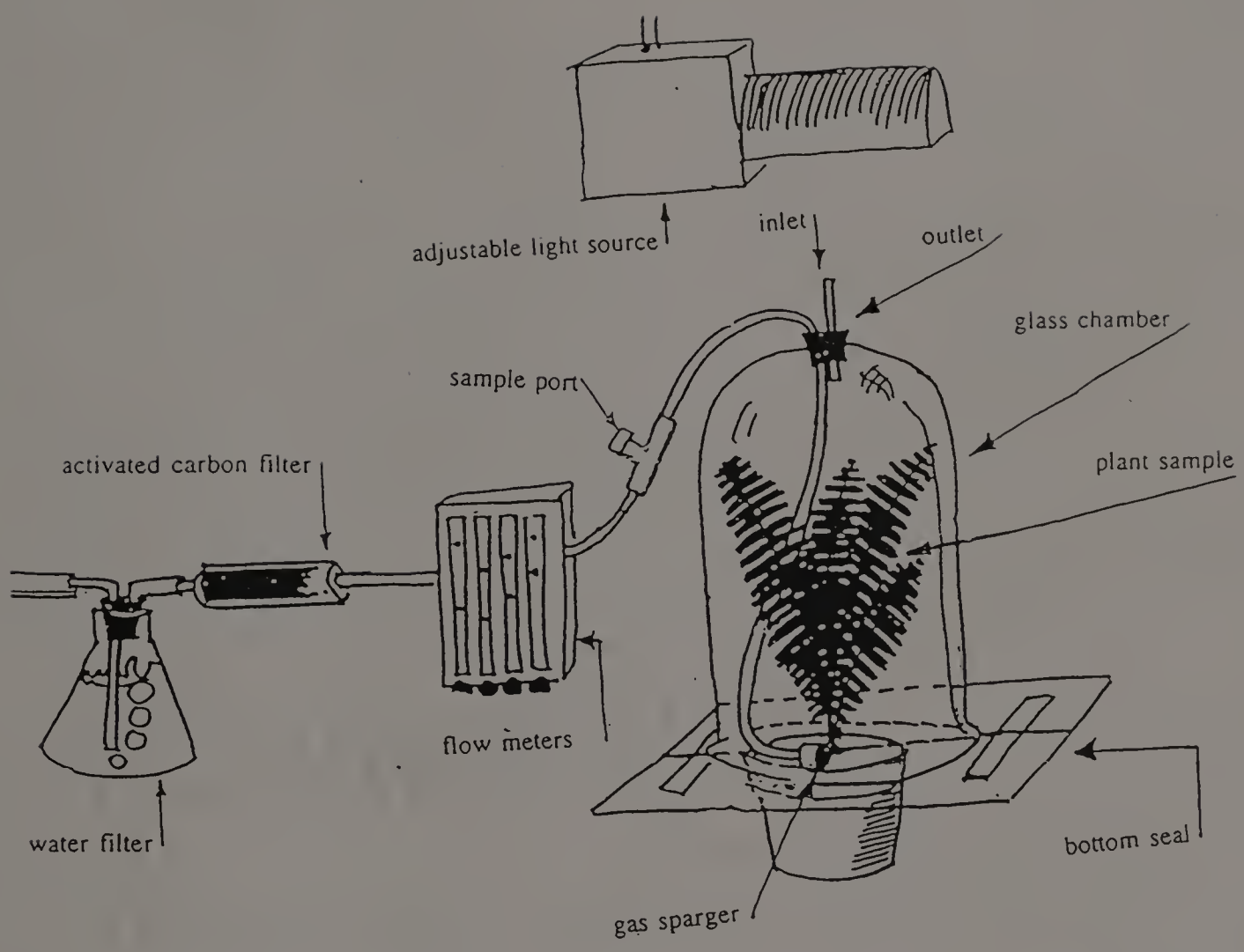

Figure 2.5 Diagram of apparatus used to determine photosynthetic response under varying light conditions.

2.6 Crown Response to Shock Induced Dormancy

On April 4, 1993, 55 crowns of the cultivar N.B. 35 were removed from cold storage and forced in greenhouse conditions. Crowns were planted in 6" pots with Pro-Mix BX potting soil and watered daily. By June 11, frond desiccation and die-back had occurred for all plants. Crowns were then placed in a cold room near 3 C° to induce artificial vernalization. A sample of 5 crowns remained under greenhouse conditions as a control.

Sample groups of 5 crowns were removed weekly and returned to greenhouse conditions until August 20 (a total of 11 increases in vernalization lengths). Crowns were monitored daily to observe when crosier emergence occurred.

CHAPTER 3

RESULTS

3.1 Shade Treatments, 1993

Shading treatments had a highly significant (1% level) effect on crown activity, with crowns under more shade being more likely to produce vegetative growth (table 3.1). The effect of time was also significant (5% level), with crown activity increasing during the season for all shaded treatments. The interaction between time and shading treatments, for all response variables, was also highly significant. This may be explained by the cumulative effects of shading treatments over time. Separate shading treatments had a distinct influence on crown activity over the season, with activity increasing proportionally with increased shading (fig. 3.1). Included as active are plants whose primary crowns have died, but from which one or more vegetative secondary crowns have later developed from rhizomes. Also included are crowns which recovered from shock induced dormancy and later became active. Nearly 80% of all crowns planted under shade cloth became active, while all of the plants exposed to full light treatments died.

For the three shade treatments, no significant difference between the number of fronds produced by

Table 3.1
Growth response to shading treatments, 1993 season.

	Days after planting		
	43	85	120
Number of plants out of 12 active			
Light level:			
22%[1]	11.0[2]	11.3	11.0
46%	9.0	11.3	11.7
73%	6.7	8.3	9.7
100%	2.0	0.0	0.0
significance[3]	l^{***},q^{*},c^{ns}	l^{***},q^{***},c^{ns}	l^{***},q^{***},c^{ns}
Number of fronds per plant			
Light level:			
22%	4.73	7.67	8.23
46%	4.73	6.73	7.85
73%	4.43	5.83	7.53
100%	4.00	0.00	0.00
significance	l^{ns},q^{ns},c^{ns}	l^{***},q^{***},c^{ns}	l^{***},q^{***},c^{***}
Mean frond length per plant (cm)			
Light level:			
22%	16.2	17.7	17.3
46%	11.0	14.7	14.9
73%	10.6	11.2	14.1
100%	0.0	0.0	0.0
significance	l^{**},q^{ns},c^{ns}	l^{***},q^{*},c^{*}	l^{***},q^{***},c^{***}

[1] Representing percent of ambient light transmitted through shade cloth.
[2] Means of three replications. Replicates consisted of a maximum of n=12 plants.
[3] *, **, ***, ns, significant at P=0.05, 0.01, 0.005, or not significant respectively. l, q, c =linear, quadratic, or cubic components, respectively.

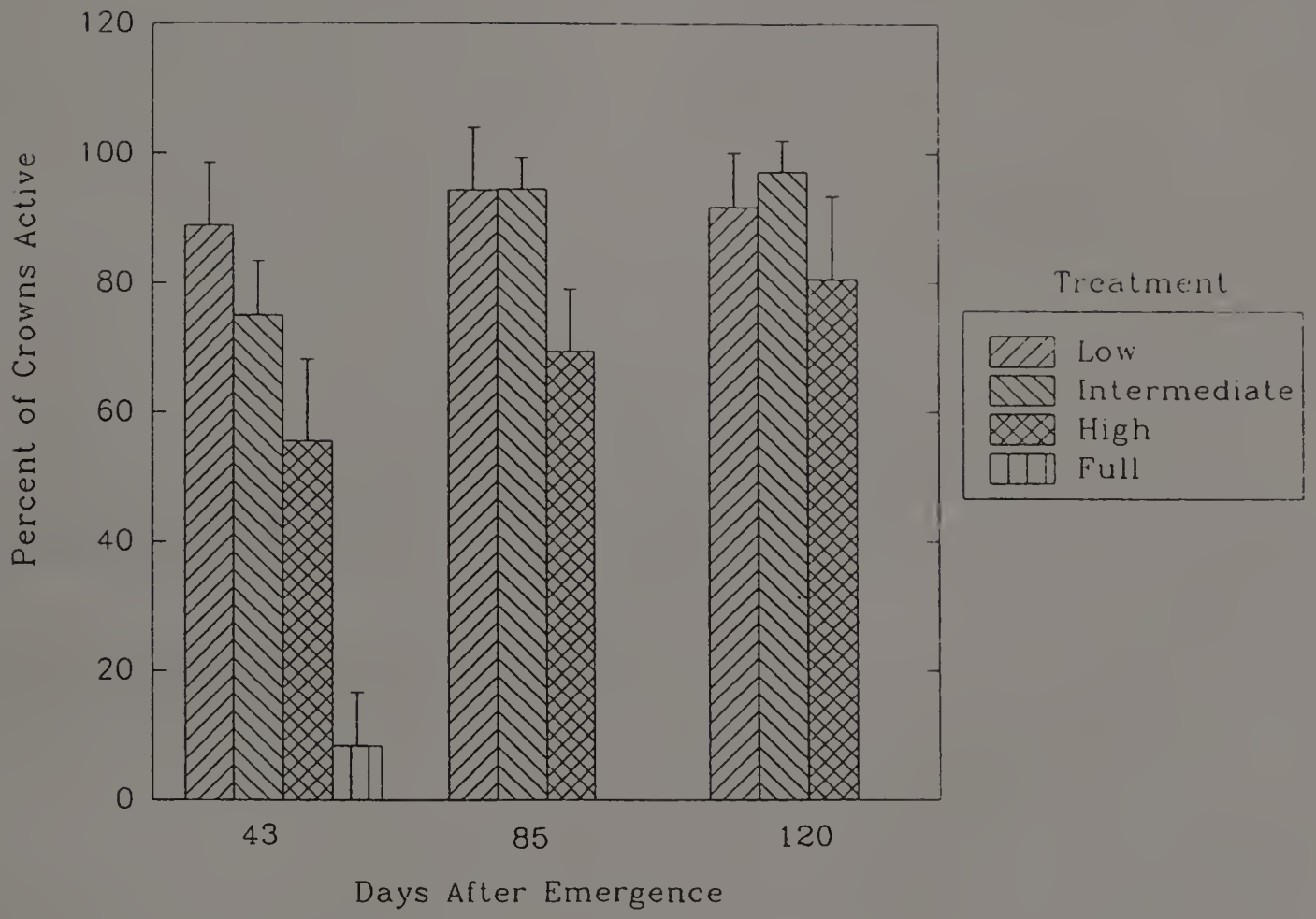

Figure 3.1 Shading effects on crown activity, 1993 season.

surviving individual crowns was indicated (table 3.1). All shade treatments had the same effect on the number of fronds produced by crowns. The only significant differences were between crowns subjected to shade treatments and those under full sun. The number of fronds per crown increased over the season from an average of 4.6 at 43 days after planting to 7.8 at 120 days after planting (figure 3.2).

The average length of fronds was significantly influenced by shading treatments (1% level) (table 3.1). Shade treatments had a graduated effect on frond lengths with longer fronds being produced by crowns that received more shading. Frond lengths of crowns under the lowest light level (22% ambient) increased in length from an average of 16.2 cm to 17.3 cm over the course of the growing season (fig. 3.3). In contrast, crowns subject to a higher light level (73% ambient) increased about 3.5 cm from 10.6 cm to 14.1 cm. Fronds produced by crowns under the lighter shade cloths (46% and 73% ambient) were initially smaller than those under the heaviest shade cloth (22% ambient), but recovered as crowns became acclimatized to the new environments.

Secondary crowns were produced by many crowns (fig. 3.4). The highest number of secondary crowns were produced by crowns under the lowest shade treatment (73% ambient) with nearly 80% of all active crowns producing one or more secondary crowns. In contrast, only some 25% of the crowns

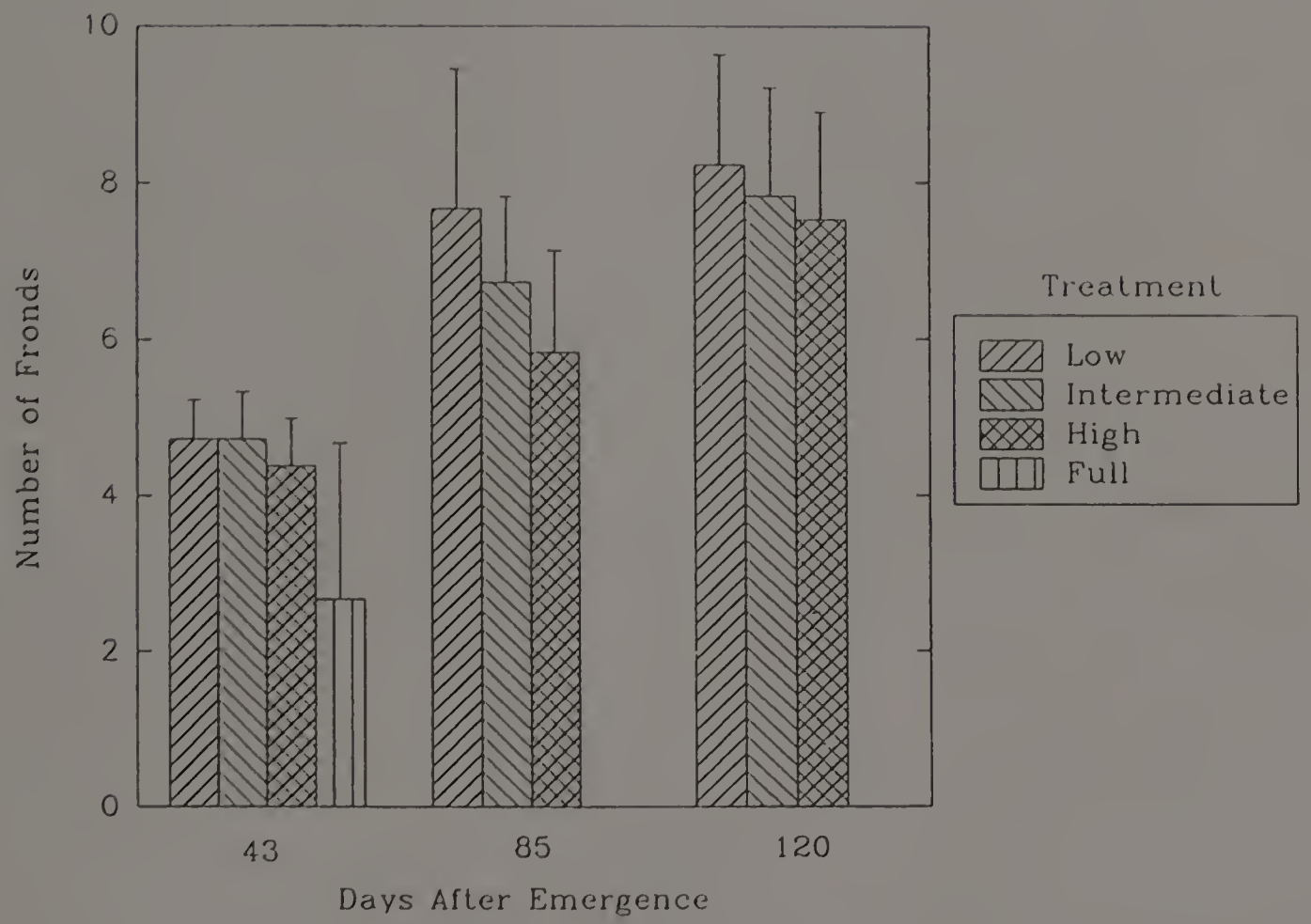

Figure 3.2 Shading effects on the number of fronds per plant, 1993 season.

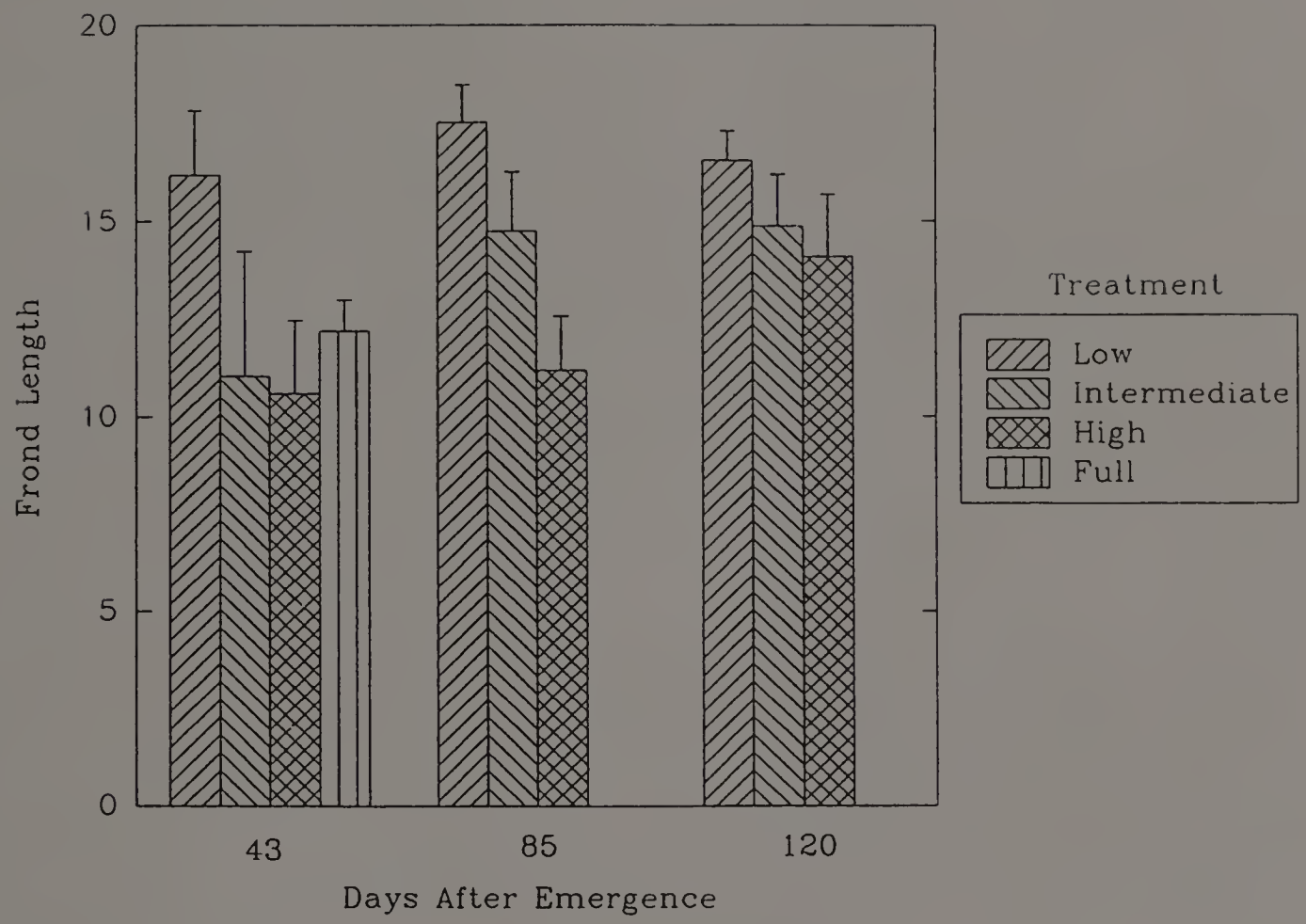

Figure 3.3 Shading effects on frond lengths, 1993 season.

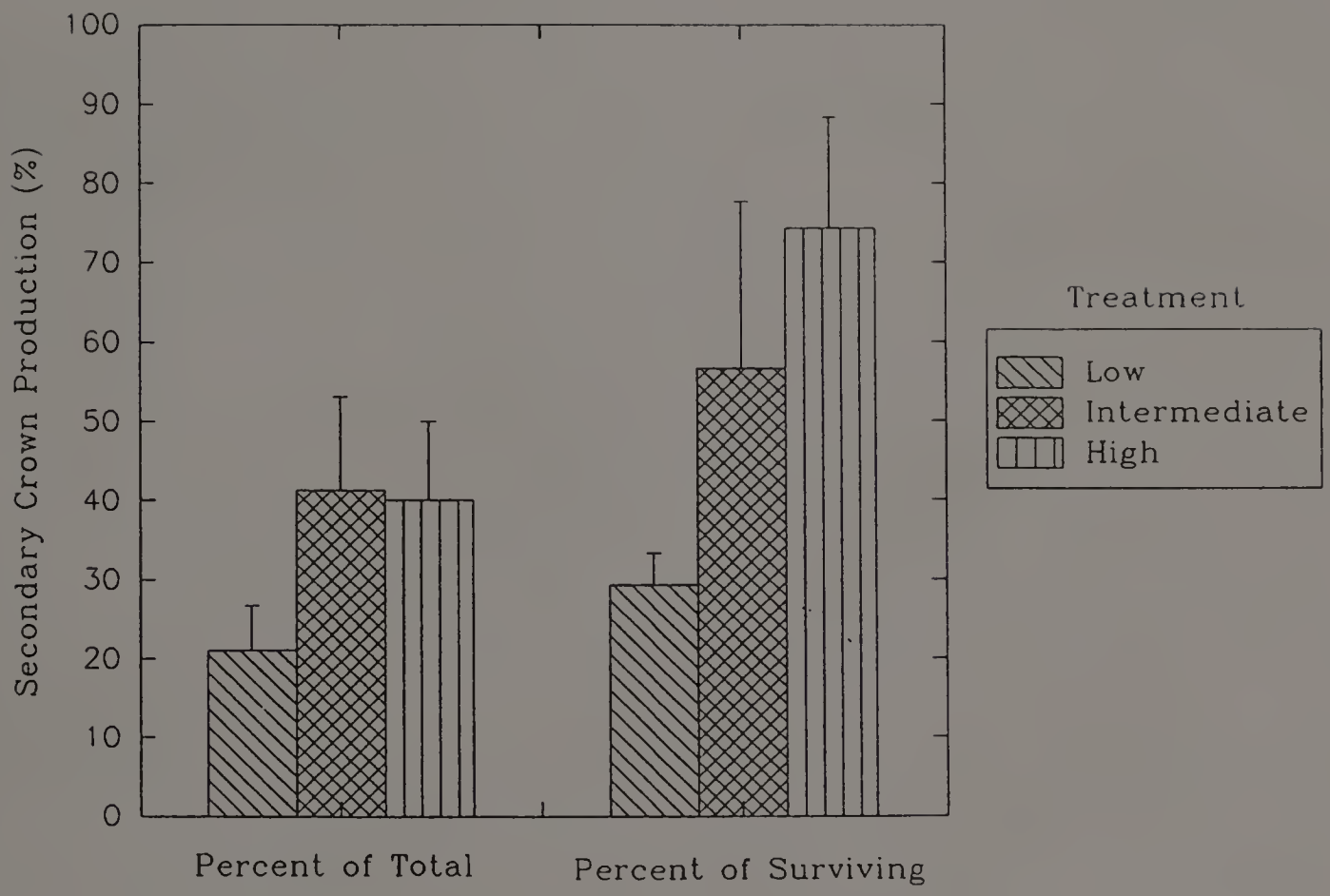

Figure 3.4 Shading effects on the production of secondary crowns, 1993 season.

subject to the highest shade treatment (22% ambient) produced secondary crowns.

Fresh weight gain by crowns over the growing season was not influenced by shade treatments. On average, crowns increased in fresh weight by a factor of 60% over their initial weight (fig 3.5).

3.2 Shade Treatments, 1994

Shading treatments did not have a significant effect on crown activity during the 1994 season (table 3.2). Non-activity ,mortality or induced dormancy, of plants increased dramatically over the season regardless of shade treatment (fig. 3.6). Initially, 85 to 100% of all crowns produced vegetative growth at 28 days after frond emergence. Shortly thereafter, high rates of frond desiccation and die back occured causing many crowns to enter shock induced dormancy or die. By 120 days after planting, only 15 to 25% of crowns in all treatments showed signs of vegetative growth.

The mean number of fronds produced by crowns was not significantly effected by shade treatments (table 3.2). Regardless of the shade treatment, the number of fronds decreased from 6 to 7 fronds per crown to between 3 to 4 fronds per crown by the end of the season (fig. 3.7).

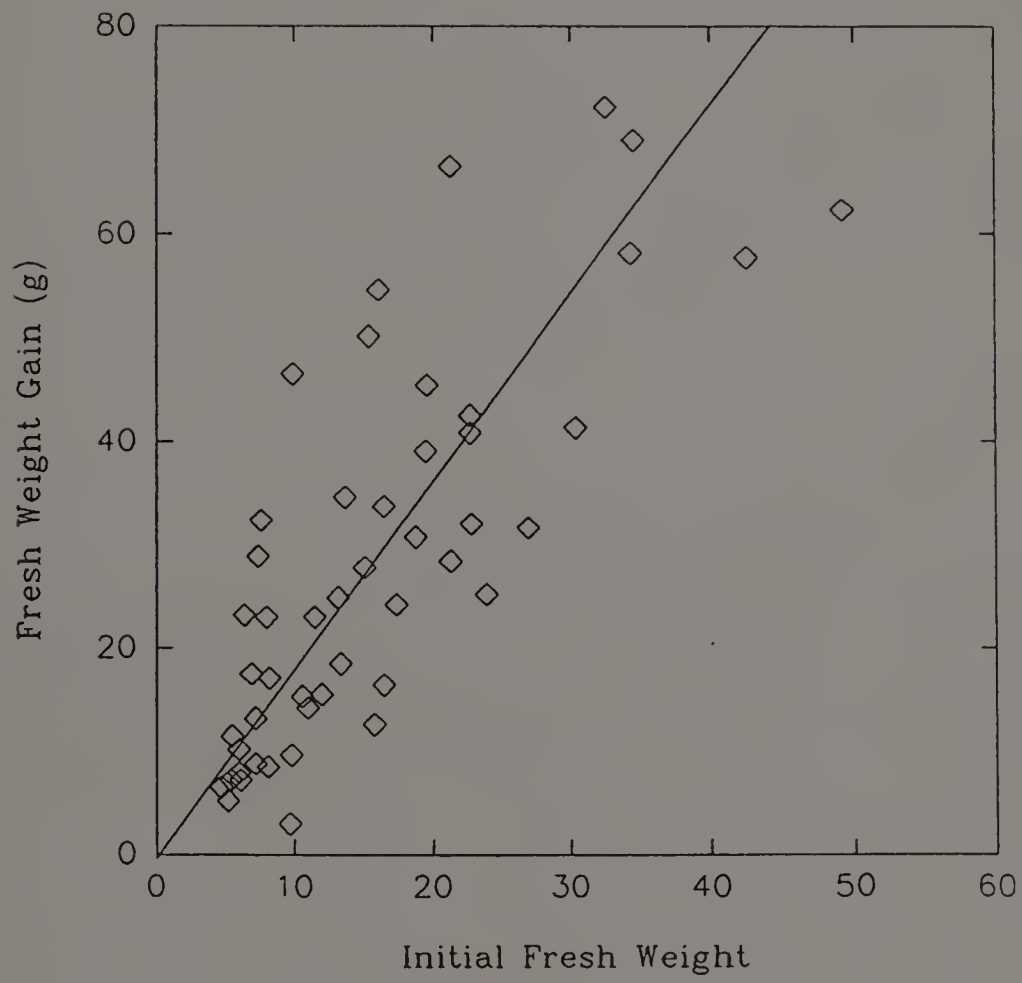

Figure 3.5 Initial crown weight versus fresh weight gain, 1993 season.

Table 3.2
Growth response to shading treatments, 1994 season.

	Days after emergance			
	28	53	78	120
Number of plants out of 12 surviving				
Light level:				
22%[1]	13.67[2]	12.00	11.00	3.33
46%	15.67	12.00	10.33	2.67
73%	14.33	11.97	9.67	4.33
100%	16.00	11.67	10.33	2.33
significance[3]	l^{**}, q^{ns}, c^{***}	l^{ns}, q^{ns}, c^{ns}	$l^{ns}, q^{ns}\ c^{ns}$	l^{ns}, q^{ns}, c^{ns}
Number of fronds per plant				
Light level:				
22%	6.70	5.63	2.73	2.60
46%	6.63	4.73	2.37	1.90
73%	6.17	4.03	2.20	1.90
100%	6.07	3.97	2.66	2.43
significance	l^{ns}, q^{ns}, c^{ns}	l^{***}, q^{ns}, c^{ns}	l^{*}, q^{ns}, c^{ns}	l^{ns}, q^{ns}, c^{ns}
Mean frond length per plant (cm)				
Light level:				
22%	48.83	50.60	54.17	54.80
46%	45.80	48.70	49.50	19.07
73%	46.13	46.47	45.93	40.43
100%	39.83	41.03	39.33	16.00
significance	l^{**}, q^{ns}, c^{ns}	l^{**}, q^{ns}, c^{ns}	l^{**}, q^{ns}, c^{ns}	l^{*}, q^{ns}, c^{*}

[1] Representing percent of ambient light transmitted through shade cloth.
[2] Means of three replications. Replicates consisted of a maximum of n=12 plants.
[3] *, **, ***, ns, significant at P=0.05, 0.01, 0.005, or not significant respectively. l, q, c =linear, quadratic, or cubic components, respectively.

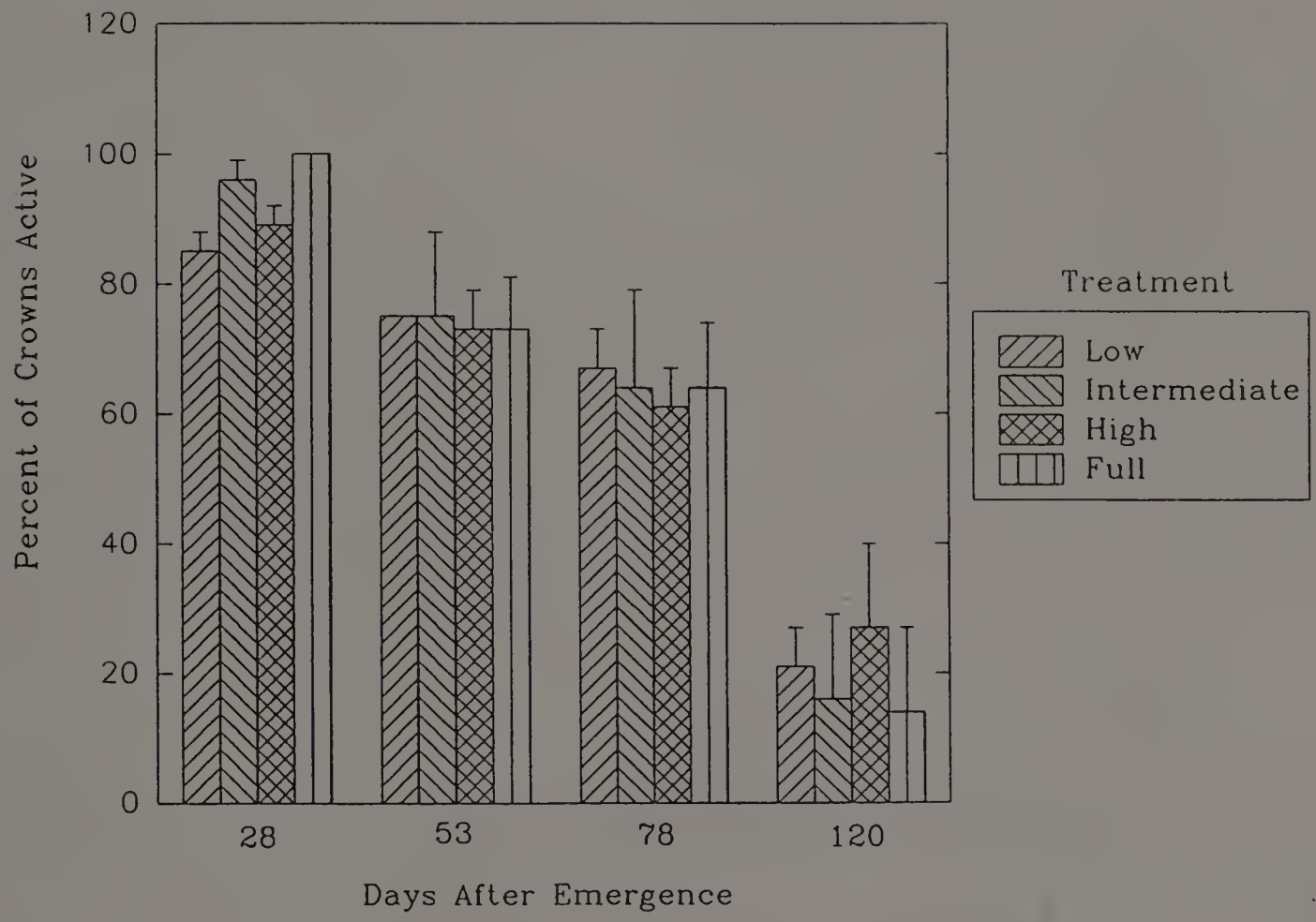

Figure 3.6 Shading effects on crown activity, 1994 season.

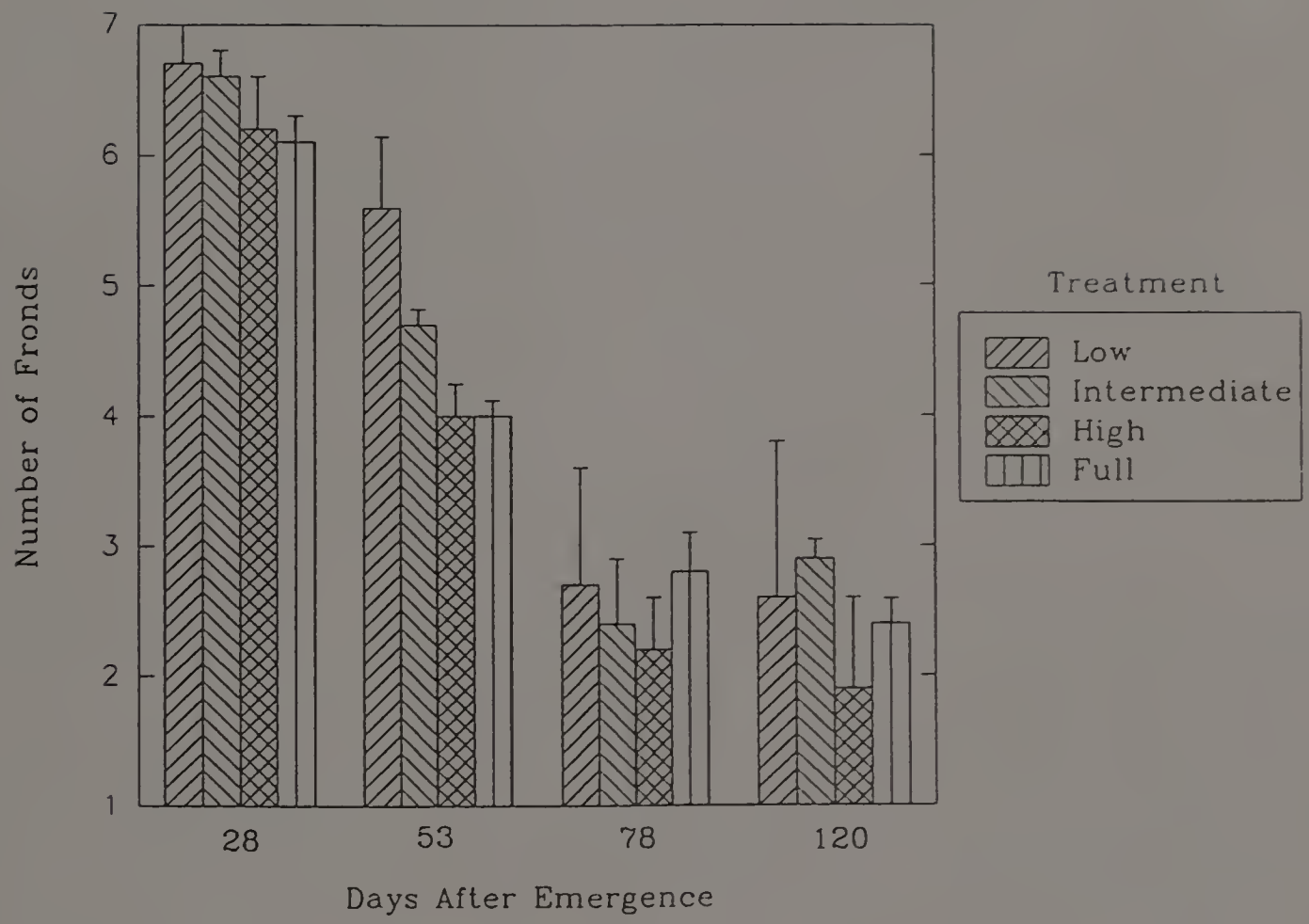

Figure 3.7 Shading effects on the number of fronds per plant, 1994 season.

Shading treatments did have a significant effect on the average length of fronds produced by crowns (Table 3.2), but treatment within time separations indicate that shading only had a significant effect on frond lengths towards the end of the growing season. The interaction between time and shading treatments was also highly significant. This may be explained by the cumulative effects of shading treatments over time. Crowns that were subject to lower light intensities produced slightly larger fronds than those under higher intensities (fig. 3.8).

No secondary crowns were produced during the 1994 season.

3.3 Planting Density

Planting density treatments had a significant effect on crown activity (5% level) (table 3.3). Crowns planted at the highest density (20 cm spacing) had the highest percentage of active crowns (fig. 3.9). By the end of the season some 60% of crowns planted 20 cm apart were active while, in contrast, only 10% of crowns planted 60 cm apart were active (table 3.3). Some crowns that had initially entered shock induced dormancy were able to recover by mid-

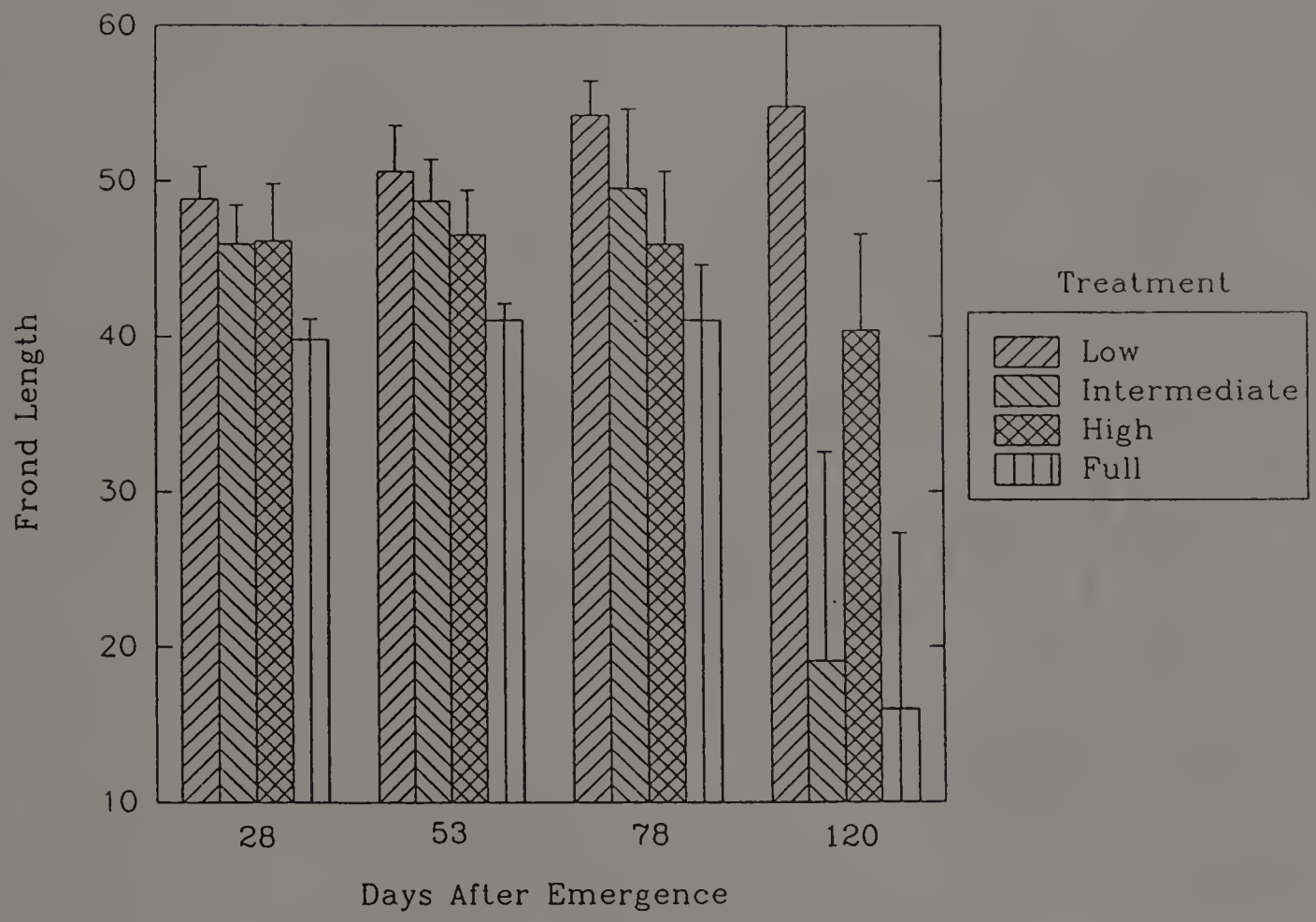

Figure 3.8 Shading effects on frond lengths, 1994 season.

Table 3.3
Growth response to planting density treatments.

Planting Density	Weeks After Emergance 1	2	3	4	5	6
20 cm[1]						
Surviving (%)[2]	75.0[3]	84.3	91.7	91.7	83.3	75.0
Number of fronds	6.10	5.37	5.40	4.77	4.42	3.87
40 cm						
Surviving (%)	58.3	58.3	58.3	66.7	58.3	41.7
Number of fronds	5.93	4.77	3.73	3.43	2.90	2.10
60 cm						
Surviving (%)	58.3	75.0	66.7	58.3	25.0	8.3
Frond number	6.23	4.48	3.10	2.83	1.40	0.67

[1] Distance between plants.
[2] Percent of initial plants surviving.
[3] Means of three replications. Replicates consited of a maximum of n=4 plants.

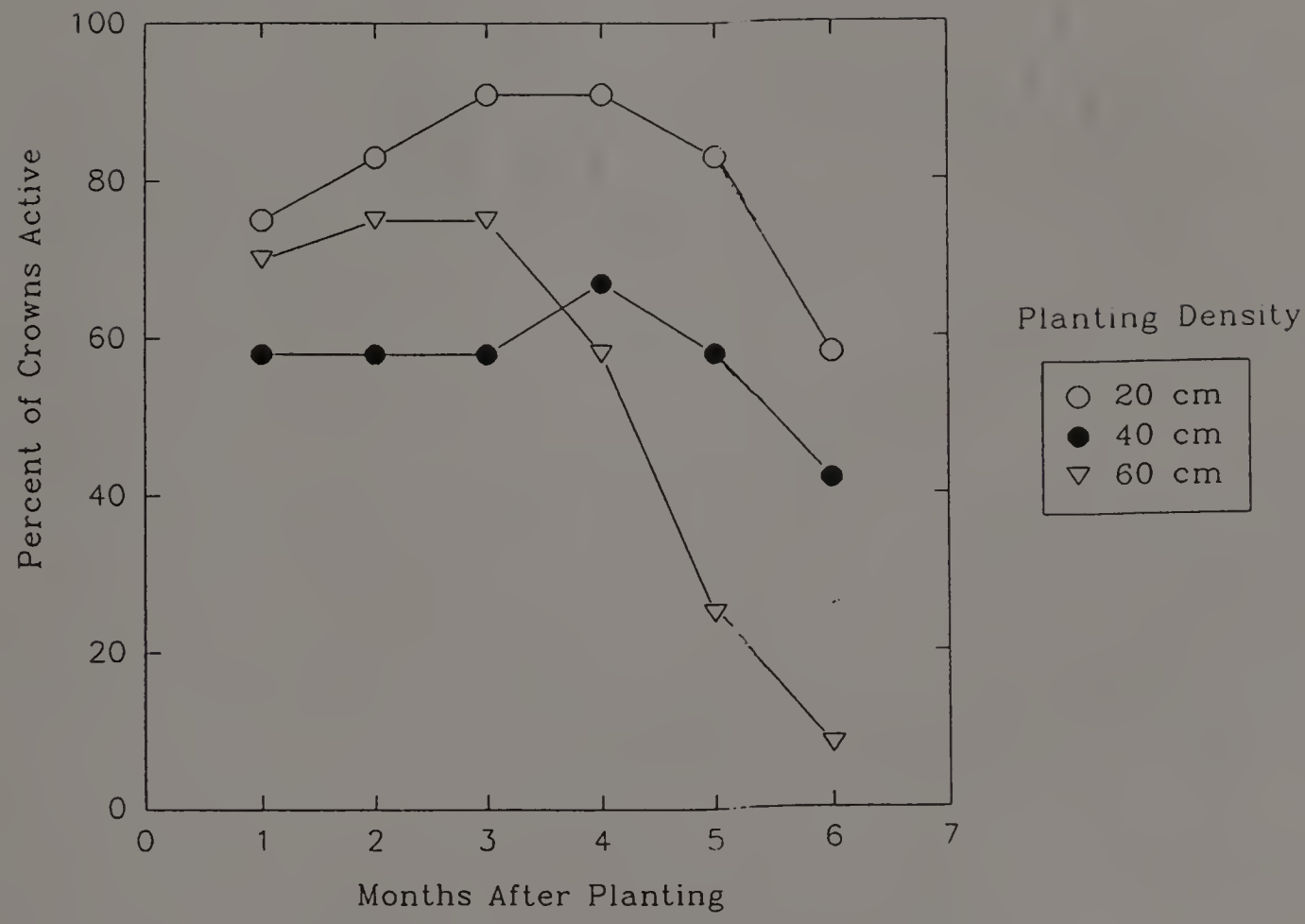

Figure 3.9 Planting density effects on crown activity.

season and produce vegetative growth. This phenomena was most visible at the 20 cm planting density treatment. Plant viability at all planting densities began to decline within 3 months after frond emergence. Decline occurred sooner and more rapidly at lower planting density treatments.

The effects of planting density on the number of fronds produced by crowns was highly significant (table 3.3). Crowns in all planting densities initially produced an average of 6.0 fronds per crown. Treatment effects then became more evident with crowns planted at higher densities keeping their fronds longer until by 6 months after planting the average number of fronds decreased to 3.87, 2.10, and 1.67 for the 20 cm, 40 cm, and 60 cm planting densities respectively (fig 3.10).

3.4 Frond Tissue Response

Shading significantly affected tissue conductivity (table 3.4). Differences in shading effects were noticible from the first week onward. Tissue conductivity increased steadily over the course of the experiment (fig. 3.11). The rate at which tissue conductivity measurements increased was indirectly proportional to the level of shading a particular treatment received.

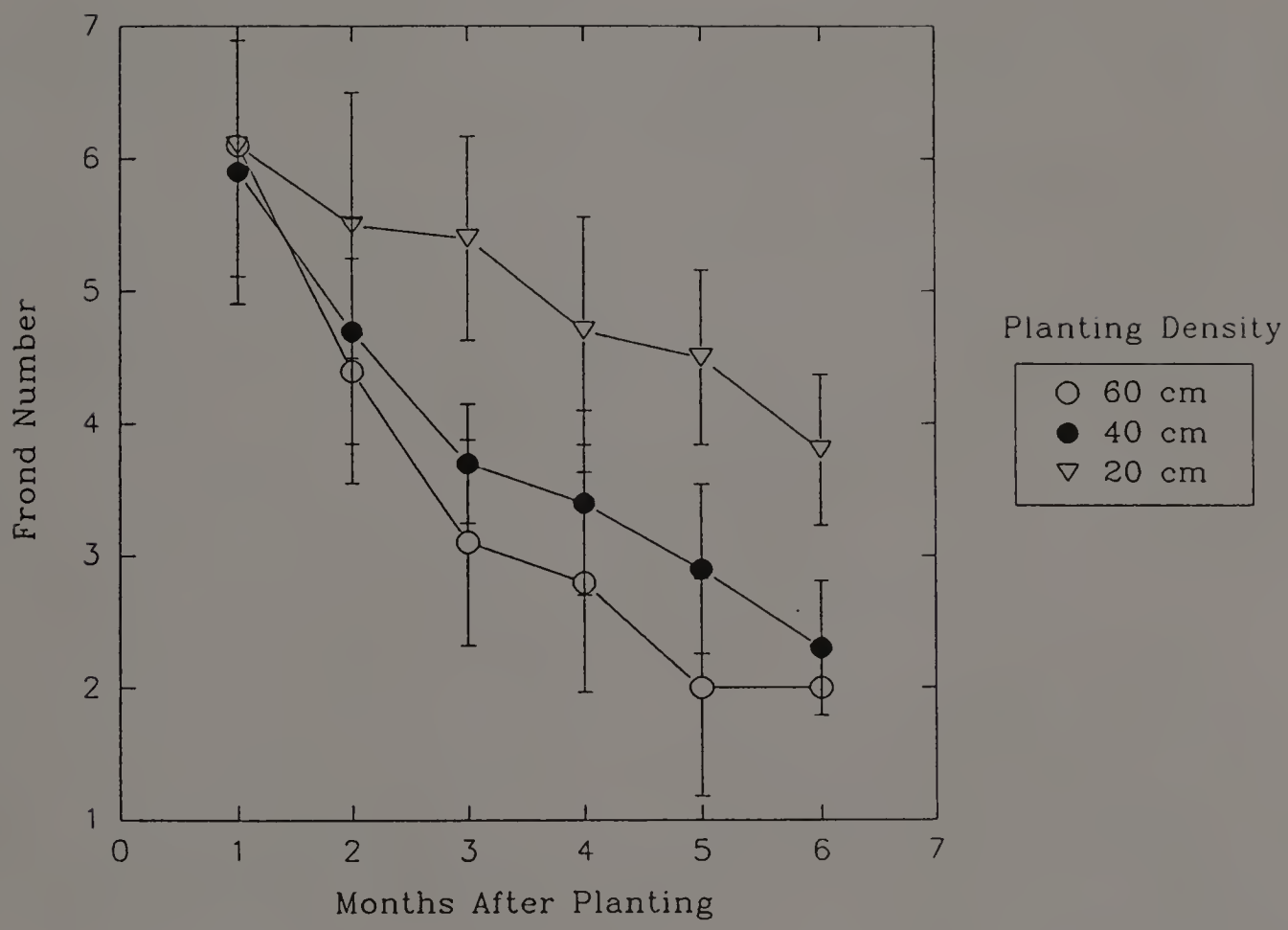

Figure 3.10 Planting density effects on the number of fronds per plant.

Table 3.4
Frond tissue response.

	Weeks After Frond Emergance					
	1	2	3	4	5	6
Tissue conductivity (μmols/cm*100)						
Shading treatment:						
22%[1]	2.47[2]	3.51	3.87	5.37	6.50	7.30
46%	2.50	3.97	5.36	8.64	10.52	11.80
73%	3.91	7.29	8.59	13.75	17.32	21.27
100%	5.63	8.37	13.23	17.64	20.75	28.30
significance[3]	l^{***},q^{***},c^{ns}	l^{***},q^{**},c^{***}	l^{***},q^{***},c^{ns}	l^{***},q^{ns},c^{*}	l^{***},q^{ns},c^{ns}	l^{***},q^{ns},c^{**}
Chlorophyll a content (mg/g tissue)						
Shading treatment:						
22%	2.38 a	3.24	2.92	3.02	3.00	2.71
46%	1.84 b	2.31	2.17	2.06	1.84	1.71
73%	1.49 c	2.41	1.67	1.11	1.02	0.92
100%	0.88 d	1.54	1.27	1.04	0.73	0.73
significance	l^{***},q^{ns},c^{**}	l^{***},q^{ns},c^{ns}	$l^{***},q^{***}c^{*}$	l^{***},q^{***},c^{ns}	l^{***},q^{***},c^{ns}	l^{***},q^{***},c^{***}
Chlorophyll b content (mg/g tissue)						
Shading treatment:						
22%	11.44	15.26	12.00	13.82	13.55	13.42
46%	8.78	12.54	11.61	10.43	10.00	9.03
73%	5.48	10.37	9.87	5.29	4.65	3.34
100%	4.61	7.91	7.67	4.36	2.53	2.09
significance	l^{***},q^{ns},c^{ns}	l^{***},q^{***},c^{**}	l^{***},q^{**},c^{**}	l^{***},q^{***},c^{***}	l^{***},q^{***},c^{***}	l^{***},q^{***},c^{**}

[1] Representing percent of ambient light transmitted through shade cloth.
[2] Means of three replications. Replicates consisted of a maximum of n=12 plants.
[3] *, **, ***, ns, significant at P=0.05, 0.01, 0.005, or not significant respectively. l, q, c =linear, quadratic, or cubic components, respectively.

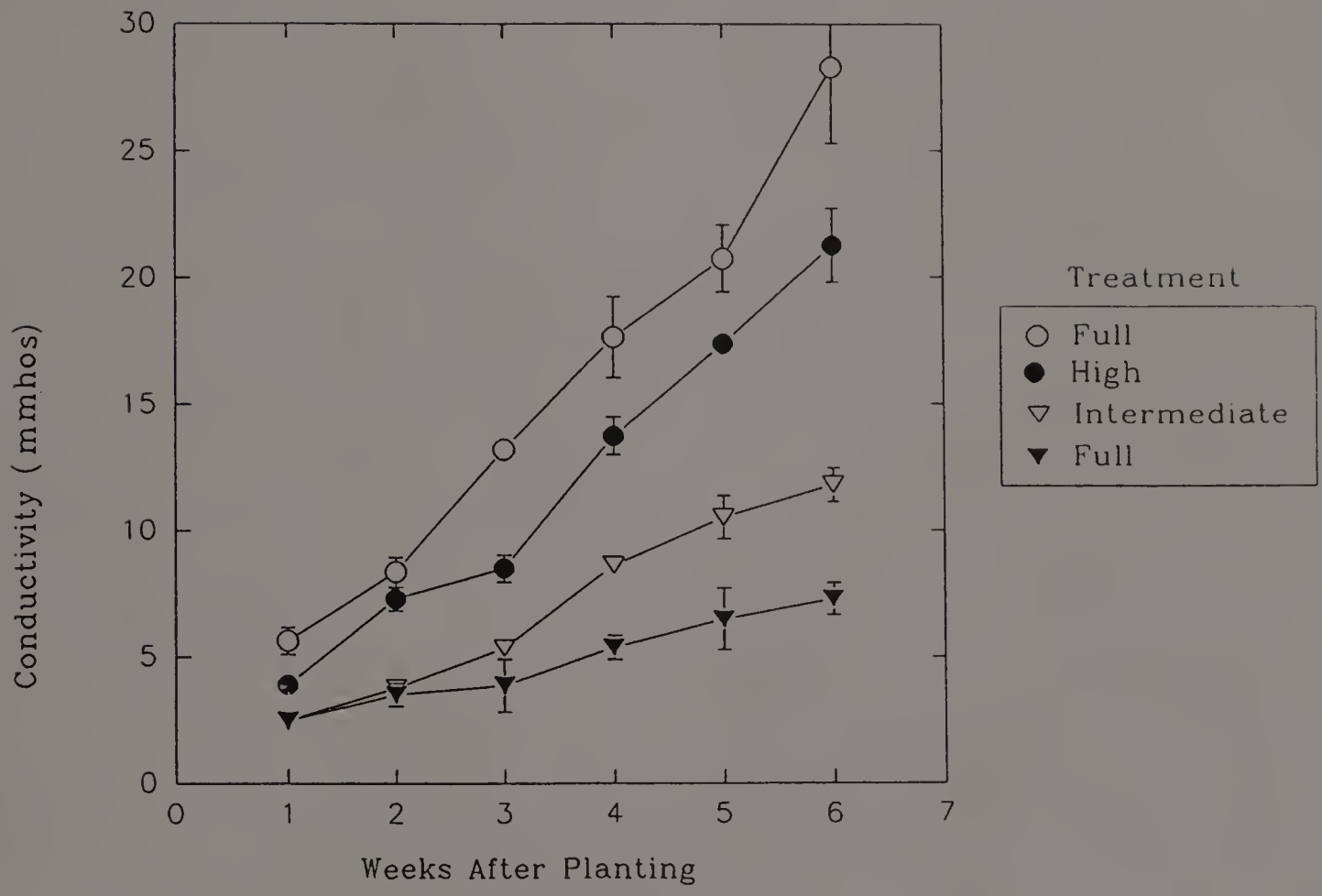

Figure 3.11 Shading effects on frond tissue conductivity.

The effect of shading on both chlorophyll a and b contents was highly significant (Table 3.4). Tissue chlorophyll increased between the first and second weeks after frond emergence and then declined steadily until the end of the experiment (figures 3.12 and 3.13). The rate of chlorophyll decline was indirectly proportional to the level of shading, the higher the light level, the more chlorophyll loss.

The interaction between time and shading treatments, for all response variables, was highly significant. This may be explained by the cumulative effects of shading treatments over time causing a varied response to identical treatments.

3.5 Photosynthetic Response

A photosynthetic light response curve was generated (table 5, figs. 3.14 and 3.15). The rate of photosynthesis increased with increasing light intensity, reaching 26 μmol CO_2 m^{-2} s^{-1} with a light saturation value occurring at about 400 μmol PAR m^{-2} s^{-1}. The light compensation point was estimated from the x-intercept to be about 27 μmol PAR m^{-2} s^{-1}. PAR levels could not be raised above 500 μmol/m^2 without raising temperatures in the chamber to unreasonable levels,

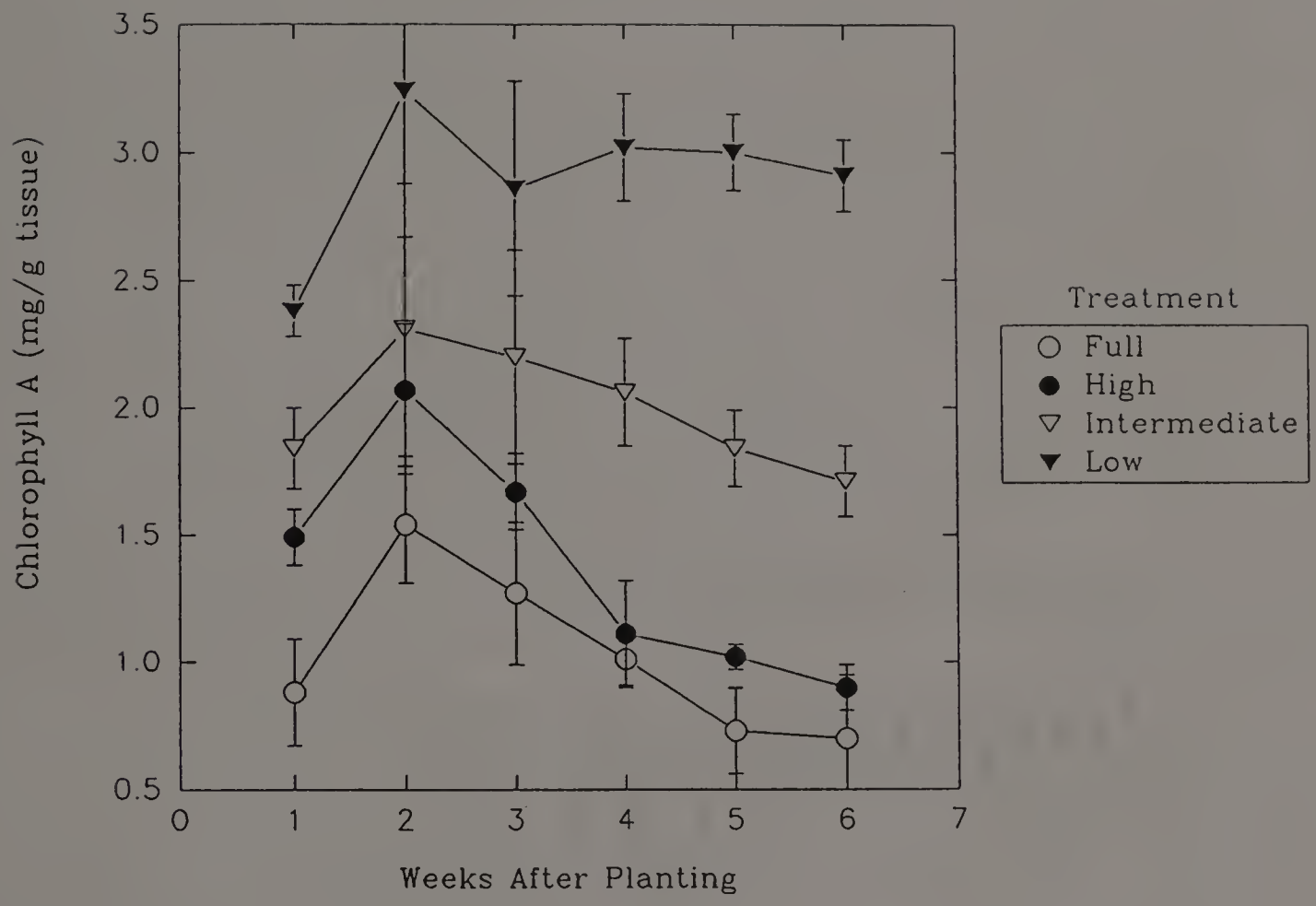

Figure 3.12 Shading effects on frond tissue chlorophyll a content.

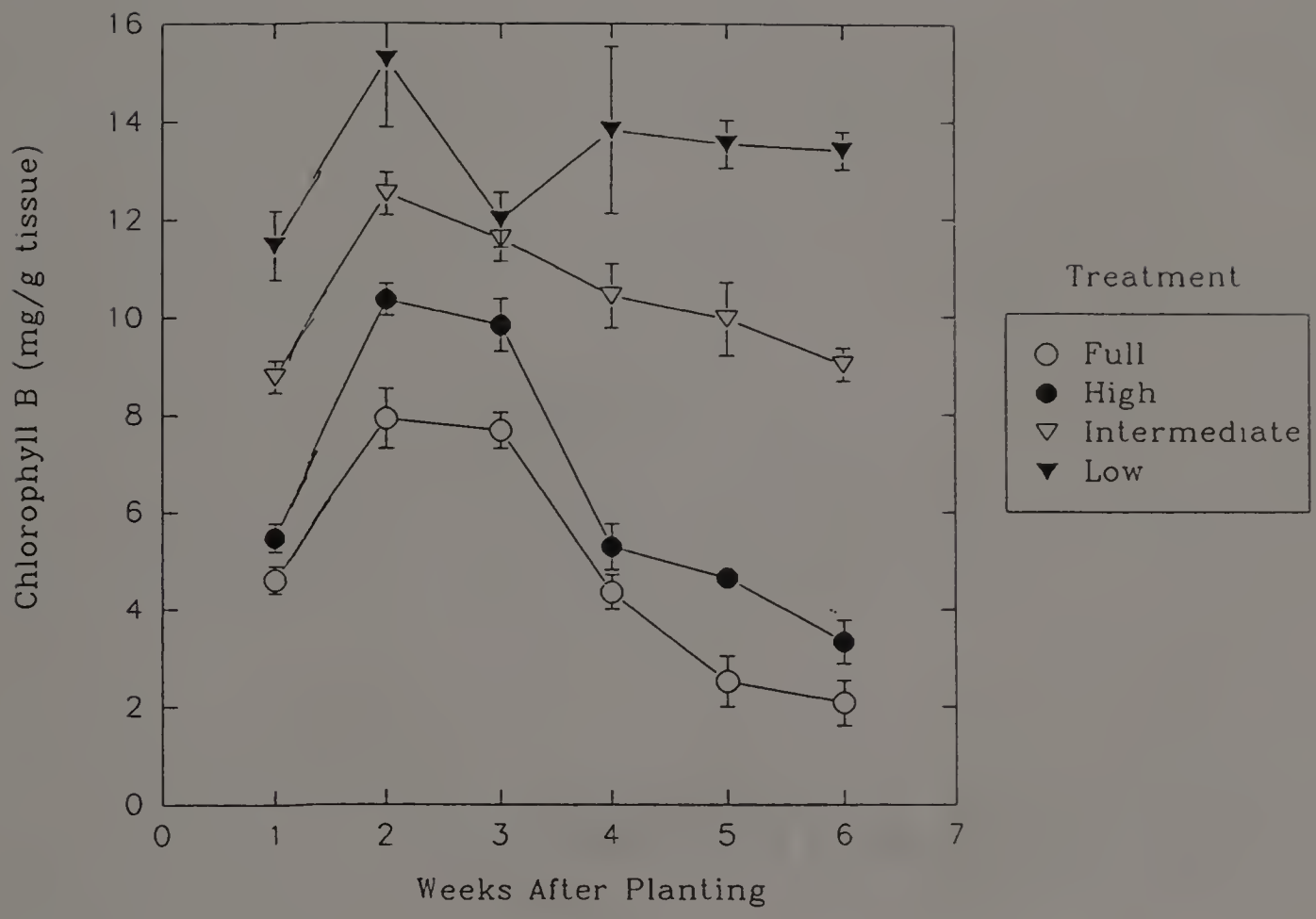

Figure 3.13 Shading effects on frond tissue chlorophyll b content.

Table 3.5
Photosynthetic response.

	Photosynthetically active radiation (PAR) (*u*mols/m^2)					
	0	60	125	260	400	600
Photosynthesis						
*u*mol $CO_2/m^2/sec$[1]	-6.89[2]	7.93	13.30	18.79	23.10	22.62
*u*mol $CO_2/g/sec$[3]	-45.62	62.77	102.67	126.47	164.26	151.20

[1] Carbon exchange rate on a leaf area basis.
[2] Means of 3 replications.
[3] Carbon exchange rate on a fresh weight basis.

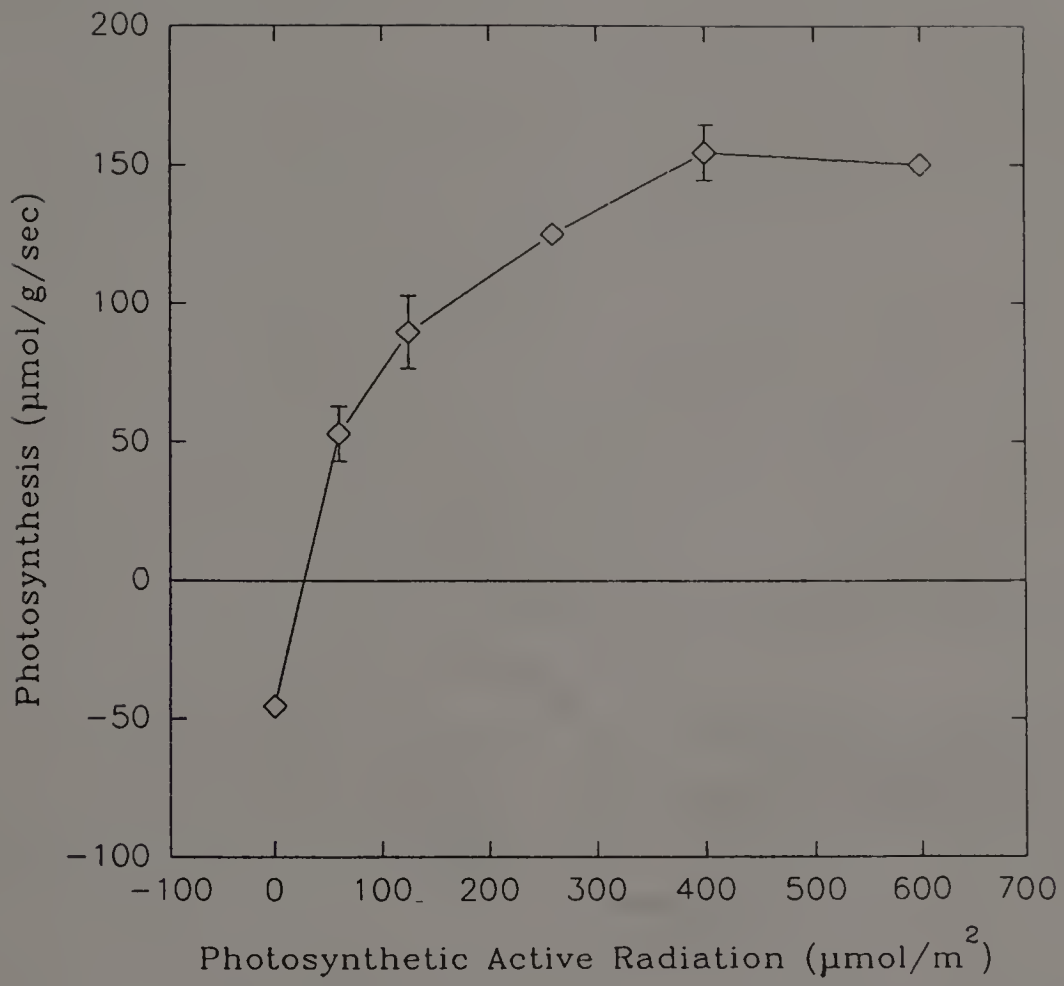

Figure 3.14 Photosynthetic response on a fresh weight basis.

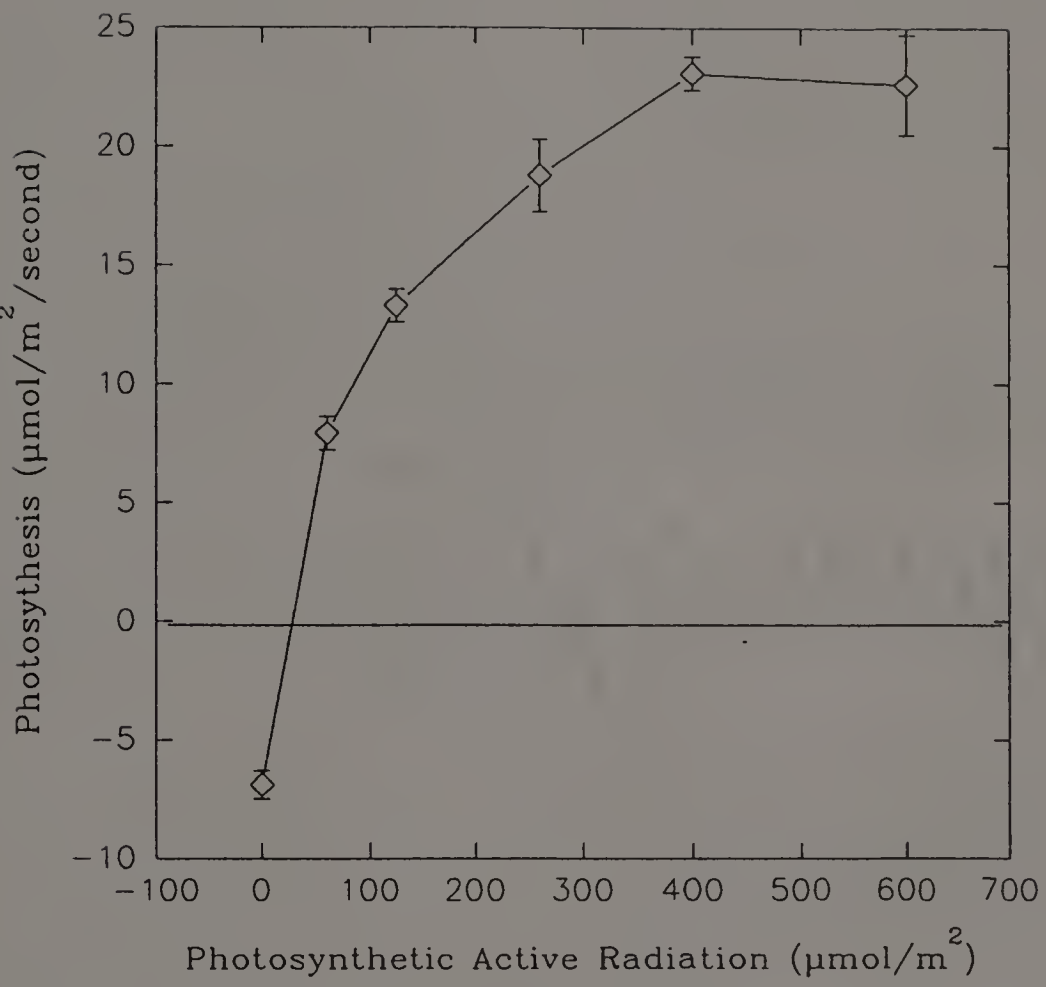

Figure 3.15 Photosythetic response on a leaf area basis.

preventing analysis of photosynthetic response light levels higher than that level.

3.6 Crown Response to Shock Induced Dormancy

Crowns needed a minimum of 4 weeks vernalization to break shock induced dormancy (table 3.6) Some 40% broke dormancy by 4 weeks, however, the results suggest that at least 6 to 7 weeks of vernalization are required for all treated crowns to break dormancy (figs 3.16 and 3.17). Crown take an average of 9 days to resume vegetative growth after breaking dormancy.

Table 3.6
Crown response to shock induced dormancy.

	Weeks of induced vernalization									
	1	2	3	4	5	6	7	8	9	10
Dormancy broken (%)[1]	0	0	0	40	60	100	100	100	100	100
Days to break dormancy[2]	--	--	--	12.5	8.7	12.0	12.0	9.4	9.0	9.0

[1] Percent of crowns that broke dormancy out of 5 individuals.
[2] Days to break dormancy following removal from cold storage at 3 C.

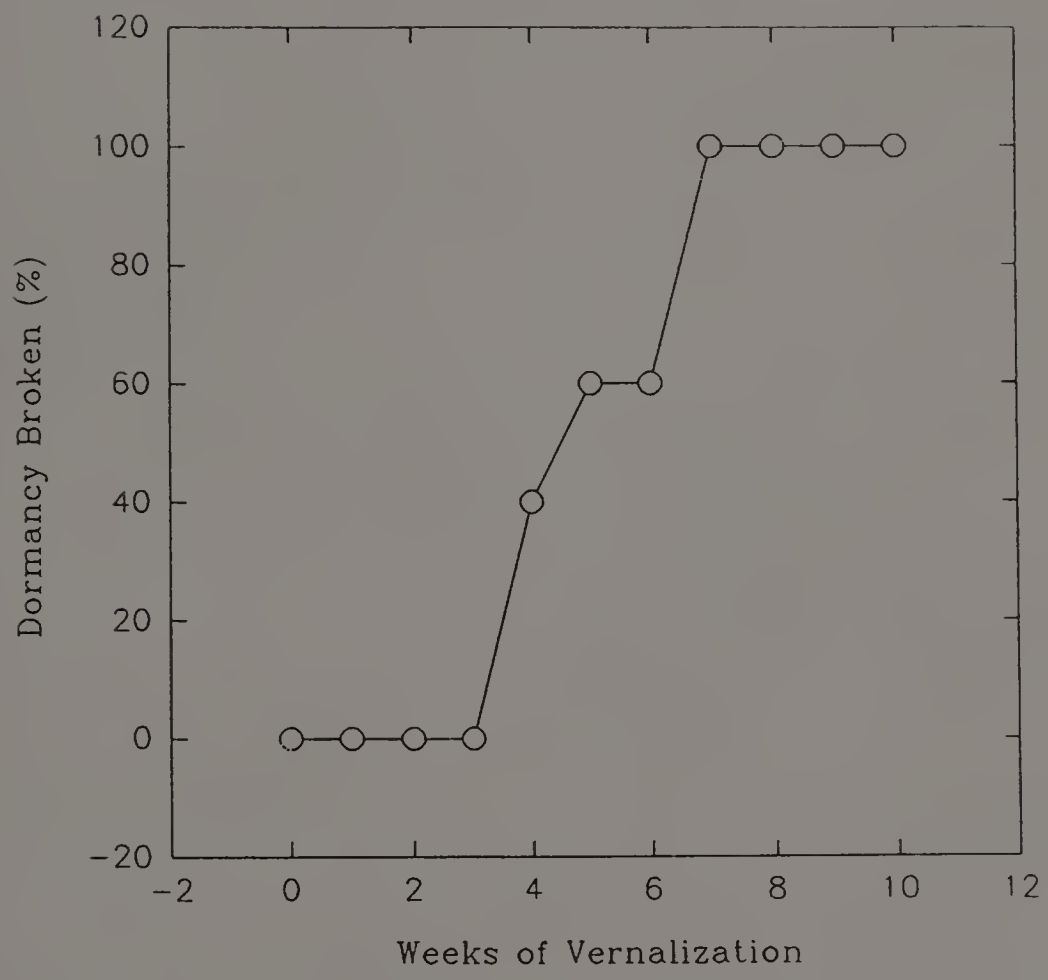

Figure 3.16 Percent of crowns breaking dormancy in response to induced vernalization.

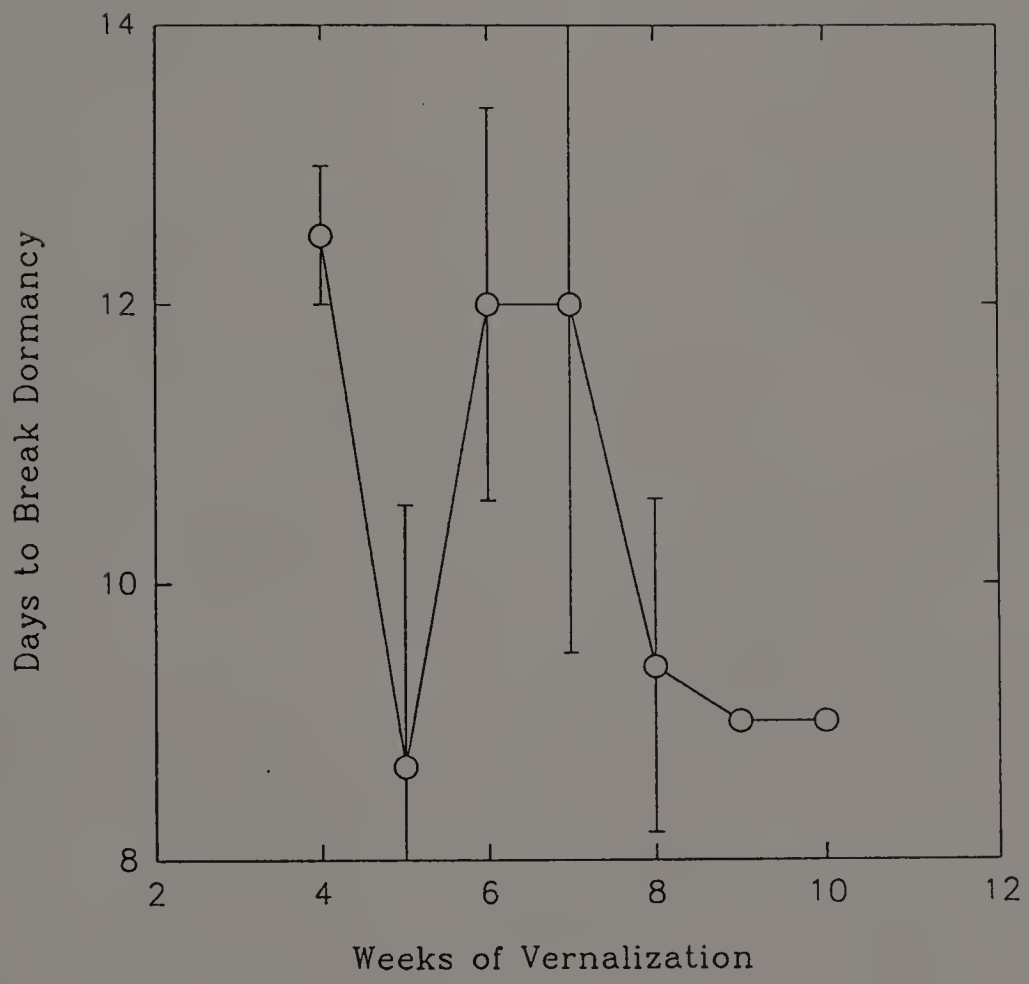

Figure 3.17 Days to frond emergence after crown removal from induced vernalization.

CHAPTER 4

DISCUSSION

4.1 Shade Treatments, 1993

Crowns planted in the spring suffer from severe transplanting shock, suggesting that the cultural practices recommended by Dykeman (1980 and 1991) for New Brunswick growers may be unsuitable in Massachusetts. Despite the initial shock of transplanting, crowns have a limited ability to recover and acclimatize to field conditions. Crown recovery from transplanting shock was proportional to the amount of shading crowns received. Crowns grown under low light levels were more likely to produce vegetative growth consisting of fronds which were longer and more numerous than those on crowns under high light levels. Despite clear initial separations between treatments 120 days after planting the only difference between treatments is between the three that received some shading and the treatment that did not.

Interestingly, crown growth at high light levels produced more secondary crowns, suggesting that higher light levels actually promote rhizome growth and increase the production of secondary crowns. Because crowns subject to the high light levels were clearly smaller and less healthy

than crowns in other treatments the reason for the increased production of secondary crown is unclear. It may be an attempt by crowns to evade poor local conditions by sending rhizomes and clones to neighboring areas. A longer term study would be needed to determine whether such events would increase stand establishment.

4.2 Shade Treatments, 1994

Using a regionally selected cultivar, U.M. 1, fall planting significantly altered growth patterns. Growth during the 1993 season was initially poor due to the shock of transplanting with plants recovering in proportion to the level of shading. Crowns of the 1994 season initially grew well, but then declined rapidly. Because initial growth was so vigorous, a fall planting had a very beneficial effect on crown survival and growth. Transplanting stresses appeared largely reduced with a fall planting.

The decline of crowns and increases in mortality and induced dormancy associated with fall planting suggests that crowns of the cultivar U.M. 1 are less suited to field conditions than crowns of the cultivar N.B. 35. In 1994, frond numbers declined rapidly, regardless of growth conditions, and no secondary crowns were produced. In 1993 crowns of the cultivar N.B. 35, despite a transplanting

shock, grew more vigorously and produced both new fronds and secondary crowns. These observations suggest that crowns of the U.M. 1 cultivar are more vulnerable to adverse conditions than crowns of the N.B. 35 cultivar. Because shading treatments for both seasons were identical, the exact nature of this sensitivity in unclear. Increased sensitivity to other stresses, such as heat and water stress, are suggested, but unproven.

4.3 Planting Density

High planting densities did improve individual plant development leading to improved stand establishment. Close planting densities offer other benefits besides mutual shading, due to mutual support, fronds were more raised less subject to breaking. Plants in all treatments declined over the growing season, but the 20 cm planting density experienced this decline later and to a lesser degree than other treatments. High plant densities cause decreased air movement in plant stands, leading to decreased evapo-transpirational demands and increased soil moisture (Geiger, 1961). Another beneficial plant to plant interaction might come from rhizome connections in mature stands, which may improve water distribution within the stand.

High planting density regimes may not prove economical for the commercial grower, but they might be amended. Crowns might be planted in strips or clusters and allowed to spread in fields intended for fiddlehead cultivation. High density planting might also prove useful in ornamental and vegetable gardens.

Closer planting causes mutual shading and beneficial microclimate effects which support plant growth. Plants were grown at ambient light levels, suggesting that other factors, besides light intensity, such as water relation and heat stress problems, might be responsible for the poor plant development experienced in the field shading experiments.

4.4 Frond Tissue Response

Results demonstrate that light levels do have a significant effect on frond tissues. Conductivity measurements increased proportionaly with increased light levels and chlorophyll content decreased in proportion with increased light levels. The experiment was performed for a period of 6 weeks, or roughly one third the length of a full season, and no fronds under any treatment experienced desiccation, and no crowns were shocked into dormancy.

All light levels gradually caused tissue damage, but it is unclear how much membrane damage and chlorosis must occur before a frond in not functional. Even 6 weeks under ambient light conditions was insufficient to cause frond die-back or desiccation. If tissue damage continued at the same rates over the season then crowns in the field, under lower light levels, should have survived the majority of the season. This, again, suggests other factors besides light intensity may be responsible for poor plant development seen in field shading experiments.

Crowns grown in this experiment were generally healthier and more vigorous than those grown under field conditions. One or more of several factors may be responsible for this result. A high peat potting soil mixture (Pro-mix BX) has better water retention properties than field soil low in organic matter, causing improved water relations. The potting soil may also have allowed for more rapid and increased root growth, also improving water relations. Greenhouse studies with plants grown in potting soil under shade had frond desiccation occurring after two to three weeks of growth, suggesting that other factors, possibly temperature, may be responsible for frond desiccation. Plants in this experiment were planted late in the season, September 3, to avoid high seasonal temperatures and lower temperatures and slightly shorter day lengths may

have decreased the amount of evapo-transpirational stress encountered by crowns resulting in healthier plants.

Crowns of the cultivar U.M.1 were used in this experiment and it is unclear what the response of other genotypes would be. Experiments based on studying tissue responses to adverse conditions may prove useful in selecting genotypes which are more suitable for growth in field conditions.

4.5 Photosynthetic Response

Results suggest that the ostrich fern is efficient at utilizing low levels of PAR and that the ostrich fern may be physiologically unsuited for growth under field light conditions. Light levels above 400 μmol/m^2 PAR had an injurious effect on photosynthesis. This is near the lowest light level treatment, or 22% of ambient light.

LSV and LCP values (LSV=400 μmol PAR m^{-2} s^{-1}, LCP=27 μmol PAR m^{-2} s^{-1}) are between those typically found for sun and shade species of plants. For example the shade species Cordyline rubra had a light saturation point of 300 μmol PAR m^{-2} s^{-1} and a corresponding photosynthetic rate of 2.5 μmol CO_2 m^{-2} s^{-1}. The sun species Zea mays exhibited a light saturation point of almost 2000 μmol PAR m^{-2} s^{-1} associated

with a photosynthetic rate of about 47 μmol CO_2 m^{-2} s^{-1} (Beadle et al., 1985).

Crowns of the cultivar U.M. 1 were used in this experiment and it is uncertain what the photosynthetic response of other genotypes would be. Photosynthetic response curves may prove useful for selecting genotypes which are suitable for growth in field conditions.

4.6 Crown Response to Shock Induced Dormancy

Crowns enter shock induced dormancy as protection against adverse environmental conditions. Crowns may survive a period of adverse conditions by entering dormancy and then exiting when conditions are more favorable. It is unclear whether light, temperature or drought stress induces dormancy.

Crowns grown under field conditions were able to recover from shock induced dormancy without cold treatments while crowns in the greenhouse were not, suggesting shock induced dormancy may be or may have a temperature dependant response. Further experiments would be required to better understand these phenomena.

CHAPTER 5

CONCLUSIONS

Results suggest that the ostrich fern is marginally suited for growth in field conditions in Western Massachusetts. The ostrich fern is sensitive to many environmental conditions encountered in the field. Light levels are just one of the environmental conditions that differ between native stands and field conditions. Forest canopies transmit only 5-30% of photosynthetically active radiation through to stands of ostrich ferns with occasional sunflecks contributing moments of 100% transmittance (personal observation). Light has been demonstrated to cause tissue damage, but not at a rate damaging enough to explain field results indicating that other factors may be more responsible for poor plant development.

Lacking a cuticle, having a shallow root system, and having fern vascular tissues, all make the ostrich fern susceptible to drought stress. Under hardwood canopies where radiant energy is low and wind movement is reduced, evapo-transpirational demands are also reduced. Native stands are also usually located near sources of water. The increased radiant and heat energy and increased air movement experienced in the field creates the potential for undue evapo-transpirational demands on frond tissues. In

addition, slow root and frond development reduces the ferns ability to rapidly acclimatize to changed conditions, especially for recently transplanted crowns.

Any cultural practice that effects water relations will have an effect on plant growth. Transplanting creates severe stress on ostrich fern tissue. During the 1993 season crowns were transplanted in the spring and the transplanting shock caused a high rate of mortality and shock induced dormancy. The high incidence of frond desiccation indicated that water transport to the fronds was not adequate to balance increased evapo-transpirational demands, suggesting that, despite irrigation, frond tissues were simply not getting enough water. The most likely cause of this was the insufficient time available for new root development and rhizome damage from tissue removal for fresh weight purposes.

In contrast, crowns planted in the fall that had no root tissue removed had healthy initial vegetative growth across all treatments. As the season progressed plant mortality increased dramatically regardless of the shade treatment, suggesting the importance of cultivar choices and not poor water relations per se. If crowns of a cultivar selected by Dykeman had been used in 1994, maybe growth over the entire growing season would have been improved. The selection of genotypes suited for field conditions may prove vitaly important for improved stand establishment.

Another factor that has been shown to contribute to poor plant development is the lack of beneficial community interactions. Crowns planted in high density planting regimes not only offer each other mutual shading, but mutual frond support and beneficial microclimate effects, improving plant development. The ostrich fern has evolved to grow in a stand like fashion and reproduction is primarily accomplished through rhizome growth and the micro-climates near second generation crowns is significantly influenced by their progenitors. Rhizome connections between individuals in a mature stand may also prove vital to plant health. Community interactions are so important that when planted at high densities crowns of the U.M.1 genotype were able to survive the length of the season, whereas more isolated crowns were quickly damaged from environmental stresses. These interactions support the notion that once established a stand of ostrich ferns may be quite stable and can support vigorous growth.

Heat stress problems are suggested by results of several experiments. Temperature is also a determinant of evapo-transpiration and it is unclear whether tissue damage is the direct result of temperature damage or caused secondarily through water stress (Levitt, 1980). Direct cellular damage from heat is unlikely, because crowns in the planting density experiment were able to survive field conditions. Although, the fact that some aspects of shock

induced dormancy may be temperature dependant was demonstrated in greenhouse studies.

Results indicate that we may be looking more at the problem of stand establishment and of genotype selection than of inherent poor plant/environment relations. All field studies were supported for only one season of growth and two, three and four year studies of stand establishment would be needed to indicate whether the causes of frond desiccation were induced by inherent physiological limitations, cultivar selection, or problems enhanced by the stress of transplanting and the inability of crowns to acclimatize. Comparing genotype responses to temperature, light intensities and drought stress may prove useful in choosing candidate genotypes which are most suited to field conditions.

APPENDIX

ANALYSIS OF VARIANCE TABLES

Table 1.

Shading effects on crown mortality, 1993 season.

Source	DF	Mean Square	F Value
Treatment	3	224.765	70.57**
Time	2	4.333	9.45*
Treatment*Time	4	3.296	12.95**
Rep	2	0.000	
Rep*Treatment	5	3.185	
Rep*Time	4	0.458	
Rep*Treatment*Time	8	0.254	
$Treatment:Time_1$		56.083	45.54**
$Treatment:Time_2$		86.083	106.01**
$Treatment:Time_3$		89.194	72.43**
Total	28		

** Significance at the 1% level, * Significant at 5% level, N.S. No Significance.

Table 2.

Shading effects on number of fronds, 1993 season.

Source	DF	Mean Square	F Value
Treatment	3	1.8391	2.54 N.S.
Time	2	24.4344	19.53**
Treatment*Time	4	0.4722	6.18**
Rep	2	16.4139	
Rep*Treatment	5	0.7235	
Rep*Time	4	1.2511	
Rep*Treatment*Time	8	0.0764	
Treatment:$Time_1$		.393	5.21*
Treatment:$Time_2$		35.650	472.25**
Treatment:$Time_3$		46.663	618.095**
Total	28		

** Significance at 1% level, * Significant at 5% level, N.S. No Significance.

Table 3.

Shading effects on frond lengths, 1993 season.

Source	DF	Mean Square	F Value
Treatment	3	41.9324	18.94**
Time	2	18.5336	7.56**
Treatment*Time	4	3.9938	11.05**
Rep	2	23.7159	
Rep*Treatment	5	2.2134	
Rep*Time	4	2.4502	
Rep*Treatment*Time	8	0.3613	
Treatment:$Time_1$		18.540	18.94**
Treatment:$Time_2$		124.100	126.10**
Treatment:$Time_3$		183.280	183.28**
Total	28		

* Significance at 5% level, ** Significance at 1% level, N.S. No Significance.

Table 4.

Shading effects on plant mortality, 1994 season.

Source	DF	Mean Square	F Value
Treatment	3	0.076	0.01 N.S.
Time	3	297.299	221.82**
Treatment*Time	9	2.299	1.33 N.S.
Rep	2	6.063	
Rep*Treatment	6	7.118	
Rep*Time	6	1.340	
Rep*Treatment*Time	18	1.729	
Treatment:$Time_1$		3.667	0.90 N.S.
Treatment:$Time_2$		0.123	0.03 N.S.
Treatment:$Time_3$		0.889	0.22 N.S.
Treatment:$Time_4$		2.333	0.57 N.S.
Total	47		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 5.

Shading effects on frond numbers, 1994 season.

Source	DF	Mean Square	F Value
Treatment	3	1.538	2.71 N.S.
Time	3	46.121	21.00**
Treatment*Time	9	0.388	2.40 N.S.
Rep	2	4.875	
Rep*Treatment	6	0.567	
Rep*Time	6	2.196	
Rep*Treatment*Time	18	1.162	
Treatment:$Time_1$		0.439	1.67 N.S.
Treatment:$Time_2$		1.812	6.90*
Treatment:$Time_3$		0.187	0.71 N.S.
Treatment:$Time_4$		0.407	1.54 N.S.
Total	47		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 6.

Shading effects on frond lengths, 1994 season.

Source	DF	Mean Square	F Value
Treatment	3	683.618	35.53**
Time	3	579.540	3.32 N.S.
Treatment*Time	9	180.400	2.98**
Rep	2	81.709	
Rep*Treatment	6	17.240	
Rep*Time	6	174.669	
Rep*Treatment*Time	18	60.623	
Treatment:$Time_1$		29.973	0.60 N.S.
Treatment:$Time_2$		51.377	1.03 N.S.
Treatment:$Time_3$		117.309	2.35 N.S.
Treatment:$Time_4$		1006.921	20.21**
Total	47		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 7.

Planting density effects on crown mortality, 1994 season.

Source	DF	Mean Square	F Value
Treatment	2	5914.352	6.59*
Time	5	1379.630	3.33*
Treatment*Time	10	511.574	2.53*
Rep	2	150.463	
Rep*Treatment	4	896.991	
Rep*Time	10	414.352	
Rep*Treatment*Time	20	202.546	
Treatment:Time$_1$		3246.333	10.21*
Treatment:Time$_2$		4236.072	13.31**
Treatment:Time$_3$		35208.333	110.62**
Treatment:Time$_4$		35208.333	110.62**
Treatment:Time$_5$		12208.668	37.96**
Treatment:Time$_6$		10572.917	33.218**
Total	53		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 8.

Planting density effects on mean frond number, 1994 season.

Source	DF	Mean Square	F Value
Treatment	2	16.030	61.85**
Time	5	17.329	58.22**
Treatment*Time	10	1.271	2.51*
Rep	2	0.022	
Rep*Treatment	4	0.259	
Rep*Time	10	0.298	
Rep*Treatment*Time	20	0.506	
Treatment:Time$_1$		28.242	330.93**
Treatment:Time$_2$		18.201	213.26**
Treatment:Time$_3$		15.294	179.16**
Treatment:Time$_4$		11.838	137.71**
Treatment:Time$_5$		10.882	127.49**
Treatment:Time$_6$		8.792	103.02**
Total	53		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 9.

Light intensity effects on tissue conductivity.

Source	DF	Mean Square	F Value
Treatment	3	425.379	381.11**
Time	5	313.835	449.19**
Treatment*Time	15	26.062	67.35**
Plant	2	9.997	
Plant*Treatment	6	1.116	
Plant*Time	10	0.699	
Plant*Treatment*Time	30	0.587	
$Treatment:Time_1$		16.967	13.71**
$Treatment:Time_2$		17.363	34.19**
$Treatment:Time_3$		51.596	102.43**
$Treatment:Time_4$		92.280	181.46**
$Treatment:Time_5$		124.830	245.43**
$Treatment:Time_6$		266.941	524.93**
Total	70		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 10.

Light intensity effects on chlorophyll a content.

Source	DF	Mean Square	F Value
Treatment	3	11.508	195.67**
Time	5	1.185	34.17**
Treatment*Time	15	0.161	6.00**
Plant	2	1.011	
Plant*Treatment	6	0.059	
Plant*Time	10	0.036	
Plant*Treatment*Time	30	0.268	
$Treatment:Time_1$		1.186	5.09**
$Treatment:Time_2$		1.451	6.23**
$Treatment:Time_3$		1.513	6.49**
$Treatment:Time_4$		2.571	11.03**
$Treatment:Time_5$		3.102	13.31**
$Treatment:Time_6$		2.431	10.43**
Total	70		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

Table 11.

Light intensity effects on chlorophyll b content.

Source	DF	Mean Square	F Value
Treatment	3	258.862	1478.57**
Time	5	37.900	193.73**
Treatment*Time	15	5.939	41.77**
Plant	2	6.242	
Plant*Treatment	6	0.175	
Plant*Time	10	0.196	
Plant*Treatment*Time	30	0.142	
$Treatment:Time_1$		29.520	199.89**
$Treatment:Time_2$		29.380	198.93**
$Treatment:Time_3$		11.716	79.32*
$Treatment:Time_4$		59.469	402.63**
$Treatment:Time_5$		75.543	511.46**
$Treatment:Time_6$		82.884	561.16**
Total	70		

** Significance at 1% level, * Significance at 5% level, N.S. No Significance.

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