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THE INFLUENCE OF LIGHT INTENSITY ON GROWTH AND CHLOROPHYLL IN ARCTIC, SUBARCTIC, AND AL-PINE POPULATIONS OF DESCHAMPSIA CAESPITOSA AND TRISETUM SPICATUM

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INTRODUCTION

Investigations on several species which grow in both the arctic and alpine tundras have shown that the populations tend to be adapted to the environmental characteristics of their respective habitats. The arctic populations of *Oxyria digyna*, e.g., appear to be adapted to the unique photoperiod and temperatures of the Arctic, whereas the alpine populations tend to respond best in simulated alpine conditions (Mooney and Billings, 1961). Similar responses for several arctic and alpine populations of *Trisetum spicatum* (L.) Richt. to simulated arctic and alpine conditions have also been noted (Clebsch, 1960). Adaptations of the photosynthetic apparatus of various populations of *Deschampsia caespitosa*

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(L.) Beauv. to some of the unique environmental factors of the Arctic and Alpine are also known (Tieszen, 1965). Apparently ecotypic differentiation (Lawrence, 1945) and physiological adaptability are important phenomena which help account for the distribution of the *Deschampsia caespitosa* complex in both the Arctic and the Alpine.

Light intensity is one of the environmental factors which differ between the arctic and alpine environments (Bliss, 1956). Even though the theoretical daily totals of undepleted solar radiation may be higher in the Arctic in June than at comparable elevations in temperate regions (Gates, 1962), the intensity in the Alpine must certainly be much greater than in the Arctic, since the light in the Arctic is received on a 24-hour basis, whereas in the Alpine it is received in 16 hours or less. The recorded net radiation values for the Arctic indicate that during the growing season the Arctic receives an average of less than 500 langleys per day (Bliss, 1956; Sørensen, 1941; Wilson, 1960). In the Colorado Alpine, on the other hand, the net radiation during the summer frequently exceeds 800 langleys per day, and occasionally around June 21 it attains 1000 langleys per day (Spomer, 1962). Light intensities which exceed 16,000 foot-candles have been recorded in Colorado from Mt. Evans and Trail Ridge (Spomer, 1962), and the senior author has recorded similarly high values from Rollins Pass and Summit Lake. Radiation values as great as 2.20 langleys per minute indicate that it is not uncommon for the net radiation to exceed the solar constant (Spomer, 1962). It should be emphasized that the light intensities will differ more markedly between the Arctic and a continental Alpine than they will between the Arctic and a maritime alpine region, e.g., Mt. Washington in New Hampshire (Hadley and Bliss, 1964).

That light in the Arctic is limiting to plant processes has been shown by various workers (Müller, 1928; Stålfelt, 1925; Kostytschew, Tschesnokov, and Bazyrina, 1930). Polunin's indication (1955) that in the Arctic suitable conditions of light rarely persist for long contrasts with Cartellieri's suggestion (1940) that in the Alpine light limits photosynthesis only in the mornings and evenings. The excessive light is believed to cause a depression in chlorophyll content and a bleaching in upper palisade layers (Montfort, 1950), as well as morphological characteristics which were recognized by Bonnier (1895). The influence of the extreme intensity of the alpine noon sunlight is shown by the mid-day depression observed in photosynthesis (Cartellieri, 1940; Pisek, 1960).

Since light is an environmental factor which is extremely intense in the Alpine and weak in the Arctic and since the weak light of the Arctic limits some plant processes while the intense light in the Alpine possibly inhibits some of these same processes, one might expect arctic plants to be adapted to low light intensities and alpine plants to high light intensities. This investigation is an attempt to determine the responses of arctic, subarctic, and alpine populations of two grass species, *Deschampsia caespitosa* and *Trisetum spicatum*, to various light intensities.

MATERIALS AND METHODS

The alpine plants of *Deschampsia caespitosa* and *Trisetum spicatum* were collected at Rollins Pass, Boulder County, Colorado, at an elevation of 11.600 feet. The northern grasses were kindly supplied by Drs. John J. Koranda, A. E. Porsild, Simon Laegaard, and Albert Johnson. The populations of D. caespitosa were from St. Michael and the Colville River delta of Alaska, and the populations of T. spicatum were collected in central Ungava, Canada, and near Godhavn, Greenland. Since the populations from central Ungava, Canada, and St. Michael, Alaska, were obtained from the lower latitudinal limits of the arctic tundra, they will be referred to as subarctic. Clones were prepared from plants grown in the greenhouse, and only one clone per population was utilized. Voucher specimens have been deposited at the herbarium of Augustana College, Sioux Falls, South Dakota. Details on plant care and treatment have been reported (Tieszen, 1965), and it need only be added that the plants were fertilized and sprayed with insecticides at regular intervals. In addition, before the experiments were initiated, the alpine population of D. caespitosa was sprayed with "Orthorix" fungicide to prevent infection by a yeast, which was found to parasitize the alpine population preferentially.

The experiment was set up with four light intensities in a greenhouse. The light intensity incident upon an open area in the greenhouse was designated as "1", and intensities $\frac{1}{2}$, $\frac{1}{4}$, and $\frac{1}{8}$ as great as those of the open area were established with filters which approximated neutral density. Ten ramets of each population were placed under each light intensity at the beginning of the experiment. These ramets contained an average of slightly more than one shoot per plant, and the leaves were cut back so that the initial plant heights were the same within each population. The photoperiod was not controlled and represents the naturally occurring photoperiod between March and June. The light intensity in the greenhouse did not exceed 5000 foot-candles for extensive periods until after the end of May, and during the major part of each day it was around 2000 to 3000 foot-candles. The temperature was maintained below 25° C at all times, and during the night the low was usually between 18 and 20° C. The experiment was conducted for eleven weeks, and periodic determinations of growth were made.

At the termination of the experiment young, fully expanded leaves were analyzed for chlorophyll content according to the method of Arnon (1949). The check for total chlorophyll was made at a wavelength of 652 millimicrons, and Bruinsma's correction factor (1961) was utilized.

RESULTS

Growth, in terms of numbers of leaves produced, was best for each population of D. caespitosa and T. spicatum under full light intensity (Figures 1-6, Table I). The alpine population of D. caespitosa showed a more marked reduction in



leaf production with a reduction in light intensity than did the arctic and subarctic populations (Figures 1-3). The northern populations developed more leaves than the alpine population under all light intensities, and, in general, shoot production followed this same pattern, although the alpine population consistently had a higher leaf-to-shoot ratio than the northern populations.

In *T. spicatum* the alpine population produced more leaves under $\frac{1}{2}$ and $\frac{1}{4}$ light intensity, relative to the maximum produced, than the arctic and subarctic populations (Figures 4-6). Under $\frac{1}{8}$ light intensity, however, only the population from central Ungava increased in its relative leaf production. The population from Greenland lived only six weeks at $\frac{1}{8}$ light intensity. The alpine population possessed the lowest actual number of leaves per plant at all light intensities. The Greenland population possessed the most leaves, except, of course, at $\frac{1}{8}$ light intensity, where this population failed to survive. The leafto-shoot ratio in all three populations of *T. spicatum* did not vary with light intensity during growth, and there were no apparent differences in this ratio in these populations.

Differences in plant height and growth form are readily apparent in Figures 7 and 8. In both species the shoots of the plants which were grown under high light intensities were quite erect, whereas the shoots under low light intensities were often very lax and even prostrate. The Greenland population of T. spicatum was characteristically lax, and the very long leaves of this population (Table II) were usually so flat and prostrate that most of the upper surfaces were exposed to the sun at right angles.

Leaf width decreased (Figures 9 and 10) with a reduction in light intensity during growth in all populations of *D. caespitosa* and *T. spicatum*. This decrease in width amounted to a reduction in each population of around 30 percent from full light intensity to $\frac{1}{8}$ light intensity. In both species the alpine populations possessed the narrowest leaves under all light intensities. Associated with the consistent decrease in leaf width was the decrease in density-thickness (weight per unit area) in all populations (Figures 11 and 12). This decrease was caused by a decrease in leaf thickness.

Chlorophyll on a fresh-weight basis increased with a reduction in light intensity during growth (Figures 13 and 14). The *T. spicatum* populations showed a progressive increase in chlorophyll, whereas the *D. caespitosa* populations showed a significant increase only between 1 and $\frac{1}{2}$ light intensity. In each species and under all light intensities an arctic or subarctic population possessed more chlorophyll than the alpine population. When the chlorophyll content was

FIGURES 1-3. Percent of the maximum number of leaves for the Rollins Pass (1), Colville (2), and St. Michael (3) populations of *Deschampsia caespitosa* grown under full (circles), one-half (squares), one-fourth (triangles), and one-eighth (crosses) light intensity.



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related to leaf area (Figures 15 and 16), there was no increase with a reduction in light intensity during growth. Usually the content remained the same, but in the Colville population of *D. caespitosa* there was a drop in chlorophyll from a high of more than 7 mg/dm² to nearly 5 mg/dm². The chlorophyll a-to-b ratio (Figures 17 and 18) was usually higher under full light intensity than under any of the reduced light conditions, and the populations generally showed a reduction in the a-to-b ratio with a reduction in light intensity.

DISCUSSION

Genetic differentiation is apparent in the populations of D. caespitosa and T. spicatum. Similar diversity has been found in each of the wide-ranging tundra species that has been investigated, e.g., Oxyria digyna (Mooney and Billings, 1961) and Trisetum spicatum (Clebsch, 1960). The arctic and subarctic populations of D. caespitosa appear to be adapted to low light conditions, since these plants grew better under such conditions than did the alpine population. However, in T. spicatum this same response was not noted, for in this species the alpine population actually grew as well under low light intensities as did the northern populations. The Greenland population of T. spicatum did not grow well under the reduced light and, in fact, did not survive long under the lowest light intensity.

In terms of growth responses, the differences between the arctic and the subarctic populations appear to be as great as those between an arctic and an alpine population. Therefore, any statements concerning "arctic populations," "arctic adaptations," or similar statements about alpine plants must be made with qualifications, for it does not appear possible to generalize for arctic and alpine plants from data available on only a few species or populations. The intense light of the alpine has been suggested as being responsible for the short growth form of many of the alpine plants (Bonnier, 1895; Wagner 1892), but it is not known if these plants are indeed stunted. In the present investigation an arctic or subarctic population in each species was taller than the alpine population under all light conditions. In D. caespitosa the alpine population attained its greatest height under full light, while neither of the northern populations showed much deviation under the various light regimes. The arctic and subarctic populations of T. spicatum showed a decrease in plant height with a decrease in light intensity, but the alpine plants showed their maximum heights under 1/2 and 1/4 light intensity. In both species the northern populations showed a distinct tendency toward a prostrate habit. This was especially evident

FIGURES 4-6. Percent of the maximum number of leaves for the Rollins Pass (4), Central Ungava (5), and Greenland (6) populations of *Trisetum spicatum* grown under full (circles), one-half (squares), one-fourth (triangles), and one-eighth (crosses) light intensity.

	Light ntensity	Weeks After Beginning of Experiment					
Population I		0	2	4	6	8	11
Deschampsia caespitosa Rollins Pass, Colorado	1	5.0	6.0	12.2	17.4	28.9	64.4
	$1/_{2}$	5.0	5.5	6.7	7.7	9.0	11.9
	1/4	5.0	4.8	6.0	6.1	6.5	7.5
	1/8	5.0	6.3	6.8	6.2	5.6	2.8
Deschampsia caespitosa Colville, Alaska	1	5.0	5.5	12.0	21.2	43.0	80.6
	$\frac{1}{2}$	5.0	6.7	12.6	18.3	33.7	60.3
	i/4	5.0	5.3	8.6	11.0	12.7	19.0
	1/8	5.0	6.4	10.0	9.0	9.3	9.7
Deschampsia caespitosa St. Michael, Alaska	1	5.0	8.5	20.0	31.7	40.9	72.9
	1/2	5.0	8.7	13.4	16.6	19.6	32.9
	1/4	5.0	7.9	9.0	10.9	12.2	19.8
	1/8	5.0	8.1	10.1	11.2	11.6	13.1
Trisetum spicatum Rollins Pass, Colorado	1	3.5	3.8	6.1	9.4	15.1	25.5
) 1/2	3.5	4.0	6.4	7.1	8.8	17.2
	1⁄4	3.5	3.1	3.7	5.5	6.9	8.5
	1/8	3.5	4.4	4.0	3.8	4.4	4.0
Trisetum spicatum Central Ungava, Canada	1	3.8	4.0	5.9	9.0	17.7	35.9
	la 1/2	3.8	4.9	6.8	8.1	11.0	20.5
	1/4	3.8	4.4	4.1	4.6	5.0	8.8
	1/8	3.8	4.8	4.6	5.6	5.3	6.6
Trisetum spicatum Godhavn, Greenland	1	3.8	3.9	7.5	15.0	30.3	76.6
	$1/_{2}$	3.8	3.7	5.1	8.1	9.7	22.0
	1⁄4	3.8	5.1	5.5	6.5	7.2	13.0
	1/8	3.8	3.7	2.8	1.2		

 TABLE I.

 Average number of leaves per plant as a function of light intensity during growth.

in the St. Michael, Alaska, population of D. caespitosa and the Greenland population of T. spicatum, and the decumbent leaves became more evident with reductions in light intensity during growth. This decumbent habit would certainly expose more leaf area to direct sunlight, and this might be advantageous in terms of photosynthesis in the low-light regions of the Arctic.

The wider leaves of the arctic plants than the alpine plants might also be a mechanism to spread as much leaf material as possible over a given area. A reduction in light intensity typically results in an increase in leaf area (Clausen, Keck, and Hiesey, 1940; Talbert and Holch, 1957), but in this investigation the reverse response was noted. Bonnier (1895) and Wagner (1892) found that a typical sun characteristic of alpine plants was the presence of thick leaves, a conclusion which has been confirmed by Montfort (1950). In the Arctic, leaves are usually thin (Wilson, 1957) and possess low density-thickness values (Polunin, 1955), a combination suggestive of shade adaptations. Under the conditions of this experiment, the density-thickness values of the alpine popula-

Population	Light Intensity During Growth					
	1/8	1⁄4	1/2	1		
Deschampsia caespitosa						
Rollins Pass	92	84	125	164		
Colville	155	154	141	138		
St. Michael	218	209	225	234		
Trisetum spicatum						
Rollins Pass	162	185	197	164		
Central Ungava	134	155	182	183		
Greenland	64*	183	218	244		

 TABLE II.

 Average maximum leaf length (mm) as a function of light intensity during growth.

*Measured 6 weeks after the beginning of the experiment, when the plants were nearly dead. The original leaves, cut to a length of 115 mm at the beginning, had all died.

tions were intermediate between those of the two northern populations of each species, indicating that in these species the responses noted by the above investigators have not been genetically fixed. With a reduction in light intensity during growth, density-thickness decreased in these grasses, as in most other plants (McClendon, 1962), and this response resulted from both a decrease in leaf density and thickness. The high density-thickness values in the plants from full light may have resulted from an increase in cell enlargement (Anderson, 1955), an increase in the number of cells or layers (Pieters, 1960; Montfort, 1948), and/or a reduction in the size of the intercellular air spaces (Hanson, 1917).

Genetic differentiation in terms of chlorophyll contents is apparent in the populations of both D. caespitosa and T. spicatum. The alpine population of D. caespitosa possessed lower chlorophyll concentrations under all light conditions than the Colville, Alaska, population, but its chlorophyll values were not much different from those of the St. Michael, Alaska, population. It should be stressed that the St. Michael, Alaska, population was more similar to the alpine population than was the Colville, Alaska, population for all factors examined. Even in growth characteristics and appearance these two populations are similar. It is possible that this subarctic population occupies an intermediate position with respect to adaptations to the arctic and alpine environments. The Greenland population of T. spicatum showed poor growth under the reduced light intensities, and associated with this was a very low chlorophyll content under all light intensities. The relationship between chlorophyll content and growth under low light intensities indicates that the plants which grew best under low light conditions were those which possessed the highest concentrations of chlorophyll, especially on a leaf-area basis. These data indicate that some arctic populations may possess more chlorophyll than certain alpine populations, and the similar



FIGURE 7. Representative plants of *Deschampsia caespitosa* from Rollins Pass (left), St. Michael (center), and Colville (right) after fifteen weeks at full (A), one-half (B), one-fourth (C), and one-eighth (D) light intensity.

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FIGURE 8. Representative plants of *Trisetum spicatum* from Rollins Pass (left), Central Ungava (center), and Greenland (right) after fifteen weeks at full (A), one-half (B), one-fourth (C), and one-eighth (D) light intensity.

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FIGURE 9. Average leaf width in populations of *Deschampsia caespitosa* from Rollins Pass (circles), Colville (squares), and St. Michael (triangles).



FIGURE 10. Average leaf width in populations of *Trisetum spicatum* from Rollins Pass (circles), Central Ungava (squares), and Greenland (triangles).



FIGURE 11. Leaf density-thickness (mg/cm²) in the Rollins Pass (circles), Colville (squares), and St. Michael (triangles) populations of *Deschampsia caespitosa*.

finding for *Oxyria digyna* (Mooney and Billings, 1961) might indicate that arctic populations in general possess more chlorophyll than their alpine counterparts.

A reduction in chlorophyll content on a fresh-weight basis under high light intensity is what one would normally expect, and the responses of the arctic populations do not appear to be different from those of the alpine populations. This generally confirms Montfort's suggestion (1953) that the depression of chlorophyll content by high light intensity is as great in alpine plants as in others. This reduction could be due to a destruction of chlorophyll or a reduced synthesis. Interestingly, on a fresh-weight basis there was not an increase in chlorophyll with a reduction in light intensity, and in the Colville, Alaska, population of D. caespitosa there was even a progressive decrease in chlorophyll content.

The decrease in the chlorophyll a-to-b ratio under reduced light conditions was observed in all populations and was accompanied by an increase in total carotenoids. This increase in "accessory pigments" was also found by Björkman and Holmgren (1963) in *Solidago virgaurea*, and some populations of this species also possessed higher rates of photosynthesis under low light intensities. The influence of the content of accessory pigments on photosynthesis is not known, but its universal change with intensity suggests some adaptive value. It might play some role in coordinating the activities of the two light reactions now known to take part in photosynthesis. The population of each species which grew best under the low light conditions was also the one which possessed the highest chlorophyll content as well as being the one which showed the greatest



FIGURE 12. Leaf density-thickness (mg/cm²) in the Rollins Pass (circles), Central Ungava (squares), and Greenland (triangles) populations of *Trisetum spicatum*.



FIGURE 13. Total chlorophyll on a fresh-weight basis in the Rollins Pass (circles), Colville (squares), and St. Michael (triangles) populations of *Deschampsia caespitosa*. Brackets represent 95 percent confidence intervals.



FIGURE 14. Total chlorophyll on a fresh-weight basis in the Rollins Pass (circles), Central Ungava (squares), and Greenland (triangles) populations of *Trisetum spicatum*. Brackets represent 95 percent confidence intervals.

change in the chlorophyll a-to-b ratio. The relationships between the pigment concentration and the chlorophyll a-to-b ratio and photosynthesis are also not known, but growth under low light intensities could conceivably be enhanced by an increase in the rate of photosynthesis under these conditions.

The process of adaptation to the environment of the Arctic and the Alpine evidently involves some genetic differentiation, but from the information derived from this investigation it can be seen that all northern populations of any one species do not necessarily react in the same manner. The St. Michael, Alaska, population of D. caespitosa, for example, was more similar to the alpine population than to the Colville, Alaska, population in a number of characteristics including leaf width, density-thickness, and chlorophyll on an area basis. An analysis of a larger number of populations from arctic, subarctic, and various alpine locations will be needed to determine the significance of the intermediate responses of this subarctic population. In T. spicatum the pattern was similar, but in this species the Greenland population actually possessed less chlorophyll than the alpine population, and the alpine population showed better growth under low light than did the Greenland plants. The adaptive nature of some of these physiological differences might become more apparent as more of the environmental factors are investigated, and the adaptive value of any one character would presumably be most evident in arctic and alpine transplants or in simulated arctic and alpine environments. It is hoped that further studies will reveal the significance of the adaptive changes and population differences found in this investigation.



FIGURE 15. Total chlorophyll on a leaf-area basis in the Rollins Pass (circles), Colville (squares), and St. Michael (triangles) populations of *Deschampsia caespitosa*. Brackets represent 95 percent confidence intervals.



FIGURE 16. Total chlorophyll on a leaf-area basis in the Rollins Pass (circles), Central Ungava (squares), and Greenland (triangles) populations of *Trisetum spicatum*. Brackets represent 95 percent confidence intervals.



FIGURE 17. Chlorophyll a-to-b ratios in the Rollins Pass (circles), Colville (squares), and St. Michael (triangles) populations of *Deschampsia caespitosa*.



FIGURE 18. Chlorophyll a-to-b ratios in the Rollins Pass (circles), Central Ungava (squares), and Greenland (triangles) populations of *Trisetum spicatum*.

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