RESULTS

Visual Observations

When plants from the three treatments in both the greenhouse and growth chamber experiments were visually compared, certain differences were apparent. Plants grown in the two sun simulations had the greatest number of tillers and leaves per plant. Their leaves were green, short and thick, upright in growth habit and their cross-section was shaped as an open vee. In contrast, the plants grown in the canopy shade simulation had the fewest tillers and leaves per plant. The leaves were very long and droopy in growth habit, tightly rolled, and thin, i.e., etiolated. Canopy shade plants were actually yellow-green in appearance.

Responses of the diffuse skylight-grown plants were between those described above. These plants had an intermediate number of tillers and leaves per plant, were moderately upright in growth, and their leaves were shaped as a semi-open vee. Leaves on plants under growth chamber conditions were the shortest of the experiment and were also the darkest green, whereas greenhouse-grown leaves were as long as sun leaves and only slightly darker green. The plants were sufficiently different in growth habit from each other so that even an inexperienced observer could have correctly identified a plant's growth environment, given the above information.

Although the growth chamber treatments only had one-half
of the total spectral energy of the greenhouse, plants grown in the growth chamber showed greater plant response or increased growth. A possible explanation for this unexpected result may be that the more controlled air temperatures in the growth chamber permitted more growth.

Morphological and physiological measurements at the 3 time periods are summarized in Tables 1 and 2 and analyses of variance for these measurements appear in Appendix Tables I-IV. Each measurement will be individually presented and discussed in following sections.

Morphological Measurements

Weight. Fresh and dry weights were measured and the ratio of these weights was computed. Fresh weight and dry weight followed nearly identical rates of increase with time (Figs. 5 and 6). The sun, skylight, and canopy shade plants in the growth chamber had greater fresh and dry weights than did plants from similar treatments in the greenhouse, although the growth chamber provided only one-half of the total radiant energy of the greenhouse. At week 3, all plants had approximately equal weights, but by weeks 4 and 5, plants grown in both sun spectra had significantly greater weight.

Fresh weight/dry weight ratio. The fresh weight/dry weight ratio decreased with time in plants from all treatments (Fig. 7). Plants from the high light or greenhouse experiment had higher values for this ratio than those from similar treatments in the
TABLE 1

SUMMARY OF GROWTH MEASUREMENTS OF GOLFROOD RED FESCUE GROWN UNDER GREENHOUSE SIMULATIONS OF SUNLIGHT (S), CANOPY SHADE (CS), AND SKYLIGHT (SL), MEASURED 3, 4 AND 5 WEEKS AFTER SEEDING* (MEAN OF 2 REPLICATIONS)

<table>
<thead>
<tr>
<th>TIME OF MEASUREMENT</th>
<th>TYPE OF MEASUREMENT</th>
<th>Average No. of Leaves/Plant</th>
<th>Total Chlorophyll g ug/g dry top</th>
<th>Total Carotenoid g ug/g dry top</th>
<th>Dark Respiration g CO₂ dry top/hr</th>
<th>Compensation Point mW/cm² 400-760 nm</th>
<th>Photosynthesis dry top/mg CO₂ dry top/hr</th>
<th>Photosynthesis Chlorophyll Chlorophyll mg CO₂/ug Chlorophyll hr</th>
</tr>
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<tbody>
<tr>
<td>WEEK 3</td>
<td>Treatment</td>
<td>Dry Wt</td>
<td>Fresh Wt</td>
<td>Fresh Wt /Dry Wt</td>
<td>0.034a</td>
<td>0.267a</td>
<td>7.78b</td>
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<td>SL</td>
<td>CS</td>
<td>g</td>
<td>g</td>
<td>g</td>
<td>0.031a</td>
<td>0.270a</td>
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<td></td>
<td></td>
<td>0.030a</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WEEK 4</td>
<td>Treatment</td>
<td>Dry Wt</td>
<td>Fresh Wt</td>
<td>Fresh Wt /Dry Wt</td>
<td>0.089a</td>
<td>0.649a</td>
<td>7.26b</td>
<td>2.51a</td>
</tr>
<tr>
<td>SL</td>
<td>CS</td>
<td>g</td>
<td>g</td>
<td>g</td>
<td>0.049b</td>
<td>0.400b</td>
<td>7.85a</td>
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<td></td>
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<td>0.058b</td>
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<tr>
<td>WEEK 5</td>
<td>Treatment</td>
<td>Dry Wt</td>
<td>Fresh Wt</td>
<td>Fresh Wt /Dry Wt</td>
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<td>1.050a</td>
<td>6.54b</td>
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<td>SL</td>
<td>CS</td>
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<td>g</td>
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*Means followed by the same letter within a time and measurement are not significantly different at the 1% level.
### Table 2

**Summary of Growth Measurements of Golfrood Red Fescue Grown Under Growth Chamber Simulations of Sunlight (S), Canopy Shade (CS), and Skylight (SL), Measured 3, 4 and 5 Weeks After Seeding**  
(Mean of 2 Replications)

<table>
<thead>
<tr>
<th>Time of Measurement</th>
<th>Treatment</th>
<th>Week 3</th>
<th>Week 4</th>
<th>Week 5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dry Wt</td>
<td>Fresh Wt /Dry Wt</td>
<td>Fresh Wt</td>
<td>G Fresh Wt /Dry Wt</td>
</tr>
<tr>
<td>SL.060a</td>
<td>.417a</td>
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<td>.842a</td>
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<td>7.53a</td>
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</tr>
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<td>.567b</td>
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<td>.834b</td>
<td>6.31b</td>
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</table>

*Means followed by the same letter within a time and measurement are not significantly different at the 1% level*
Fig. 5. Influence of simulated light spectra on shoot dry weight of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

![Graph showing dry weight over weeks after planting for different light treatments.]

Fig. 6. Influence of simulated light spectra on shoot fresh weight of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
Fig. 7. Influence of simulated light spectra on shoot fresh weight/dry weight of Golfood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). *(Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
growth chamber experiment. This difference was small when comparing the two sun treatments, but was much more evident when comparing the skylight and canopy shade treatments. The decrease in fresh weight/dry weight ratio with increasing age may be the result of a lower ratio of new growth to existing plant matter as the plant increased in age, assuming that the new growth contained more water per cell than did older plant material. It is also possible that cells were accumulating more storage products and wall constituents than they contained at a younger age. Plants grown in the canopy shade treatment had significantly higher fresh weight/dry weight ratios at all times. This indicates a higher percentage of water in tissue under canopy shade treatments as compared to tissue from the other treatments.

**Average number of leaves.** Average number of leaves per plant at weeks 3, 4, and 5 and the length of first leaf and number of tillers per plant at week 6 were measured. The number of leaves per plant increased with time in all treatments (Fig. 8). Low light growth chamber conditions permitted plants to produce more leaves per plant than did the same radiation spectrum treatments in the greenhouse. At week 3 all plants in both the growth chamber and the greenhouse had approximately the same number of leaves. At week 4, canopy shade-grown plants had fewer leaves than did sun or skylight-grown plants and at week 5, all plants were different from each other, with sun spectra plants producing the greatest number of leaves.

**Average number of tillers.** The number of tillers per plant
Fig. 8. Influence of simulated light spectra on number of leaves/plant of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
was measured on 6-week-old plants (Fig. 9). Low light conditions again permitted more tillering than did corresponding treatments in high light greenhouse conditions. Both chamber and greenhouse sun spectra simulations permitted development of significantly more tillers per plant than did skylight treatments, which, in turn, permitted more tillering than did canopy shade.

Leaf and tiller number were the only gross measurements where all plants in both greenhouse and growth chamber treatments were statistically different from each other. This indicates that the sun or a complete spectrum is very important in leaf and tiller initiation and that a canopy shade spectrum is the least favorable. This study did not find reports on leaf or tiller number in relation to various spectra, although many researchers note spectral influence on leaf elongation, leaf area, leaf morphology, and leaf shape (Popp, 1926; Logan and Krotkov, 1969; Erner et al., 1972).

Leaf length. The length of the first leaf of six-week-old plants was measured (Fig. 10). Full sun-treatment plants were compared with those from the experimental treatments. Unfiltered sun plants were grown in the greenhouse and were maintained at nearly the same temperature, relative humidity, and air movement as were the greenhouse treatment plants. In both high light (greenhouse) and low light (growth chamber) experiments, canopy shade plants had the longest leaves. However, plants in greenhouse skylight or sun conditions had longer leaves than did those under similar treatments in the growth chamber.
Fig. 9. Influence of simulated light spectra and full sun on number of tillers/plant of Golfroad red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C).* 
(Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
Fig. 10. Influence of simulated light spectra and full sun on length of first leaf of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). * (Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
Growth chamber plants in the skylight treatment had the shortest leaves and sun plants were intermediate in length. In the greenhouse experiment, the skylight and sun plants had leaves of about the same length. Plants grown in unfiltered sunlight in the greenhouse had very short leaves, and were comparable to growth chamber skylight plants.

Since canopy-shade plants had long leaves with low dry weights, increased leaf length is due to loose cell arrangements and excessive cell elongation. Popp's (1926) plants in a spectral greenhouse of 529-720 nm (corresponding to this study's canopy shade treatment) had long, slender stems with greatly elongated internodes and few branches. The stem tissues had a rather loose cell organization with thin-walled cells showing little differentiation and poor development of secondary and strengthening tissues. Practically all his plants had to be supported after 2 or 3 weeks of growth. Popp's observations coincide with those made in this research.

**Stomates.** Stomates have frequently been studied in shade and sun leaves (Penfound, 1931), but the sun and shade environments often had either undefined spectra or the radiant fluxes were not equal. Variations in either of these parameters could account for the reported differences between sun and shade leaves. When stomates of 6-week-old fescue plants were examined, using a leaf impression technique, stomates from plants under all six treatments were found to be nearly the same size (Fig. 11). Stomatal width was 1 μ and the length was approxi-
Fig. 11. Influence of simulated light spectra and full sun on stomate size of Golfrood red fescue.

Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). *(Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.

Fig. 12. Influence of simulated light spectra and full sun on number of stomates of Golfrood red fescue.
mately 6 \mu. Stomates of leaves from plants grown in unfiltered sunlight had a stomatal length of 5 \mu; the difference is not significant.

Stomatal densities (number of stomates/100 \mu^2) were, however, different, with canopy shade-grown plants having fewer stomates per area than did either sun or skylight-grown plants (Fig. 12). Plants from both the high and low light canopy shade and skylight treatments were similar, but in the sun simulation, leaves on chamber-grown plants had a slightly higher stomatal density. The lower stomate density for the canopy shade plants could be the result of leaf etiolation. Because the larger cells in the canopy shade plants caused greater separation of stomates, density was reduced. Correspondingly, unfiltered sunlight plants had very short leaves with a very high stomate density. A value for stomatal area was calculated by multiplying stomatal number by size for each treatment (Fig. 13). The resulting numbers show that the skylight plants had the greatest stomatal area and the canopy shade plants the least.

**Pigments.** Although color difference between plants from different treatments was observed, when isolated pigments (chlorophyll and carotenoids) were compared on a dry weight basis, only the growth chamber skylight plants had more pigments (Figs. 14 and 15). Pigment content did not change with time for any treatment group, nor was there any difference between groups, even though the plants looked quite different. The greater pigment
Fig. 13. Influence of simulated light spectra and full sun on total stomatal area of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C).

(Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
Fig. 14. Influence of simulated light spectra on total chlorophyll of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

Fig. 15. Influence of simulated light spectra on total carotenoid of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
content of skylight treatment plants may be due to the fact that the skylight spectrum most closely matches the spectrum for chlorophyll synthesis from protochlorophyll (Koski, French, and Smith, 1951) with a high peak at 440 nm and a smaller peak at 650 nm. Shirley (1929) found that his different radiation spectra resulted in plants with approximately the same chlorophyll concentration, but plants in the canopy shade house (529-720 nm) tended to be lower in chlorophyll, and plants in the skylight house (374-585 nm) tended to have more chlorophyll. These results agree with those found in this research.

The high carotenoid content of the growth chamber skylight-grown plants may have acted to protect chlorophyll from photodestruction as described by Anderson and Robertson (1960). Our findings showed that chlorophylls a and b exactly paralleled the total chlorophyll and did not vary either within or between treatments. The chlorophyll a:b ratio was 3:2, not the expected 3:1 ratio. This unexpected ratio was confirmed by methods of Mahlberg and Venketeswaran (1966), and of Madison and Andersen (1963) who used slightly different extracting solvents, absorption readings, and computation formulae. Even full sun plants showed the 3:2 ratio. The only correlation between higher pigment content and morphogenic effects is found in the growth chamber skylight treatment, where the plants had a higher carotenoid content and short leaves. These short leaves may have been due to a destruction of auxin by blue-light-absorbing riboflavin-carotenoid complexes (Galston and Hand, 1949).
Physiological Measurements

A morphological feature is an expression of physiological processes otherwise not evident (Daubenmire, 1959). What is actually measured in physiological or in developmental morphological studies are phenotypic expressions of genetic potential; structure and function are inseparable. To determine the extent that the plants in this study had physiologically adapted to the light treatments, measurements were made of dark respiration, light compensation point, and high light apparent photosynthesis at weeks 3, 4, and 5.

Dark respiration and light compensation. Dark respiration decreased threefold during the 3 weekly measurement periods in all treatments (Fig. 16). Similar results were reported as early as 1920 by Kidd, West and Briggs (1920) for sunflower. In this research, the actual respiration rates per plant were too variable to establish clear trends. Probably the only true measurement of respiration rate would be based on cell number or cell size, and would therefore be more independent of plant age. On a dry weight basis, plants from the low light variables in the growth chamber had slightly lower dark respiration rates for the skylight and canopy shade treatments than did similar plants grown in the high-light greenhouse conditions. The only statistically significant difference in the study was a lower rate for plants from the greenhouse sun simulation at week 3, although the sun simulation plants had lower respiration rates in all measurements. This depressed respir-
Fig. 16. Influence of simulated light spectra on dark respiration of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). *(Mean of 2 replications)*

*Means followed by the same letter within a treatment are not significantly different at the 1% level.*
ation rate at an earlier age can be rationalized by assuming that sun-spectrum plants matured at a faster rate than did the other plants. This interpretation is supported by evidence of earlier seedling independence and numbers of leaves and tillers, and is further supported by the data on light compensation points.

The light compensation point of a plant is the minimum light energy required for a plant to make photosynthate at a sufficiently high rate to balance its use in respiration. Theoretically, at the compensation point there is no net change of carbon within the plant and the plant could survive, but not grow, at this light intensity. The compensation point is an indicator of the plant's photosynthetic efficiency, i.e., a measure of the ability to make maximum use of a small light flux, and hence its ability to survive in light-deficient or light-competitive environments. For all treatments the compensation point decreased with age (Fig. 17), but to a greater extent than did respiration. Respiration was reduced threefold in 3 weeks while the compensation point was depressed tenfold. Reduced compensation points are thus due to more than just lower respiration rates and may be related to a more efficient photosynthesis and more reserve energy substrate that could be converted for efficient dark metabolism. Plants from all treatments in the low light variables had lower compensation rates at the 3 week measurement than did plants from corresponding treatments in the greenhouse. However, by week 4 corresponding plants performed similarly. Only at week 3 and 4 did the plants
Fig. 17. Influence of simulated light spectra on compensation point of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C). (Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.
from the sun simulation have a significantly lower compensation point and, at week 5, all plants had equivalent abilities to utilize light and to survive at low light intensities. Clearly, spectral differences did not affect a plant's final ability to photosynthesize in low light, although they retarded its development. The lower compensation point of sun-grown plants also suggests a greater physiological maturity at an earlier age than the other plants.

When light compensation points were measured directly after dark respiration and immediately following high light photosynthesis, the same results were obtained, showing that the compensation point is a very stable physiological function and is not greatly changed by preceding bright light. If a plant is in a rapidly changing light environment, such as intermittent cloud cover or a sunflecked canopy shade, and is operating at compensation levels, the sudden exposure to bright light will not impair the plant's ability to return quickly to photosynthetic operation at the previous light level. This may be of adaptive significance, for it would allow a plant to utilize sudden high light energy without jeopardizing its normal rate for subsistence.

**Photosynthetic measurements.** Once a seedling has reached independence, it must photosynthesize to provide energy substrate to at least the level of compensation and, if the plant is to mature, it must photosynthesize above this minimum existence level. Hence, photosynthetic capacities are of great
adaptive significance. The plants show considerable between-treatment variability at weeks 3 and 4, but at week 5 all plants had nearly equivalent photosynthetic rates calculated on a dry weight basis (Fig. 18). Although there were no differences between the performance of sun simulation plants at week 3 in either greenhouse or growth chamber, there was a much lower rate for skylight and canopy shade plants in the high light greenhouse than in the growth chamber. At week 5, plants from all treatments in the high light experiment performed much more identically than plants from the growth chamber. In comparing the treatments within an experiment, it was found at week 3 that the sun-grown plants had a much higher photosynthetic rate than did the other plants and even at week 4, only in the greenhouse experiment were skylight-grown plants comparable to the sun plants. The equivalent rates measured at week 5 may be a result of all the plants finally reaching a level of physiological maturity associated with a stable vegetative growth rate. Sun-grown plants reached this level around week 3 and maintained a fairly constant photosynthetic rate throughout the study. In the greenhouse, both skylight and canopy shade-grown plants reached this level around the fourth week, while in the growth chamber, the plants were nearly as developed as sun treatment plants, and slowly reached the maturity plateau.

The data on plant weight, leaf characteristics, tillering and stomatal density suggested that a higher photosynthetic rate in sun-grown plants might be responsible for observed dif-
Fig. 18. Influence of simulated light spectra on high light photosynthesis of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C).

(Mean of 2 replications)

*Means followed by the same letter within a treatment are not significantly different at the 1% level.

Fig. 19. Influence of simulated light spectra on high light photosynthesis/chlorophyll of Golfrood red fescue. Plants were grown in treatments of direct sun (S), skylight (SL), and canopy shade (CS) in a greenhouse (G) and growth chamber (C).

(Mean of 2 replications)
ferences. Measurements of photosynthetic capacity supported interpretations of the growth data.

When photosynthetic rates were based on chlorophyll content, slightly different results were obtained (Fig. 19). The difference was in the greenhouse experiment, where the skylight-grown plants had a photosynthetic rate as high as the sun-grown plants at week 3, and the canopy shade plants had a lower rate at all 3 measurements.

Assuming photosynthetic rate based on chlorophyll content to be an integration of light treatment, light receptor, and light response, the measurement could be considered an indicator of photosynthetic efficiency per unit of receptor pigment. With this premise, plants grown in the sun simulation were highly efficient, while those under the canopy shade treatment were less efficient in harvesting and utilizing available light. This would account for the photosynthetic performance and subsequent growth of these plants, but it must be remembered that the photosynthetic measurements were made under white light and not in the light where the plants were growing, and are a measure of plant capacity.