MORPHOLOGICAL, ANATOMICAL, AND PHYSIOLOGICAL RESPONSES OF POA PRATENSIS L. 'MERION' AND FESTUCA RUBRA L. 'PENNLAWN' TO REDUCED LIGHT INTENSITIES

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Morphological, Anatomical, and Physiological Responses of *Poa pratensis* L. 'Merion' and *Festuca rubra* L. 'Pennlawn' to Reduced Light Intensities

presented by

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ABSTRACT

MORPHOLOGICAL, ANATOMICAL, AND PHYSIOLOGICAL RESPONSES OF *POA PRATENSIS* L. 'MERION' AND *FESTUCA RUBRA* L. 'PENNLAWN' TO REDUCED LIGHT INTENSITIES

By

James Freeman Wilkinson

Kentucky bluegrass (*Poa pratensis* L.) and red fescue (*Festuca rubra* L.) are both capable of adequate growth in full sun, whereas red fescue usually provides a more suitable turf in the shade. The objectives of this investigation were to characterize the morphological, anatomical, and photosynthetic-respiratory responses of Merion Kentucky bluegrass and Pennlawn red fescue to reduced light intensities. It was anticipated this information might elucidate the shade adaptive mechanisms of red fescue. Light intensities of 2.7, 5.4, 10.8, 21.5, and 43 klux were established in separate growth chambers. Light quality, soil moisture, and soil temperature were standardized among growth chambers.

Morphological Responses

Leaf length of both cultivars increased with decreasing light intensity to 10.7 klux, but decreased at intensities below 10.7 klux. Each cultivar had narrower leaves with successive reductions in light intensity. Shoot angle was measured on plants grown singly. Both cultivars displayed a horizontal growth habit at high light intensities. The red fescue remained relatively horizontal under low light, whereas the Kentucky bluegrass exhibited a vertical growth habit.

Both cultivars responded similarly in terms of clipping, dry weight, leaf area, percent moisture, and chlorophyll content. Clipping weights decreased, and percent moisture increased under low light intensities. Clipping leaf area was greatest at 10.7 klux, and decreased at higher or lower light intensities. Chlorophyll/dm^2 decreased, but chlorophyll/g increased as light intensity was reduced.

Plant shoots and roots were separated following the final clipping. Shoot and root growth decreased under lower light intensities. However, the red fescue produced greater shoot weight than the Kentucky bluegrass under the lowest intensity, whereas the Kentucky bluegrass was superior at the highest light intensity. The Kentucky bluegrass produced less leaf area, fewer shoots/cm^2, and fewer tillers/plant with each decrement of lower light, while the red fescue produced equal numbers in these categories through 5.4 klux. Thus, Pennlawn red fescue was superior to Merion Kentucky bluegrass at low light intensities only in terms of shoot growth below the cutting height (verdure).

Anatomical Responses

Pennlawn red fescue displayed greater cuticle, vascular, and support tissue development at low light intensities. Stomatal density of both cultivars decreased under reduced light. Stomatal pore length did not vary with light intensity.

Chloroplast density decreased with reduced light intensity for both cultivars. The distribution of chloroplasts was not affected by light intensity. The Kentucky bluegrass displayed increased thylakoid and grana stack development at reduced light intensity, whereas the red fescue chloroplast ultrastructure remained unchanged.

Shade adaptation of Pennlawn red fescue may be related to greater development of the cuticle, vascular, and support tissues, and chloroplast ultrastructure. Stomatal and chloroplast size and distribution responses of the two cultivars to reduced light intensity were similar, and cannot be associated with the ability of Pennlawn red fescue to provide a more desirable turf than Merion Kentucky bluegrass in the shade.

Photosynthetic-Respiratory Responses

Infrared CO_2 analysis was used to measure assimilation rates of swards and individual plants. Both cultivars displayed decreased net photosynthesis (P_N) and dark respiration (R_D), lower light saturation levels, and lower light compensation points when grown under reduced light intensity. Swards generally had lower P_N and R_D rates, but higher light saturation levels and light compensation points than the individual plants.

Both cultivars responded similarly to reduced light intensity in terms of P_N, light saturation levels, and light compensation points. These factors could not be associated with the ability of Pennlawn red fescue to provide a more desirable turf than Merion Kentucky bluegrass in the shade. R_D of individual plants of the red fescue was reduced at the lowest light intensity, whereas the R_D of the Kentucky bluegrass was not. This response may contribute to the positive CO_2 balance of the red fescue at reduced light intensities, and thus to its shade adaptability.

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By

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To my wife Cheryl for her love and understanding through my years of graduate study.

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INTRODUCTION

Maintenance of an attractive turf in shade presents numerous difficulties for even the most skilled professional turfmen. A 1966 Pennsylvania survey of 326 golf courses indicated growing turf in shade to be the number one management problem (12). It has been estimated 20% of the turf grown in the U.S. is subjected to some degree of shade (3).

Kentucky bluegrass (*Poa pratensis* L.), the most widely grown cool season turfgrass, has not performed satisfactorily in shade in the past (4, 19). Red fescue (*Festuca rubra* L.), on the other hand, is capable of providing a more suitable turf in shade. It would be desirable to more fully understand the shade adaptive mechanisms of red fescue. If the mechanisms were elucidated, it may be possible to rapidly screen turfgrass species and cultivars for shade tolerance.

The objectives of this investigation were to study the morphological, anatomical, and photosynthetic-respiratory responses of Merion Kentucky bluegrass and Pennlawn red fescue to reduced light intensity. Each aspect was studied individually, and the results are presented in three separate sections. It was anticipated this information might elucidate some of the shade adaptive mechanisms of red fescue. Factors affecting the growth of turf in shade besides light intensity (light quality, soil moisture, disease, tree roots) were controlled or eliminated.

<u>POA</u> <u>PRATENSIS</u> L. 'MERION' AND <u>FESTUCA</u> <u>RUBRA</u> L. 'PENNLAWN' AT REDUCED LIGHT INTENSITIES: I. MORPHOLOGICAL RESPONSES

ABSTRACT

The objectives of the study were to characterize the morphological responses of Kentucky bluegrass and red fescue to reduced light intensity. Merion Kentucky bluegrass and Pennlawn red fescue were grown in separate growth chambers under light intensities of 2.7, 5.4, 10.7, 21.5, and 43 klux. Light quality, soil moisture, and soil temperature were standardized among chambers. Plants were clipped weekly at 5 cm for 14 weeks.

Leaf length and width were determined prior to clipping. Leaf length of both cultivars increased with decreasing light intensity to 10.7 klux, but decreased at intensities below 10.7 klux. Each cultivar had narrower leaves with successive reductions in light intensity. Shoot angle was measured on plants grown singly. Both cultivars displayed horizontal growth at high light intensity. The red fescue remained relatively horizontal under low light intensities, whereas the Kentucky bluegrass exhibited a vertical growth habit.

Clipping weight, percent moisture, leaf area, and chlorophyll content were determined after clipping. Both cultivars responded similarly. Clipping weights decreased, and percent moisture increased under lower light intensities. Clipping leaf area was greatest at 10.7 klux, and decreased at higher or lower light intensities. Chlorophyll/dm^2 decreased, but chlorophyll/g increased as light intensity decreased. The Kentucky bluegrass was comparable to the red fescue under low light intensity in all four of the above categories.

Plant shoots and roots were separated following the final clipping. Shoot and root production decreased under lower light intensities. However, the red fescue produced greater shoot weight than the Kentucky bluegrass under the lowest intensity, whereas the Kentucky bluegrass was superior at the highest light intensity. The Kentucky bluegrass produced less leaf area, fewer shoots/cm^2, and fewer tillers/plant with each decrement of lower light, whereas the red fescue produced equal numbers in these categories through 5.4 klux. Thus, Pennlawn red fescue was superior to Merion Kentucky bluegrass at low light intensities only in terms of shoot growth below the cutting height (verdure).

The superiority of red fescue under shade has been related to competition with tree roots, and the loss of Kentucky bluegrass due to disease infestation. These factors were not present in this study. Since the red fescue produced superior verdure under low light intensities, it must possess additional shade adaptation mechanisms.

INTRODUCTION

Both Kentucky bluegrass (Poa pratensis L.) and red fescue (Festuca rubra L.) form high quality turfs in full sun, but red fescue generally provides a more desirable turf under shaded conditions (3, 5). Maintenance of turf in shade presents unique problems. A 1966 Pennsylvania survey of 326 golf courses indicated growing turf in shade to be the number one turf problem (4). It has been estimated 20% of the turf grown in the U.S. is subjected to some degree of shade (2).

The morphological responses of grasses associated with reduced light intensities include: decreased shoot, root, rhizome, and stolon growth; reduced shoot density and tillering; decreased root to shoot ratio; thinner leaves; longer internodes; increased leaf length; and upright growth habit (3). Lighter green color and increased succulence also have been found under low light intensities. A comprehensive study comparing the morphological responses of Kentucky bluegrass and red fescue to reduced light intensity has not been made.

Wood (12) compared the growth of eight Kentucky bluegrass and eight red fescue cultivars in a controlled climate chamber study under light intensities from 2.4 to 32.3 klux. Shoot and root growth of both species was comparable at 16.2 and 32.3 klux. Red fescue cultivars generally outperformed Kentucky bluegrass cultivars at 2.4 and 5.4 klux. Wood reported both species responded to reduced light intensities by more flaccid, paler green, and narrower leaf blades. A field study also showed red fescue cultivars superior to Kentucky bluegrass cultivars in the shade. Beard (1) grew several turfgrass species and mixtures beneath shade trees. Red fescue was superior to Kentucky bluegrass in terms of turfgrass quality ratings and shoot density counts. Red fescue-Kentucky bluegrass mixtures were predominantly red fescue after two years. Wilson (11) grew red fescue, orchardgrass (Dactylis glomerata L.) and white clover (Trifolium repens L.) at light intensities of 2.2, 6.5, and 19.4 klux. Growth of orchardgrass and clover was reduced with each decrement of reduced light intensity. Red fescue grew as well at 6.5 as at 19.7 klux, indicating greater tolerance to reduced light intensities than orchardgrass or clover, but was seriously impaired at 2.2 klux.

Many aspects of the shade environment in addition to reduced light intensity affect turfgrass growth: altered light quality, moderation of temperature extremes, increased disease incidence, decreased wind movement and evapotranspiration, and tree root competition (3). The adaptive mechanisms of shade tolerant species may involve acclimation to these factors. Beard (1) has shown red fescue more disease tolerant than Kentucky bluegrass under shaded conditions. Although the red fescue was thinned by _Helminthosporium_ leafspot in its first year of growth, a more suitable turf resulted in subsequent years. Kentucky bluegrass was unable to survive due to powdery mildew (_Erysiphe graminis_ D.C.). Whitcomb (9) compared the clipping yields of Kentucky bluegrass, red fescue, rough bluegrass (_Poa trivialis_ L.), and perennial ryegrass (_Lolium perenne_ L.) beneath shade trees, with and without tree root competition. Kentucky bluegrass shoot growth was impaired more by the tree roots than the other species. Whitcomb and Roberts (10) demonstrated Kentucky bluegrass rooting to be severely restricted by trees having shallow feeder roots.

The objectives of this study was to characterize the morphological responses of Merion Kentucky bluegrass and Pennlawn red fescue to reduced light intensities. Other factors influencing turfgrass growth in shade (altered light quality, disease incidence, soil temperature and moisture levels, tree root competition) were eliminated. It was anticipated this information might give further insight into shade adaptation mechanisms of red fescue.

MATERIALS AND METHODS

Light

Light intensities of 2.7, 5.4, 10.7, 21.5, and 43 klux (1.4, 2.4, 5.0, 7.5, and 11.4 x 10^3 μw cm^{-2}, respectively) were established in separate growth chambers. Preliminary studies indicated 2.7 klux was the lowest light intensity at which Merion Kentucky bluegrass could persist. A Weston Illumination Meter, Model 765, and a YSI-Kettering, Model 65 Radiometer were used for the light measurements. A 14 hr photoperiod was used.

Light quality was first standardized among the chambers utilizing similar make bulbs and the same proportion of fluorescent to incandescent bulbs. An ISCO, Model SR Spectroradiometer indicated only slight variation in light quality among chambers. The variation in light quality within each chamber was not significant. The light was weak in the red and blue regions, strong in the green and infrared (Figure I.1). A similar light quality has been found beneath deciduous tree canopies (8).

Light intensities were established by raising and lowering chamber shelves. Plant material at 43 klux was within 0.50 m of the bulbs. Leaf temperature, measured with a Stoll-Hardy, Model HL4 Radiometer, and canopy temperature, measured with a copper/constantan thermocouple and potentiometer, were no more than 2 C above the soil temperature.

Separate growth chambers were used for each light intensity in order to establish uniform soil temperatures, and to avoid the use of shading materials or screens which may significantly alter the turfgrass microenvironment.

Light intensity varied markedly within each chamber, with variation increasing toward the chamber sides. All plant material was kept close to the center of the chamber, and was rotated every other day.

Soil

A sandy loam soil mix was used. Soil temperatures were maintained at 20 C, and were monitored using a bulb thermometer inserted 5 cm into the soil.

Uniform soil moisture was maintained utilizing 1.25 cm tensiometers (Irrometer Company, Riverside, California). The tensiometers were inserted into pots seeded with Kentucky bluegrass. Data were not taken from these pots. Soil moisture levels were monitored with the tensiometers, and all pots watered accordingly. All pots were saturated weekly with a complete Hoagland's solution (6).

Plant Material

Merion Kentucky bluegrass and Pennlawn red fescue were seeded in 10 cm diameter (12 cm depth) plastic pots at 3 seeds/cm^2. Seeds were germinated in a greenhouse. Three replications of each cultivar were placed under each light intensity when the seedlings were 1 cm in height. Additional pots were thinned to one seed per pot for shoot angle determinations.

Parameters Measured

After plants reached 5 cm in height, clippings above 5 cm were collected weekly using hand clippers with a collection pan attached. Several measurements were made prior to weekly clipping. (a) Average leaf length above the 5 cm cutting height. (b) Leaf width was measured on the youngest fully expanded leaf, 1 cm from the leaf collar. Leaf widths were placed into classes of 0-0.5, 0.5-1, 1-1.5, 1.5-2, and > 2 mm. Three measurements were taken for each replication. (c) Shoot angle. Shoot angle was difficult to estimate on plants within an established turf. Pots with a single plant were included under each light intensity. Shoot angle determinations were made prior to weekly clipping at 5 cm, vertical being 0°, horizontal 90°.

Leaf clippings were collected and placed in plastic bags to prevent desiccation. Several parameters were measured. (d) Total fresh weight. (e) Leaf area. A 10 to 20 leaf subsample was taken from the fresh clippings. Fresh weight was determined, the leaves taped to paper, and a photocopy made. Leaf area of the subsample was then estimated using a planimeter. The leaf area: leaf weight ratio established for the subsample was used to estimate the total clipping leaf area. The estimate included only one leaf surface. (f) Chlorophyll content. A second subsample (approximately 1 g) was removed from the fresh clipping sample, weighed, placed in a flask, and covered with 50 ml of methanol. The flasks were stoppered and left in a dark cabinet overnight. Samples were then ground for two minutes in a Virtis Mixer, Model 45, filtered under vacuum, and brought to a volume equivalent to 1 liter. Absorbancy was measured at 650 and 665 nm with a

Perkin-Elmer, Model 27 Spectrophotometer. MacKinney's (7) formula for total chlorophyll in methanol solutions was utilized. Chlorophyll was expressed as mg/dm^2 and mg/g dry weight. (g) Dry weight. The remaining fresh clippings were weighed, dried at 70 C, and reweighed. Dry weight was determined including subsamples taken for leaf area and chlorophyll estimations. (h) Percent moisture on a fresh weight basis was determined.

The final clipping was made 14 weeks after germination. All plants were cut off at the soil surface and several parameters determined. (i) Total fresh weight. (j) Number of shoots/pot. (k) Number of tillers/plant. (l) Leaf area, determined using the same technique described for clipping leaf area. (m) Dry weight, determined as previously described. (n) Root dry weight. Four subsamples were removed from each pot, using a 1.5 cm circular soil sampling device. The soil and roots were dried at 70 C, ashed at 500 C, and reweighed. The loss in weight, corrected for the original soil organic matter content, was taken as root weight. The sides and bottom of the pots were avoided when the soil samples were taken.

Statistical Analysis

A completely randomized block analysis of variance was made on the two cultivars at each light intensity. The determined variances at each light intensity were pooled, and a single LSD value (.05 level) was determined for each parameter measured.

RESULTS

Clippings were collected weekly between the 5th and 14th week following germination. Cultivar responses to reduced light intensities were similar throughout this period. Results presented are those obtained during the 11th week.

Leaf length above the cutting height increased with decreasing light intensity to 10.7 klux (Figure I.2). Leaf length decreased at the two lower light intensities. Although both cultivars responded similarly, the red fescue leaf length was less than the Kentucky bluegrass at any one light intensity. Leaf width (Figure I.2) decreased with each decrement of decreasing light. The response of the two cultivars was similar.

Shoot angle measurements are shown in Table I.1. The angle measured was the angle of the shoot from the vertical. Both cultivars displayed a horizontal growth habit at the higher light intensities. The Kentucky bluegrass had an upright growth habit under low light intensities, whereas the red fescue remained relatively horizontal.

Both cultivars responded similarly in clipping dry weight and percent moisture (Figure I.3). Clipping dry weight was maintained under decreasing light intensity to 10.7 klux, but declined rapidly below 10.7 klux for both cultivars. The Kentucky bluegrass produced more leaf growth than the red fescue at light intensities greater than 10.7 klux, but there was no difference below 10.7 klux. Percent moisture of both cultivars increased with each decrement of reduced light, ranging from 68% at 43 klux, to 83% at 2.7 klux.

Clipping leaf area (Figure I.4) increased with decreasing intensities to 10.7 klux, and then decreased under lower light intensities. The increased leaf area was due to the extended leaf length. The Kentucky bluegrass had a greater clipping leaf area than the red fescue above 10.7 klux, whereas the two cultivars did not differ below 10.7 klux.

Both cultivars responded similarly in terms of chlorophyll content (Figure I.5). Chlorophyll/dm^2 decreased with decreasing light intensities. This decrease corresponded with the lighter green color of leaves observed at the lower light intensities. Chlorophyll/g dry wt. increased with each decrement of decreasing light intensity.

Dry shoot weight below the cutting height and root weight are shown in Figure I.6. While shoot growth of the Kentucky bluegrass was greater than the red fescue at the highest light intensity, the red fescue outperformed the Kentucky bluegrass at the lowest intensity. Root growth was reduced under low light (Figure I.6). No difference could be found in the root production between the two cultivars. The most marked reduction in the root-shoot ratio occurred between 43 and 21.5 klux for both cultivars.

Merion Kentucky bluegrass had decreased leaf area below the cutting height with each decrement of reduced light intensity (Figure I.4). Pennlawn red fescue maintained leaf area under decreasing light to 10.7 klux. Although leaf area of the red fescue decreased below 10.7 klux, the reduction was less for the red fescue than the Kentucky bluegrass at 2.7 and 5.4 klux.

The shoot density of the Kentucky bluegrass declined below 21.5 klux, whereas shoot density of the red fescue did not decline until the light intensity was lower than 5.4 klux (Figure I.7). Tillering of the Kentucky bluegrass was severely restricted at light intensities below 21.5 klux (Figure I.7). Tillering of the red fescue did not appear to be affected by light intensities as low as 5.4 klux.

DISCUSSION

Merion Kentucky bluegrass and Pennlawn red fescue responded differently to reduced light intensity in terms of shoot weight and leaf area below the cutting height, tillers/plant, shoot density, and leaf angle. The red fescue produced superior verdure at the lower light intensities, thus providing a more suitable turf. Shoot density and tillering of the red fescue did not decline until light intensities were below 5.4 klux. Perhaps more shade tolerant ground cover species should be used at light intensities below 5.4 klux if there is no sunflecking.

The Kentucky bluegrass displayed an upright growth habit under low light intensities, whereas the red fescue remained relatively horizontal. A shade adaptive mechanism of red fescue may be involved. The more horizontal growth habit of red fescue shoots may enhance light interception within the shade environment. Also, less photosynthetically active, young leaf tissue will be removed by mowing.

The two cultivars responded similarly to reduced light intensities in the following parameters: leaf length, leaf width, clipping area, clipping yield, percent moisture, chlorophyll content, and root growth. The Kentucky bluegrass was superior at the higher light intensities in terms of leaf length, clipping weight, and clipping leaf area. Although the red fescue provided a better turf than the Kentucky bluegrass in shade, the Kentucky bluegrass was comparable to the red fescue at low light intensities in terms of vertical shoot growth above the cutting height and root production.

The marked increase in percent moisture of leaf tissue within the shade environment may contribute to increased disease susceptibility. Plant factors besides succulence must be involved in disease susceptibility, since the response of both cultivars was similar. Red fescue does possess more disease resistance in shade than Kentucky bluegrass (1).

Disease resistance and the ability to compete with tree roots have been studied as possible explanations for the favorable shade adaptation characteristics of red fescue (1, 9, 10). Tree root competition was not a factor in this investigation, and disease was not observed at any time. Red fescue must possess additional shade adaptive mechanisms. These mechanisms may involve anatomical responses, photosynthetic efficiencies, and respiration rates.

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TABLE I.1.--Shoot angle of singly grown plants of Merion Kentucky bluegrass and Pennlawn red fescue at five light intensities. Vertical = 0°, horizontal = 90°. LSD = 12.6.

Light intensity, lux X 10^3	Shoot angle (degrees)	
	Kentucky bluegrass	Red fescue
2.7	20	38
5.4	25	55
10.7	30	60
21.5	70	70
43.1	75	80

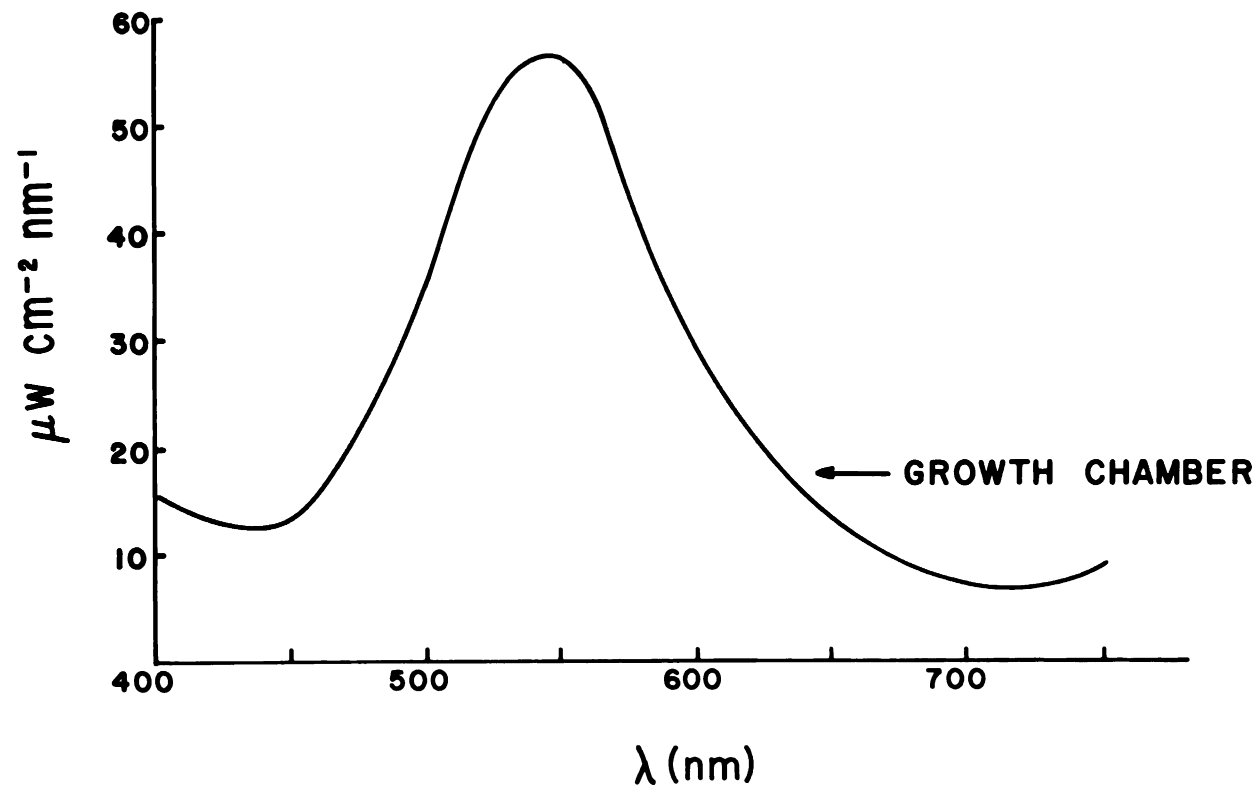

Fig. I.1.--Spectral distribution within the growth chambers.

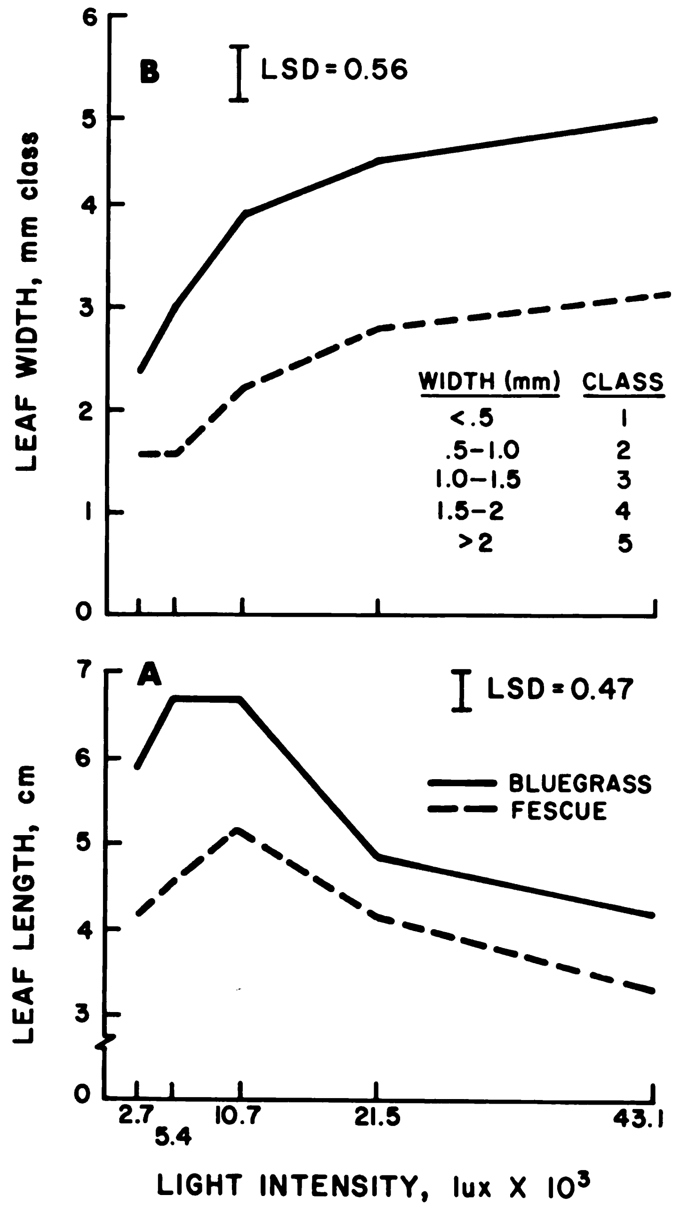

Fig. I.2.--(A) Average leaf length (cm) above cutting height, and (B) leaf width measured on the youngest, fully expanded leaf 1 cm from the collar prior to weekly clipping of Merion Kentucky bluegrass and Pennlawn red fescue at five light intensities. Leaf widths were placed into classes.

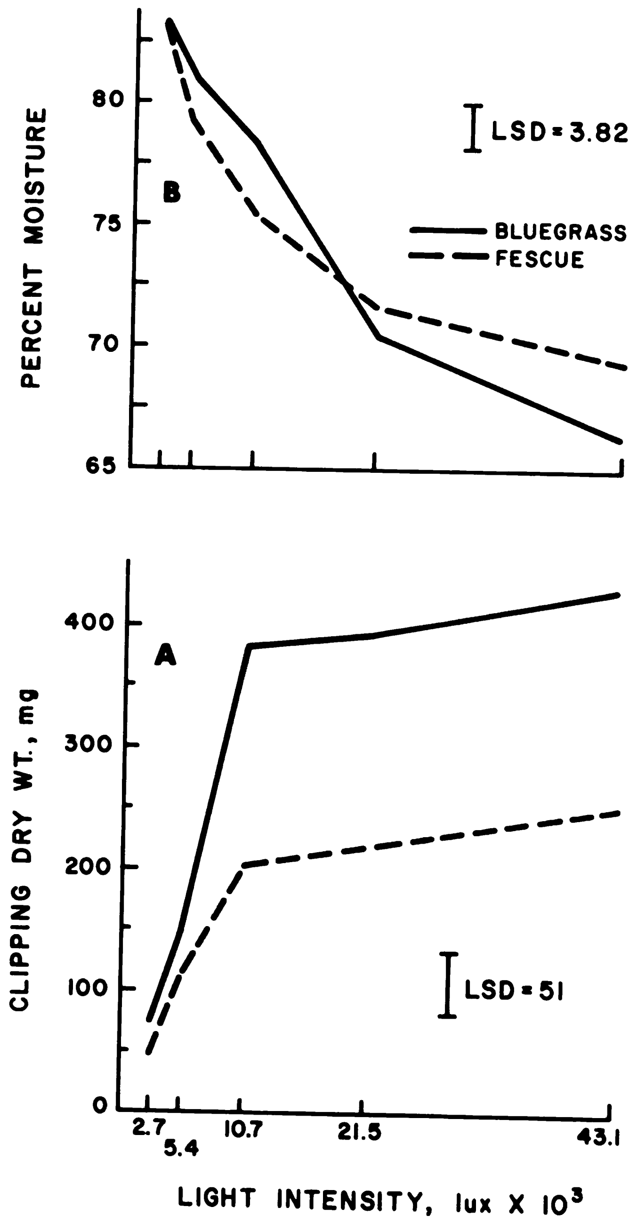

Fig. I.3.--(A) Clipping dry wt. (mg/pot) above 5 cm after 1 week's regrowth, and (B) clipping percent moisture on a fresh weight basis of Merion Kentucky bluegrass and Pennlawn red fescue at five light intensities.

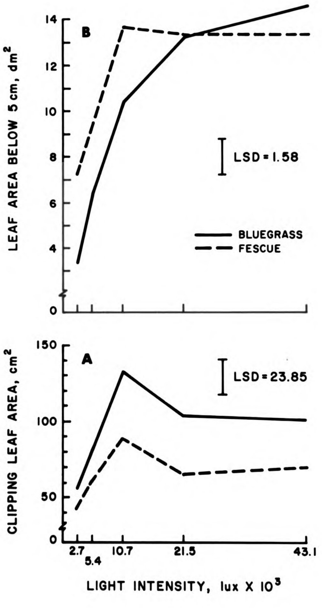

Fig. I.4.--(A) Leaf area (cm^2) of clippings collected above 5 cm after 1 week's regrowth, and (B) leaf area (dm^2) below 5 cm 14 weeks after germination of Merion Kentucky bluegrass and Pennlawn red fescue at five light intensities.

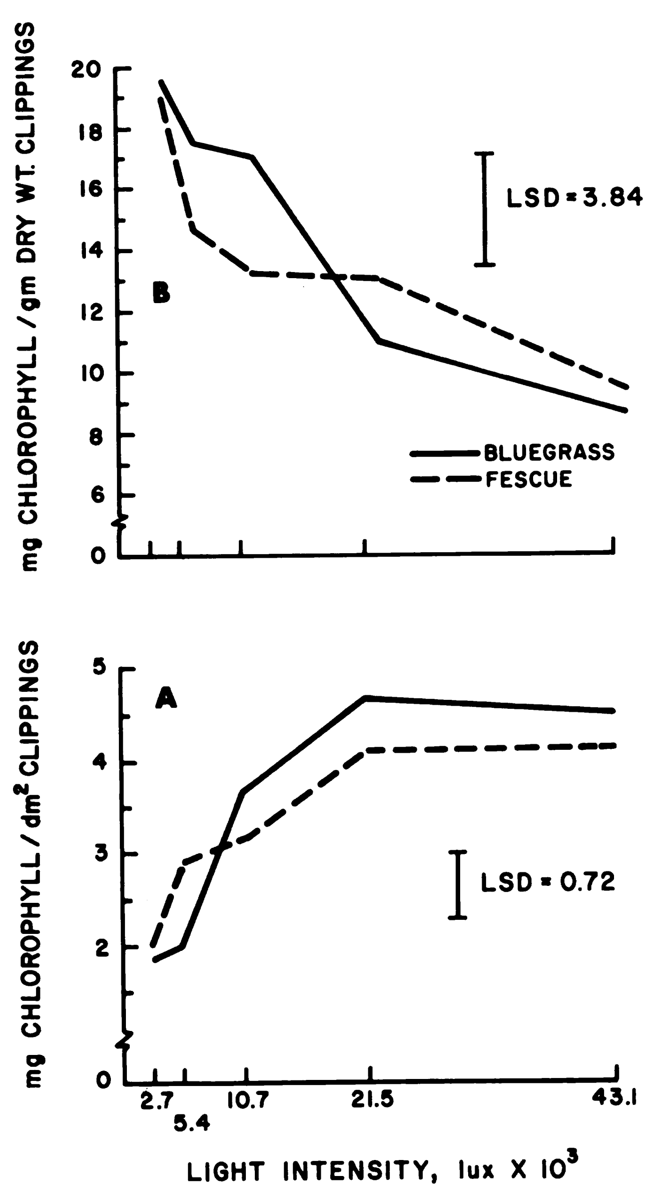

Fig. I.5.--(A) Milligrams total chlorophyll/dm^2, and (B) mg chlorophyll/g dry wt. of clippings of Merion Kentucky bluegrass and Pennlawn red fescue grown at five light intensities.

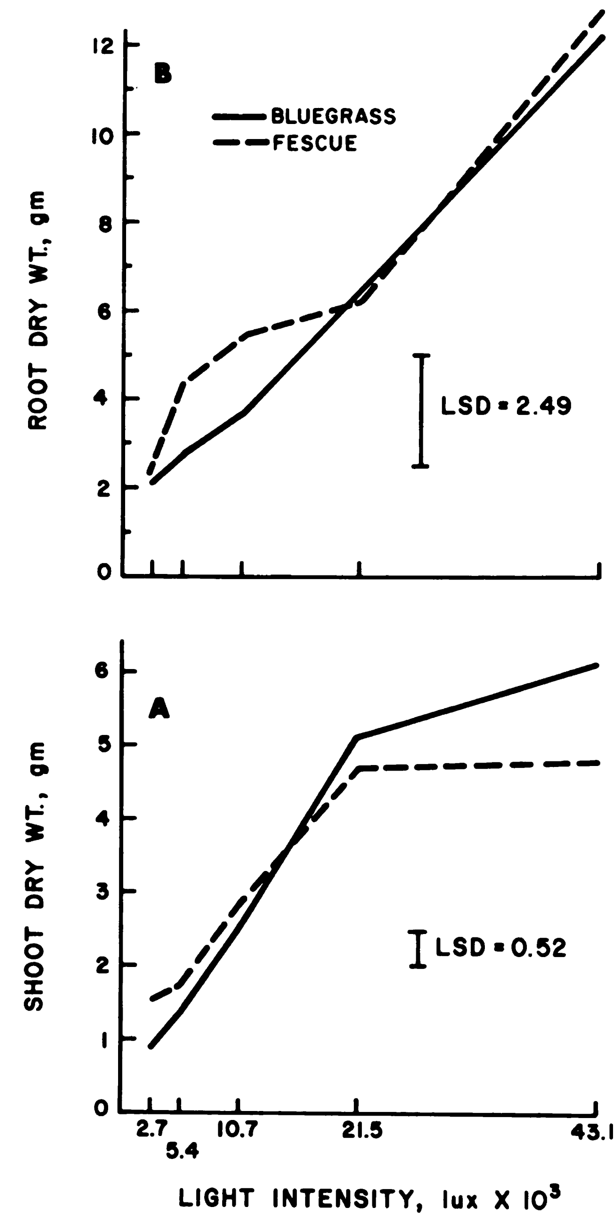

Fig. I.6.--(A) Shoot dry wt. (g/pot) below 5 cm, and (B) root dry wt. (g/pot) 14 weeks after germination of Merion Kentucky bluegrass and Pennlawn red fescue at five light intensities.

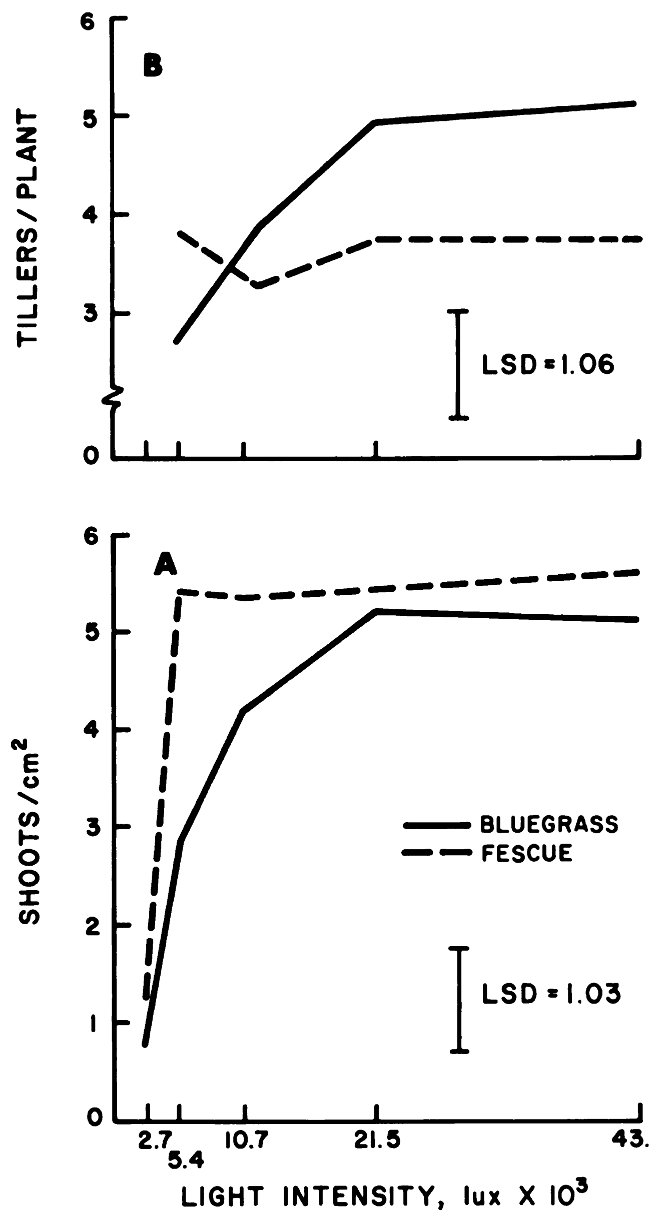

Fig. I.7.--(A) Shoots/cm^2, and (B) average number of tillers/plant 14 weeks after germination of Merion Kentucky bluegrass and Pennlawn red fescue grown at five light intensities.

POA PRATENSIS L. 'MERION' AND *FESTUCA RUBRA* L. 'PENNLAWN' AT REDUCED LIGHT INTENSITIES: II. ANATOMICAL RESPONSES

ABSTRACT

The objectives were to characterize the anatomical responses of Kentucky bluegrass and red fescue to reduced light intensities. Merion Kentucky bluegrass and Pennlawn red fescue were grown in separate growth chambers at light intensities of 2.7, 10.8, and 43 klux. Light quality, soil moisture, and soil temperature were standardized among growth chambers. Anatomical studies were conducted on the youngest, fully expanded leaf.

The red fescue had more developed cuticle, vascular, and support tissues at low light intensities. Cuticle development in red fescue at low light intensity may be an important consideration in disease resistance. Stomatal density of both cultivars decreased under reduced light intensity. Stomatal pore length did not vary with light intensity. Chloroplast density decreased with reduced light intensity for both cultivars. The distribution of chloroplasts was not affected by light intensity. The Kentucky bluegrass had increased thylakoid and grana stack

development at reduced light intensity, whereas the red fescue chloroplast ultrastructure remained unchanged.

Shade adaptation of red fescue may be related to development of cuticle, vascular, and support tissue, and to chloroplast ultrastructure. Stomatal and chloroplast size and distribution responses of the two cultivars to reduced light intensity were similar, and could not be associated with the ability of the red fescue to provide a more desirable turf than the Kentucky bluegrass in the shade.

INTRODUCTION

The superiority of red fescue (*Festuca rubra* L.) over Kentucky bluegrass (*Poa pratensis* L.) in providing a desirable turf in shade is well documented (2, 15). Loss of Kentucky bluegrass in the shade environment has been related to disease incidence (1) and tree root competition (13, 14).

Reduced light intensity alters the anatomy of plants in numerous ways: thinner, narrower leaf blades (3, 4, 6, 7, 11); less cross sectional leaf area (6, 7, 10); thinner mesophyll (3, 6, 10, 11); smaller epidermal cells (6, 8); thinner cell walls (8); reduced vascular tissue development (4, 5, 6, 11); changes in stomata frequency and size (3, 4, 11); and alteration of chloroplast size and structure (3, 4, 5, 8).

Reductions in light intensity generally decrease stomata numbers, but increase their size (3, 11). CO_2 transfer through larger stomata may compensate for decreased density at reduced light intensities. However, Björkman et al. (4) working with Atriplex patula L. at reduced light intensities, did not observe an increase in either stomata pore size or guard cell size.

Goodchild, Björkman, and Phyliotis (8) observed more chloroplasts in the mesophyll cells adjacent to the upper epidermis in several rainforests species. Chloroplasts also appeared to be large and dark green. Björkman et al. (4) found only half as many chloroplasts in leaf cross sections of A. patula under reduced light intensity. The chloroplasts appeared to be larger under low light intensities.

Björkman and Holmgren (3) studied ecotypes of Solidago virgaurea L. from exposed and shaded habitats. The exposed ecotypes displayed normal chloroplast structure under high and low light. In contrast, the shaded ecotypes had pale, irregular, fragmented chloroplasts when exposed to high light intensities. Cormack (5) observed the chloroplasts of exposed leaves of Vicia americana Muhl. to be discernable by either transmitted or phase-contrast illumination. The chloroplasts from shaded leaves were not visible using transmitted light, but were clearly defined using phase-contrast. He suggested there may be a difference in the state of the cytoplasm in which the chloroplasts were embedded.

Chloroplast ultrastructure appears to be altered at reduced light intensity. Goodchild et al. (8) found the chloroplasts of rainforest species to contain large, well developed grana stacks, with many thylakoids. The grana also appeared to be irregularly oriented, and not in one plane as usually found. Björkman et al. (4) found more thylakoids per grana stack in A. patula at reduced light intensity. He correlated decreased carboxydismutase activity with decreased volume of stroma per chloroplast. This may contribute to a decrease in the CO_2 fixing capability under low light.

The objectives of this investigation were to characterize the anatomical responses of Merion Kentucky bluegrass and Pennlawn red fescue to reduced light intensities. This information might elucidate some of the shade adaptation mechanisms of red fescue. Other shade associated factors influencing growth (altered light quality, disease incidence, soil temperature and moisture levels, tree root competition) were controlled or eliminated in this study.

MATERIALS AND METHODS

The experimental conditions were similar to those described in an earlier study (15).

Light

A 14 hour photoperiod was used. Light intensities of 2.7, 10.8, and 43 klux (1.4, 5.0, and 11.4 x 10^3 μw cm^{-2}, respectively) were established in separate growth chambers. Both Merion Kentucky bluegrass and Pennlawn red fescue provided a good turf at 43 klux in an earlier study (15). The growth of the Kentucky bluegrass was impaired at 10.8 klux, whereas the red fescue still maintained a dense turf. Although neither cultivar performed well at 2.7 klux, the red fescue was superior to the Kentucky bluegrass in terms of verdure, leaf area, shoot density, and tillers per plant.

Light quality was standardized for the three chambers utilizing similar bulbs and the same proportion of fluorescent to incandescent bulbs. An ISCO, Model SR

Spectroradiometer indicated only slight variations among or within chambers. The light was weak in the red and blue wavelengths, but strong in the green and infrared (15).

Light intensities were established by raising and lowering chamber shelves. Plant material at 43 klux was within 0.50 m of the bulbs. Leaf temperature, measured with a Stoll-Hardy, Model HL4 Radiometer, and canopy temperature, measured with a copper/constantan thermocouple and potentiometer, were no more than 2 C above the soil temperature (maintained at 20 C).

Separate growth chambers were used for each light intensity in order to establish uniform soil temperatures, and to avoid the use of shading materials or screens that can significantly alter the turfgrass microenvironment. Light intensity varied markedly within each chamber, with variation increasing toward the chamber sides. All plant material was kept in the center of the chamber, and the individual pots rotated every other day.

Soil

A sandy loam soil mix was used. Soil temperatures were maintained at 20 C, and were monitored using a bulb thermometer inserted 5 cm into the soil. Uniform soil moisture was maintained utilizing 1.25 cm tensiometers (Irrometer Company, Riverside, California). The tensiometers were inserted into separate pots seeded with Kentucky bluegrass. Soil moisture levels were monitored with the tensiometers, and all pots irrigated accordingly. All pots were saturated weekly with a complete Hoagland's solution.

Plant Material

Merion Kentucky bluegrass and Pennlawn red fescue were seeded in 10 cm diameter (12 cm depth) plastic pots at 3 seeds/cm^2. Seeds were germinated in a greenhouse and placed under each light intensity when seedlings were 1 cm in height. Plants were mown periodically at 5 cm. Occasional applications of Karathane® were made for powdery mildew (*Erysiphe graminis* D.C.) control. Plants were preconditioned for six weeks prior to sampling. Sampling lasted three weeks.

Parameters Measured

The youngest, fully expanded leaf was removed for sectioning. Fresh leaf tissue was sectioned using a Lab Line/Hooker Plant Microtome (9). The sections were fixed with FAA, and stained with safranin-fast green. Sections were traced from photographs. The tracings were cut out and weighed to determine the relative proportions and size of epidermal, mesophyll, vascular, and support tissue.

Stomatal density and size was determined using the method of Shearman and Beard (12). A nitrocellulose impression was made of the adaxial and abaxial surfaces of the youngest, fully expanded leaf. Stomata were observed at 400 X. Counts were taken randomly between the leaf edge and midvein.

Chloroplast ultrastructure was observed with a transmission electron microscope. One mm^2 sections were cut from the youngest, fully expanded leaf, and fixed in 5% glutaraldehyde in a 0.1 M phosphate buffer. The sections were subsequently fixed in 2% osmium tetroxide, dehydrated in an ethanol series, and embedded in an epoxy resin. The resin was polymerized at 50 C and sections cut 600-800 A°. thick. Chloroplasts were observed at 60 kv.

Statistical Analysis

Four replications of the cross sections, and eight of the stomatal impressions were used. A completely randomized block analysis of variance was made on the two cultivars at each light intensity. The determined variance at each light intensity was pooled, and a single LSD value (.05 level) was determined for each parameter measured.

RESULTS AND DISCUSSION

Cuticle

Both cultivars had a well defined cuticle at 43 klux, although the cuticle of the red fescue was about twice as thick as that of the Kentucky bluegrass. Leaf cross sections of the red fescue grown at 10.8 klux still had a well developed cuticle layer, whereas the cuticle of the Kentucky bluegrass was thin (Figure II.1). Neither cultivar had a well developed cuticle layer at 2.7 klux.

Disease infestation, particularly by powdery mildew, has been shown to be a major factor in the loss of Kentucky bluegrass in the shade (1). The ability of Pennlawn red fescue to produce a cuticle layer at reduced light intensities may contribute to disease resistance.

Epidermis

Both cultivars had thinner epidermal cells at reduced light intensities. The degree of reduction was similar for the two cultivars.

Leaf Tissues

The percentages of the cross sectional leaf area, composed of epidermal, mesophyll, vascular, and support tissues, are shown in Table II.1. Percent epidermal tissue increased, but mesophyll decreased under reduced light for both cultivars. The Kentucky bluegrass had a significant decrease in vascular and support tissue under decreased light, whereas the red fescue did not.

Greater development of vascular and support tissues in Pennlawn red fescue at reduced light intensity may contribute to shade adaptation. Improved vascular tissue development may lead to more rapid movement of water, nutrients, and photosynthate. Additional support tissue at reduced light intensity may impart increased wear tolerance.

Stomata

Both cultivars had decreased stomata density on the adaxial and abaxial leaf surfaces under reduced light (Table II.2). The red fescue stomata density ranked lower than that of the Kentucky bluegrass at all light intensities. Stomata pore length did not vary with light intensity (Table II.3), although the stomata of the red fescue were larger than those of the Kentucky bluegrass at all light intensities. Stomata responses could not be related to the red fescue shade adaptation.

Chloroplasts

The number of chloroplasts per cross sectional unit area decreased under reduced light for both cultivars (Figures II.2 and II.3). This is in accordance with the decrease in chlorophyll/dm^2 found earlier. Light intensity did not affect the distribution of chloroplasts within the cross sections.

The chloroplasts of both cultivars grown at 43 klux were distinct when observed under the light microscope (Figures II.2 and II.3). Chloroplasts of the red fescue grown at 2.7 klux remained distinct (Figure II.3), whereas the Kentucky bluegrass chloroplasts were not discernable when grown at the same light intensity (Figure II.2). Cormack (5) made a similar observation in *V. americana*.

Chloroplast ultrastructure was observed with a transmission electron microscope (Figures II.4 and II.5). The percent of chloroplast cross sectional area composed of grana stacks was significantly increased in Merion Kentucky bluegrass when grown at reduced light intensity (Table II.4). The percentage did not increase significantly in Pennlawn red fescue chloroplasts under low light. An increase in the number of thylakoids per grana stack was associated with the increased area of grana in the Kentucky bluegrass (Table II.5). This response has been found in other species at reduced light intensity (4, 8). Björkman et al. (4) correlated decreased carboxydismutase activity in *A. patula* with increased volume of grana (decreased volume of stroma). This could contribute to decreased CO_2 fixing capacity under low light.

In conclusion, Merion Kentucky bluegrass and Pennlawn red fescue displayed many typical anatomical responses to reduced light intensity. The red fescue differed from the Kentucky bluegrass at reduced light intensities in terms of cuticle, vascular, and support tissue development, and chloroplast ultrastructure. These factors may play important roles in the shade adaptation of Pennlawn red fescue. Increased stomata size (3, 11) and altered chloroplast distribution (8) also have been related to shade tolerance in other species. The responses of the two cultivars to these factors were similar, and they could not be associated with the ability of the red fescue to provide a more desirable turf than the Kentucky bluegrass in the shade.

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TABLE II.1.--The percentages of total cross sectional leaf area composed of epidermal, mesophyll, vascular, and support tissues of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Species	Light intensity (klux)	% of cross section area			
		Epidermal	Mesophyll	Vascular	Support
Kentucky bluegrass	43	31.15	58.73	6.42	4.45
	10.8	34.86	57.09	5.67	2.39
	2.7	39.29	55.53	3.45	1.36
Red fescue	43	21.40	68.00	5.89	4.70
	10.8	22.70	67.50	5.68	4.12
	2.7	29.00	62.30	4.62	3.80
LSD (.05)		7.42	7.01	1.88	1.90

TABLE II.2.--Number of stomata/mm^2 on the adaxial and abaxial leaf surfaces of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Species	Light intensity (klux)	Stomata/mm^2 leaf surface adaxial	Stomata/mm^2 leaf surface abaxial
Kentucky bluegrass	43	208	88
	10.8	200	16
	2.7	168	0
Red fescue	43	176	8
	10.8	128	8
	2.7	104	0
LSD (.05)		38.5	16.8

TABLE II.3.--Stomatal pore length (microns) on the adaxial leaf surface of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Species	Light intensity (klux)	Stomatal length (microns)
Kentucky bluegrass	43	26.8
	10.8	26.3
	2.7	25.9
Red fescue	43	35.6
	10.8	34.4
	2.7	33.8
	LSD (.05)	4.3

TABLE II.4.--Percent of chloroplast cross sectional area composed of grana stacks of Merion Kentucky bluegrass and Pennlawn red fescue grown at two light intensities.

Species	Light intensity (klux)	Chloroplast area (% of grana stacks)
Kentucky bluegrass	43	11.27
	2.7	29.48
Red fescue	43	13.86
	2.7	17.76
LSD (.05)		10.42

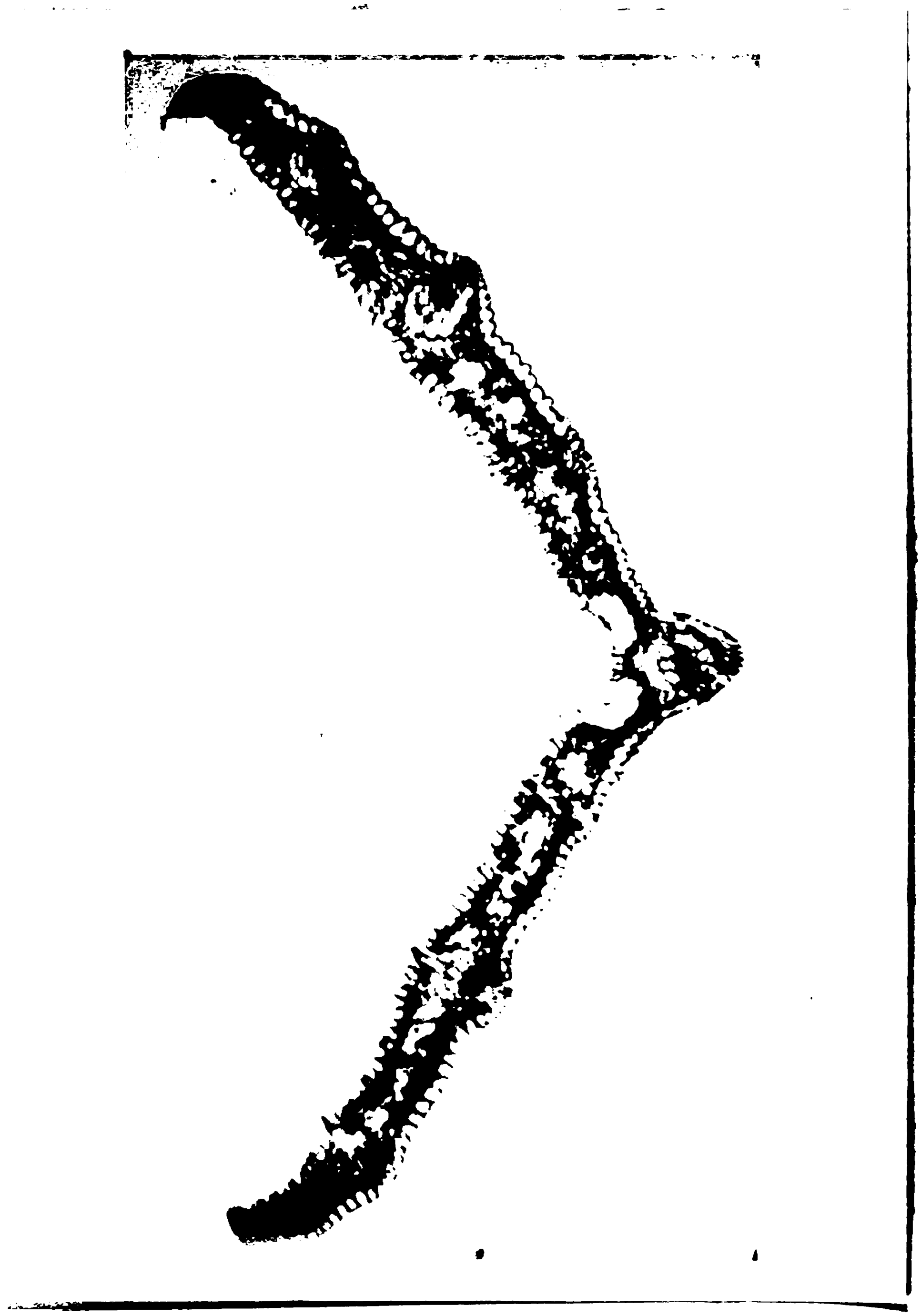

Fig. II.1. (A)

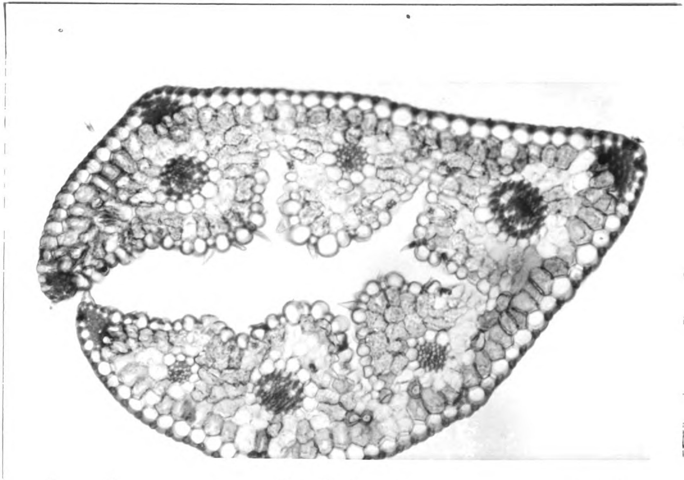

Fig. II.1. (B)

Fig. II.1.--Merion Kentucky bluegrass (A) and Pennlawn red fescue (B) leaf cross sections grown at 10.8 klux. Note the well defined cuticle layer of red fescue. X40.

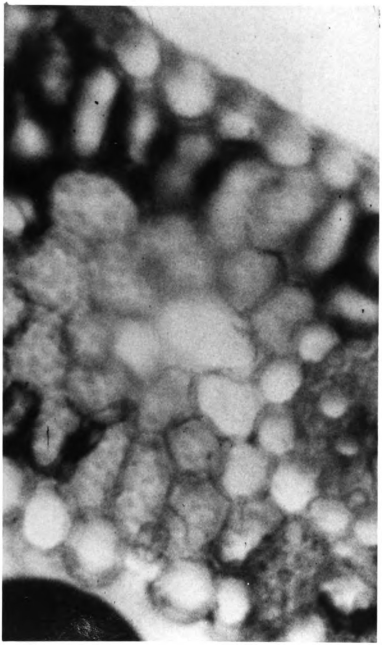

Fig. II.2. (A)

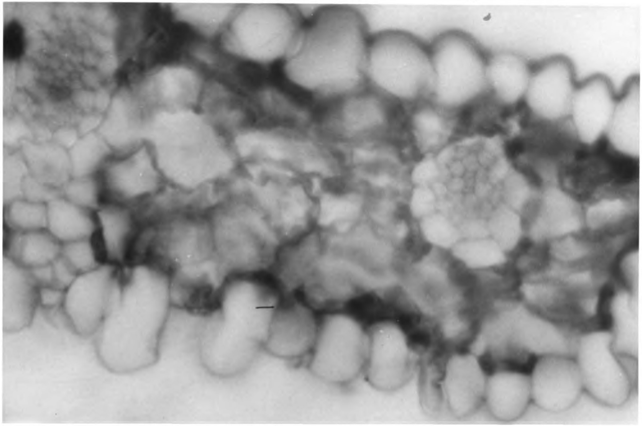

Fig. II.2. (B)

Fig. II.2.--Merion Kentucky bluegrass leaf cross sections grown at 43 (A) and 2.7 (B) klux. X400.

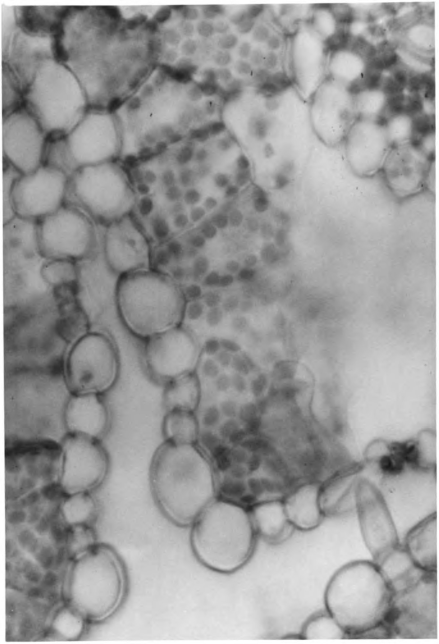

Fig. II.3. (A)

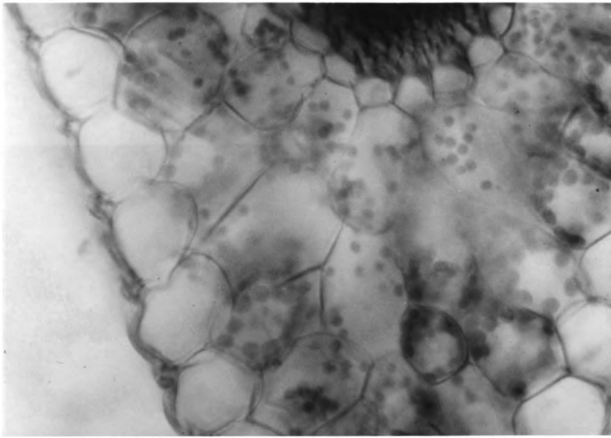

Fig. II.3. (B)

Fig. II.3.--Pennlawn red fescue leaf cross sections grown at 43 (A) and 2.7 (B) klux. X400.

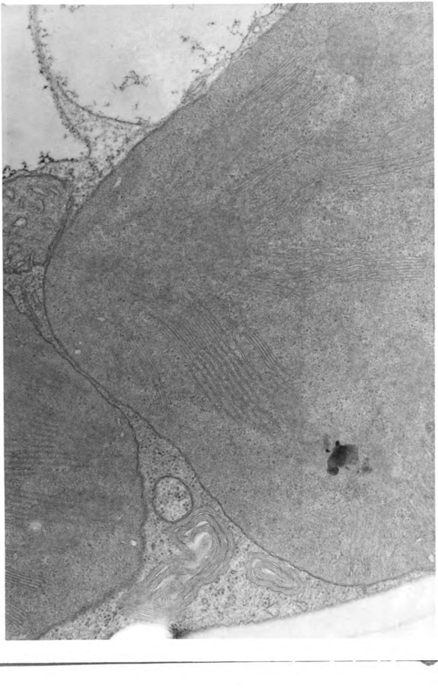

Fig. II.4. (A)

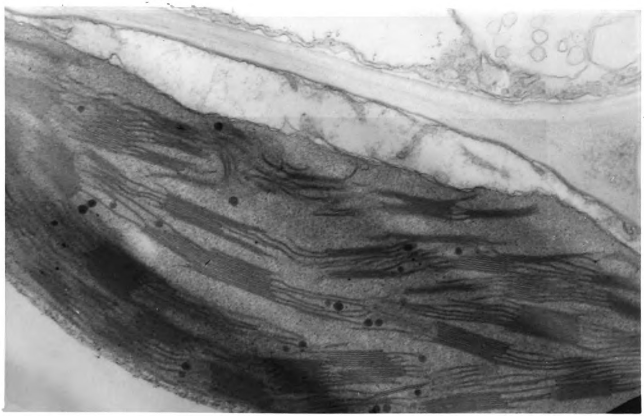

Fig. II.4. (B)

Fig. II.4.--Transmission electron micrographs of Merion Kentucky bluegrass chloroplasts grown at 43 (A) and 2.7 (B) klux. X21,000.

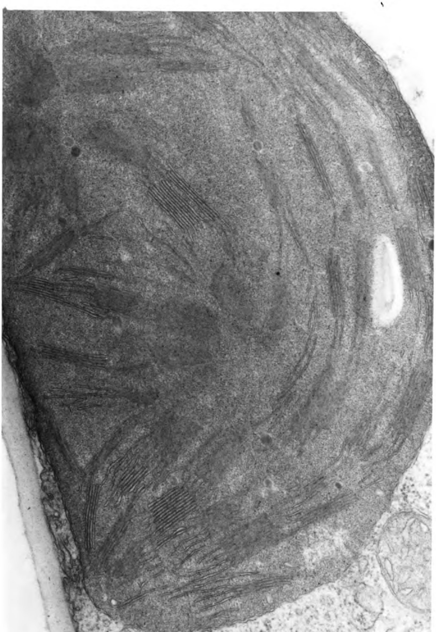

Fig. II.5. (A)

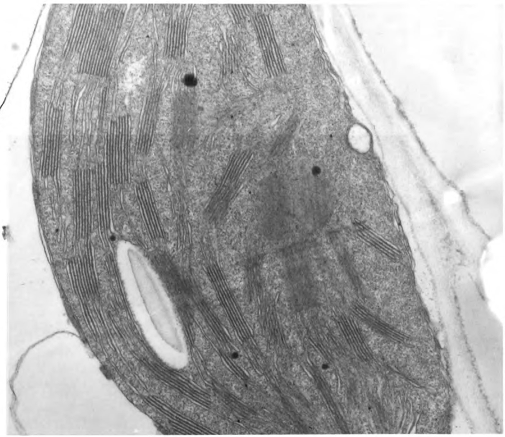

Fig. II.5. (B)

Fig. II.5.--Transmission electron micrographs of Pennlawn red fescue chloroplasts grown at 43 (A) and 2.7 (B) klux. X21,000.

POA PRATENSIS L. 'MERION' AND *FESTUCA RUBRA* L. 'PENNLAWN' AT REDUCED LIGHT INTENSITIES:

III. PHOTOSYNTHETIC-RESPIRATORY RESPONSES

ABSTRACT

The objectives were to characterize the photosynthetic-respiratory responses of Kentucky bluegrass and red fescue to reduced light intensities. Merion Kentucky bluegrass and Pennlawn red fescue were grown in separate growth chambers at light intensities of 2.7, 10.8, and 43 klux. Light quality, soil moisture, and soil temperature were standardized among chambers. Infrared CO_2 analysis was used to measure assimilation rates, light saturation levels, and light compensation points of swards and individual plants.

Both cultivars displayed decreased net photosynthesis (P_N) and dark respiration (R_D), lower light saturation levels, and decreased light compensation points under reduced light intensity. Swards generally had lower P_N and R_D rates, but higher light saturation levels and light compensation points than individual plants.

Both cultivars responded similarly to reduced light intensity in terms of P_N, light saturation levels, and

light compensation points. These factors could not be associated with the ability of Pennlawn red fescue to provide a better turf than Merion Kentucky bluegrass in the shade. R_D of individual plants of the red fescue was reduced at the lowest light intensity, whereas the R_D of the Kentucky bluegrass was not. This response may contribute to the positive CO_2 balance of the red fescue at reduced light intensities, and thus to its shade adaptability.

INTRODUCTION

Kentucky bluegrass (*Poa pratensis* L.) and red fescue (*Festuca rubra* L.) will both provide a suitable turf in full sun, whereas red fescue generally will provide more desirable turf in shade (3, 21). Disease incidence (2) and tree root competition (19, 20) have been related to the loss of Kentucky bluegrass in shade.

Reduced light intensity has a marked influence on plants by lowering the photosynthetic and respiratory rates, light compensation point, and light saturation level (1, 4, 5, 6, 8, 9, 10, 11, 12, 15, 16, 17, 23). Bohning and Burnside (10) were able to classify plants as 'sun' or 'shade' based on the higher light compensation point and light saturation level of the sun plants. Burnside and Bohning (11) later demonstrated the reversibility of this classification by placing sun plants in the shade and lowering the compensation point by up to 1 klux and saturation level by 10 klux.

The photosynthetic-respiratory balance is a critical factor in shade adaptation. For a plant to survive, net photosynthesis must exceed respiration. This balance could be improved by lowering the respiration rate or light compensation point (8, 9, 11, 15). Björkman, Ludlow, and Morrow (8) showed the positive CO_2 balance of rainforest species growing in dense shade was due to extremely low respiratory rates contributing to low light compensation points.

Björkman et al. (9) studied the response of *Atriplex patula* L., a sun plant, to reduced light intensity. Low light intensity reduced the photosynthetic rate, light compensation point, light saturation level, and respiration rate. However, the plant could not tolerate light intensities as low as the rainforest species, apparently because it could not produce as efficient a photosynthetic apparatus.

Shade tolerance may be related to photosynthetic efficiency in terms of carboxydismutase activity (6, 7, 8) or mesophyll resistance (14). Björkman (6, 7, 8) correlated high light saturation levels with high carboxydismutase activity in sun plants. He concluded low carboxydismutase activity probably is a factor limiting the capacity for light saturated photosynthesis in shade plants. Holmgren (14) explained light-saturated photosynthetic rate differences in sun and shade plants based on mesophyll resistance. He attributed higher light-saturated photosynthetic rates in exposed clones of Solidago virgaurea to lower mesophyll resistance.

Björkman (4, 5) described the initial slope of the photosynthetic rate-light intensity curve as expressing the capacity of photochemical processes. At light saturation, the photosynthetic rate is an expression of processes other than photochemical, e.g. carboxydismutase activity (6, 7, 8) and CO_2 diffusion rates (14). Björkman (4, 5) investigated the initial slope of the rate-intensity curves and light saturation levels of several species. Exposed clones had equal initial slopes regardless of preconditioning light intensity. Shaded clones had steeper slopes when grown at lower light. The light saturated photosynthetic rate was higher for the exposed ecotypes. He concluded the photosynthetic apparatus of the shaded ecotypes was able to use a low light intensity more efficiently, while the exposed ecotypes were able to use high light more efficiently.

Winstead and Ward (24) studied the physiological responses of warm season turfgrasses to shade. Tiflawn bermudagrass (Cynodon dactylon L. Pers.) displayed a decrease in net photosynthesis and respiration at low light, whereas a small increase in net photosynthesis and a decrease in respiration occurred in St. Augustinegrass (Stenotaphrum secundatum Walt. Kuntze.). St. Augustinegrass is the warm season counterpart of red fescue in regards to shade adaptation.

The photosynthetic rate and light saturation level of turf are greatly influenced by shoot density, cutting height, and mowing frequency. Alexander and McCloud (1) investigated the light compensation point and light saturation level of individual leaves and swards of bermudagrass. Isolated leaves had a light compensation point of 3.2 klux, and a light saturation of 32 klux. The light saturation level of swards cut at 5 cm and 20 cm was 75 and 54 klux, respectively. The differences were attributed to the orientation of leaves and the degree of interleaf shading.

The objectives of this study were to investigate the net photosynthetic and dark respiratory responses of swards and individual plants of Merion Kentucky bluegrass and Pennlawn red fescue under reduced light intensities. Light compensation points and saturation levels were also studied. It was anticipated this information may give further insight into the shade adaptive mechanisms of red fescue. Factors other than reduced light intensity affecting the growth of turf in shade (light quality, soil moisture, disease) were controlled or eliminated.

METHODS AND MATERIALS

Growth conditions were similar to those used in earlier studies (21, 22).

Light

A 14 hour photoperiod was used. Light intensities of 43, 10.7, and 2.7 klux (11.4, 5.0, and 1.4 x 10^3 μw cm^{-2}, respectively) were established in separate growth chambers. In an earlier study (21), both Merion Kentucky bluegrass and Pennlawn red fescue performed well at 43 klux. The Kentucky bluegrass turf quality was impaired at 10.8 klux, whereas the red fescue continued to provide a suitable turf. Shoot and root growth of both cultivars was poor at 2.7 klux, however, the red fescue was able to provide a higher quality turf than the Kentucky bluegrass.

Nominal differences existed among or within chambers in light quality (21). The light was rich in green and infrared wavelengths, weak in the blue and red regions (21). Pots were periodically rotated to compensate for variation in light intensity within chambers. Separate growth chambers were used for each light intensity to avoid using shading materials that could seriously alter the turf microenvironment.

Humidity

A relative humidity of 70 ± 5% was maintained in the growth chambers.

Growing Medium

All plants were grown in silica sand to reduce soil respiration during assimilation measurements. Plants were watered every other day with a complete Hoagland's (13) solution. Soil temperatures were maintained at 20 C during growth in the chambers.

Plant Material

Merion Kentucky bluegrass and Pennlawn red fescue were seeded in 10 cm diameter (12 cm depth) pots at 3 seeds/cm^2, and germinated in the greenhouse. Plants were moved to the growth chambers when seedlings were 2 cm in height. All plants were grown at their respective light intensities for 6 weeks prior to assimilation measurements.

Plants were mown periodically at 5 cm. Occasional applications of Karathane® were required to control powdery mildew (*Erysiphe graminis* D.C.).

CO_2 Exchange System

A waterjacketed plexiglass assimilation chamber was constructed for use with the 10 cm pots (internal volume 3.3 liters). Tap water was circulated around the chamber for temperature control. Temperatures could be maintained at 23 ± 1 C as indicated by a bulb thermometer inserted into the chamber. CO_2 was introduced into the chamber above the plants, and was removed at the base of the chamber.

The light source consisted of four 300 w reflector flood lamps. The light was passed through a water bath to reduce heat reaching the assimilation chamber. Figure III.1 compares the spectral distribution within the assimilation chamber to that of the growth chambers.

The CO_2 exchange system was closed, utilizing a FMI, Model RRP piston pump for air circulation. The flow rate was 600 ml/min. Copper tubing was used for all connections. Non-indicating Drierite provided a dessiccant.

A Beckman, Model 215 infrared gas analyzer, and a Sargent, Model SR 1 mv recorder were used.

It was found that despite growing the plants in sand, soil respiration still interfered with assimilation measurements. All pots were flooded to 1 cm over the sand surface before CO_2 measurements to reduce soil respiration. Earlier studies (18) and preliminary work showed no significant influence of flooding on photosynthetic rates in the time necessary to complete measurements.

Parameters Measured

Measurements were made for both swards of turf and individual plants. One group of measurements were taken on the turf seeded at 3 seeds/cm^2. A second series of pots were used which were thinned to 5 or 6 plants per pot to eliminate canopy effects of interleaf shading and CO_2 diffusion resistance. All assimilation rates were determined between 330 and 270 ppm CO_2. Rates were determined 4 hours after the beginning of the growth chamber photoperiod to minimize diurnal variation effects.

Dark respiration rates were measured first, followed by net photosynthetic rates at light intensities of 1.35, 2.7, 5.4, 10.8, 21.5, 43, and 64.6 klux. Rates were monitored for at least 10 minutes to obtain a straight line response at each light intensity.

After all measurements were completed, shoots were removed and the flooded pot placed back in the chamber to determine soil respiration rate. Shoot dry weight and leaf area were determined as described earlier (20).

Statistical Analysis

Four replications were utilized. A completely randomized block analysis of variance was made on the two cultivars at each light intensity. The determined variances at each light intensity were pooled, and a single LSD value (.05 level) was determined.

RESULTS AND DISCUSSION

Merion Kentucky bluegrass and Pennlawn red fescue displayed many of the typical physiological responses to reduced light intensity; reduced photosynthetic and respiratory rates, lower light saturation levels, and lower light compensation points (Tables III.1, III.2, and III.3). Swards and individual plants generally responded similarly, although the magnitude of the values was different. Swards had lower photosynthetic and respiratory rates, and higher light saturation levels and light compensation points than individual plants. Interleaf shading probably was the most important factor in reducing photosynthetic rates and increasing light saturation levels and light compensation points in the swards. Lower respiration rates in swards probably were due to CO_2 diffusion resistance within the canopy.

Photosynthetic Rates

Net photosynthesis (P_N) rates were measured at the preconditioning light intensity (Table III.1) and at light saturation (Table III.2). P_N decreased as light intensity was reduced in both instances, for swards and individual plants. Larger reductions in P_N occurred between plants grown at 43 and 10.8 klux when P_N was measured at the preconditioning light intensity as opposed to measurement at light saturation. No differences were observed in the P_N responses of the Kentucky bluegrass and the red fescue at reduced light intensities which would elucidate the shade adaptive mechanisms of red fescue.

Anatomical work (22) revealed Merion Kentucky bluegrass chloroplasts to have significantly more grana than Pennlawn red fescue at reduced light intensities. Increased grana development has been correlated to decreased carboxydismutase activity and CO_2 fixing ability (4, 5). Pennlawn red fescue did not have the ability to fix more CO_2 at reduced light intensities than Merion Kentucky bluegrass. The significance of this factor in relation to the shade adaptation of red fescue remains unknown.

Respiratory Rates

Dark respiration (R_D) rates after preconditioning to reduced light intensities are presented in Table III.1. Swards and individual plants responded differently. R_D of swards of both cultivars decreased with reduction in light intensity, although the decrease was not quite significant for red fescue. In contrast, R_D rates of individual plants of the Kentucky bluegrass did not decrease under reduced light intensity. R_D of individual plants of the red fescue was the same at 10.8 as at 43 klux, but was reduced approximately 50% at 2.7 klux.

Reduced R_D rates of swards under low light could be the result of canopy effects. The R_D values probably represent the R_D of leaves at the top of the canopy only. R_D of lower leaves and sheaths may not be accounted for due to CO_2 diffusion resistance through the canopy.

A reduction in R_D of individual plants of Pennlawn red fescue at low light intensities may be a shade adaptive mechanism. Reduced R_D would contribute to a positive CO_2 balance, despite the fact that P_N was decreased under low light. An improved photosynthetic balance has been shown a factor in the shade adaptation of other species (8, 9, 11, 15).

Light Saturation Levels

Saturation levels of both cultivars decreased under lower light (Table III.3). Saturation of swards was not reached for either species at the highest light intensity used (64.6 klux). Alexander and McCloud (1) did report the light saturation level of bermudagrass swards cut at 5 cm occurred at 75 klux.

Saturation levels of individual plants were slightly higher than those reported for individual leaves of most C_3 plants. This could be due to the fact that the entire plant was used, and not a single leaf. Some inter-leaf shading, or perhaps the presence of older leaves and sheaths would raise the saturation level. No difference in the light saturation levels of swards or individual plants of Merion Kentucky bluegrass and Pennlawn red fescue was observed that could be related to shade tolerance.

Light Compensation Points

Light compensation points of both cultivars in swards decreased under lower light (Table III.3). Compensation points were the same for individual plants at 10.8 and 43 klux, but were reduced for both cultivars at

2.7 klux. Compensation points found for individual plants are typical of those found for C_3 plants. No difference could be found in the compensation points of the Kentucky bluegrass and the red fescue at reduced light intensity.

CONCLUSIONS

The shade adaptation of several species has been related to an improved photosynthetic-respiratory balance (8, 9, 11, 15), reduced light compensation points (8, 9, 11, 15), and improved use of low light intensity as shown by an increased slope of the photosynthetic rate-light intensity curve (4, 5). The slope of the rate-intensity curve was similar for Merion Kentucky bluegrass and Pennlawn red fescue at each light intensity, although the slope did decrease with lower light. The cultivars responded similarly in terms of light compensation points (Table III.3). Only the photosynthetic-respiratory balance was observed in this study as a possible shade adaptive mechanism of Pennlawn red fescue.

The response of individual plants in Table III.1 shows only the red fescue would have a positive CO_2 balance at low light intensity over a 24 hour period. Merion Kentucky bluegrass at 10.8 and 2.7 klux displayed a negative CO_2 balance. Despite this, the Kentucky bluegrass was able to persist at these light intensities. Apparently the older leaves and sheaths of the Kentucky bluegrass were no longer photosynthetically active, and perhaps were acting primarily as a photosynthate sink. This contention is supported by earlier work (21), showing Merion Kentucky bluegrass leaf area was reduced much more than that of Pennlawn red fescue leaf area at reduced light intensities. Perhaps the older leaves of the Kentucky bluegrass senesce rapidly under low light, become a photosynthate sink, and are quickly sloughed off.

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TABLE III.1.--Net photosynthesis (P_N) measured at three preconditioning light intensities and dark respiration (R_D) of swards and individual plants of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Species	Light intensity (klux)	P_N		R_D	
		Swards	Individual	Swards	Individual
		($mg\ CO_2\ dm^{-2}\ hr^{-1}$)			
Kentucky bluegrass	43	4.92	13.30	1.61	4.55
	10.8	1.08	1.85	0.61	4.30
	2.7	0.42	1.49	0.21	4.11
Red fescue	43	3.70	11.76	1.25	2.94
	10.8	0.72	2.50	0.76	3.15
	2.7	0.27	1.61	0.29	1.56
LSD (.05)		0.85	3.01	1.36	1.20

TABLE III.2.--Light saturated net photosynthetic rates (P_N) of swards and individual plants of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Swards	Light intensity (klux)	P_N	
		Swards	Individual
		($mg\ CO_2\ dm^{-2}\ hr^{-1}$)	
Kentucky bluegrass	43	6.33	15.25
	10.8	3.93	11.00
	2.7	2.73	11.03
Red fescue	43	4.78	13.11
	10.8	3.25	11.59
	2.7	2.32	8.50
LSD (.05)		2.43	1.92

TABLE III.3.--Light saturation levels and light compensation points of swards and individual plants of Merion Kentucky bluegrass and Pennlawn red fescue grown at three light intensities.

Species	Light intensity (klux)	Light saturation level		Light compensation point	
		Swards	Individual	Swards	Individual
		(klux)			
Kentucky bluegrass	43	> 64	38	6.0	4.2
	10.8	50	32	3.2	4.4
	2.7	43	18	1.2	1.3
Red fescue	43	> 64	35	6.2	4.0
	10.8	47	32	3.5	4.2
	2.7	43	19	1.35	1.5
LSD (.05)		9.2	9.4	2.1	1.8

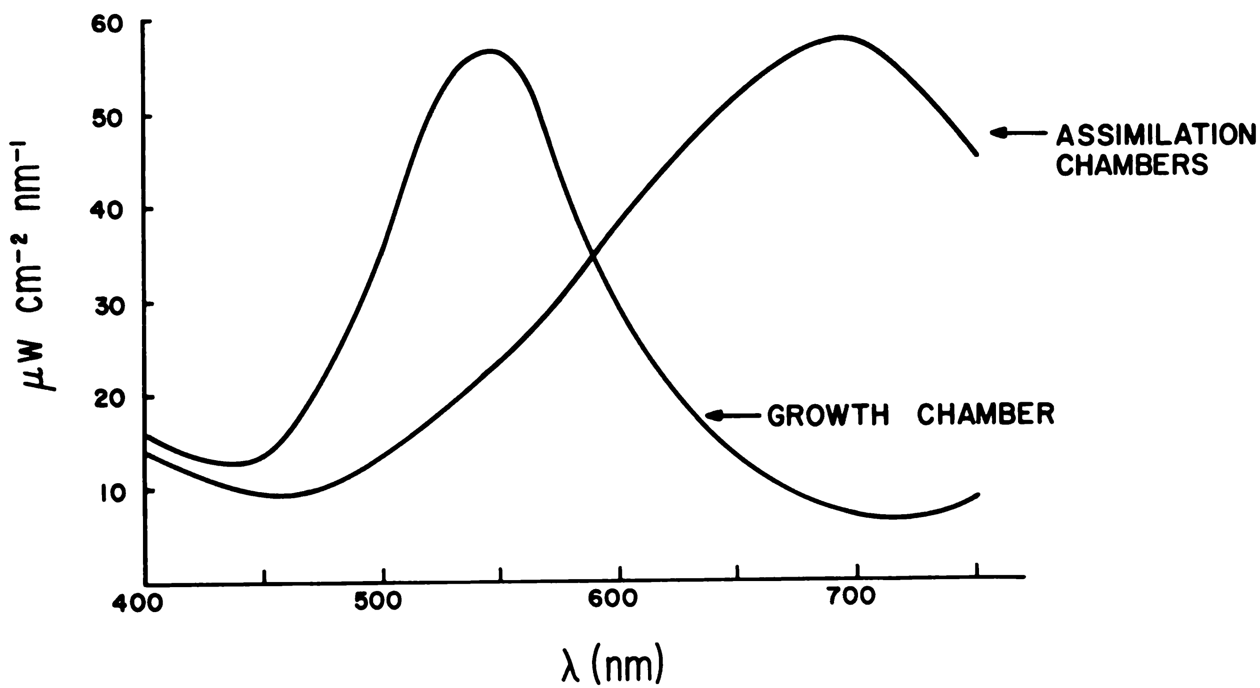

Fig. III.1.--Comparison of the spectral distribution in the assimilation chamber and the growth chambers.

CONCLUSIONS

The following conclusions can be drawn regarding the responses of Merion Kentucky bluegrass and Pennlawn red fescue to reduced light intensity:

1. The morphological responses to reduced light intensity were similar for the two cultivars in terms of leaf length and width prior to clipping, clipping weight and leaf area, percent moisture, chlorophyll content, and root growth.

2. Pennlawn red fescue provided a more desirable turf than Merion Kentucky bluegrass at reduced light intensity due to superior verdure. The red fescue was superior at reduced light intensity in terms of shoot weight and leaf area below the cutting height, shoot density, and tillering.

3. The shoot angle of Pennlawn red fescue at reduced light intensity was relatively horizontal, whereas Merion Kentucky bluegrass displayed a vertical,

upright growth habit. Red fescue may be able to persist in the shade due to less photosynthetically active leaf tissue being removed in mowing.

4. The anatomical responses to reduced light intensity were similar for the two cultivars in terms of stomata density and pore length, and chloroplast density and distribution. These factors, associated with shade adaptation in other species, cannot be associated with the ability of Pennlawn red fescue to provide a more desirable turf in the shade than Merion Kentucky bluegrass.

5. The red fescue displayed greater cuticle development at reduced light intensity than the Kentucky bluegrass. The ability of the red fescue to produce a cuticle at reduced light intensity may contribute to improved disease resistance, and as a result enhance shade adaptation.

6. The red fescue had more developed vascular and support tissue than the Kentucky bluegrass at reduced light intensity. Improved support tissue may impart increased wear tolerance to the red

fescue. Improved vascular tissue could possibly lead to improved movement of water, nutrients, and photosynthate.

7. Merion Kentucky bluegrass had increased development of grana stacks and thylakoids at reduced light intensity, whereas Pennlawn red fescue did not display such a response. This increase has been associated in other investigations to decreased carboxydismutase activity, and reduced CO_2 fixation rates at reduced light intensity. The significance of this factor in red fescue shade adaptation remains unknown.

8. The photosynthetic-respiratory responses of the two cultivars to reduced light intensity were similar in terms of reduced net photosynthesis, light saturation levels, and light compensation points. These factors cannot be associated with the ability of the red fescue to provide a more desirable turf in the shade than the Kentucky bluegrass.

9. The red fescue displayed a decrease in dark respiration (R_D) rate at reduced light intensity, whereas the Kentucky bluegrass did not. Lower R_D may contribute to a positive CO_2 balance for red fescue at reduced light intensity, and thus to its shade adaptability.

The author feels that no one factor can be looked upon at this time as the one element imparting shade adaptation to Pennlawn red fescue. The ability of red fescue to provide a suitable turf in the shade must be related to a number of complex plant and environmental factors.

It would be advantageous to recognize one shade adaptive mechanism which could be used to screen turfgrass species and cultivars for shade adaptation. This factor, if it exists, remains unknown. However, it would now appear logical to extend this study one step further. Those factors found to be involved in the shade adaptation of Pennlawn red fescue could be studied in relation to other shade adapted turfgrass species and cultivars. For instance, Nugget and A-34 cultivars of Kentucky bluegrass have been reported by several experiment stations to have improved shade tolerance. It is not known if either of these cultivars possess any of the shade adaptive mechanisms of red fescue.

Several additional mechanisms have been shown responsible for shade adaptation in other non-turfgrass species. These include: growth and physiological responses to the altered light quality found beneath deciduous trees; improved carboxydismutase activity at low light intensities; the nature and distribution of light absorbing pigments and their ability to use light of low intensity and altered quality; a low requirement for water, nutrients, or carbohydrates; ability to efficiently use light of high intensity found in sunflecks; a greater seedling competitive ability for light and nutrients. All of these factors remain to be studied in relation to red fescue shade adaptation.

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