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Effects of Daylength and Temperature on Root Elongation in Tundra Graminoids

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Summary. Effects of soil temperature and daylength on root elongation of *Carex aquatilis, Dupontia fischeri,* and *Eriophorum angustifolium* were studied under both field and phytotron conditions. Late season decrease in root elongation rate and cessation of root elongation in *Dupontia* and *Eriophorum* are shown to be controlled by decreasing daylength. During the growing season, low temperature is not a direct factor in limiting root growth in any of the three species despite the presence of permafrost and low soil temperatures in the shallow thawed soil layer. In the phytotron, temperature-dependence of root elongation is related to experimental conditions characterized by continuous light. Plants of all three species are capable of root growth at near-freezing temperatures.

Introduction

Seasonal progression of root growth in the field has been measured for many species from diverse environments (Stukey, 1941; Fernandez and Caldwell, 1975; Ares and Singh, 1974; Lyr and Hoffman, 1967). Also, temperature control of root elongation under experimental conditions has been demonstrated for a number of species (Richards et al., 1952; Whittington, 1967). In view of this, it is surprising that the effect of temperature on root elongation in nature still remains relatively unknown. There is little information on photoperiodic controls of root elongation, although the effect of photoperiod on tuber formation and root thickening in crop plants is well-known (Garner, 1936; Evans, 1975). Stahel (1972), however, did find some decrease in root growth of *Picea sitchensis* seedlings after transfer from long day to short day.

The purpose of our paper is to describe a response of root elongation to daylength in plants of three arctic species and to evaluate the interactions between soil temperature and daylength under both laboratory and field conditions. Field measurements were made at the U.S. IBP Tundra Biome Site 2 near Barrow, Alaska (71°20′N, 156°42′W) during the summer of 1974. Laboratory experimentation was done in the Duke Phytotron Unit of the Southeastern Plant Environment Laboratories.

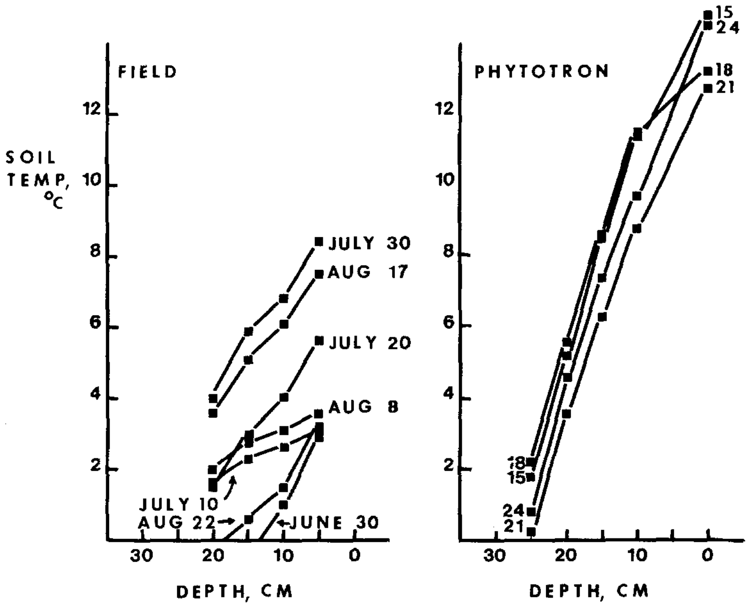

Fig. 1. Mean daily temperatures at 5 cm depth intervals in typical root observation boxes. Field data are taken from Box #11, containing a pure stand of *Eriophorum*. Phytotron data are from a *Carex* root observation box. Numbers beside phytotron data points denote daylength in hours

Research Site and Species

The environment at Barrow is characterized by extremes of photoperiod. The sun remains above the horizon continuously there from May 11 to August 2. However, the growing season of 50–80 days does not begin until the soil begins to thaw in mid-June; it extends into late August. Only during the last three weeks of August do the plants experience nights, which rapidly become longer and darker. By early September, daylength is only 15–17 h.

Soil temperatures are low throughout the growing season (Nakano and Brown, 1972), due partly to the presence of an underlying permafrost layer 300–350 m thick. The soil is frozen completely for about 9 months. Soil thawing begins with snowmelt about June 15 and proceeds until a maximum depth of approximately 30–35 cm is reached in early August. During the peak of the growing season, soil temperatures may reach 20° C just beneath the surface moss layer, dropping off sharply to 0° C at the bottom of the thawed layer. Daily temperature fluctuations in the upper soil levels can be considerable, often spanning 10–15° C; frequent fog and clouds, however, make this rather unusual. Daily mean soil temperature throughout the soil profile begins decreasing in mid-August until freezing begins both from the top down and from the bottom up in mid-to-late September (Nakano and Brown, 1972).

The Alaskan wet coastal tundra vegetation is dominated by grasses and sedges (graminoids). Near Barrow, three species—*Carex aquatilis* Honck., *Dupontia fischeri* R.Br., and *Eriophorum angustifolium* Wahlenb.—account for

57–95% of the annual aboveground primary production (Dennis and Tieszen, 1972; Tieszen, 1972; Bunnell et al., 1975). Plants of all three principal graminoid species were used in our research.

Methods

In both the field and phytotron studies, plants were grown in wedge-shaped boxes with clear Plexiglas sides (Trent, 1972; Billings et al., 1976), which allowed marking and observation of individual roots. Natural sod blocks from stands of single species were transplanted into the field boxes 1 to 3 years before measurements were made. In the phytotron, 10 individual tillers of one of the three species were planted in peat in each box. Two boxes of each species were used in the phytotron, while field measurements used 11 *Carex* boxes, 9 *Dupontia* boxes, and 10 *Eriophorum* boxes. Field boxes differed from those in the phytotron by having drainage slits at the bottom of the wedge.

Vertical temperature gradients were created in the phytotron by immersing the bottoms of the root growth observation boxes in a cold ethylene glycol bath (Trent, 1972; Billings et al., 1976). We used a bath temperature of $-4°$ C to maintain an artificial "permafrost" at 25 cm depth, with a constant air temperature in the growth chamber of 10° C. Soil temperature at any level in the vertical gradient did not vary more than 2 to 3° C through the course of the experiment (Fig. 1). The plants were grown with daily watering, weekly addition of half-strength Hoagland's solution, and constant light for two months before the first measurements were taken. Thereafter, measurements were made at 2- to 3-day intervals. After 40 days of measurement under continuous light, photoperiod was reduced to 21 h, and, after 39 and 43 days, respectively, to 18 and 15 h.

Root box temperatures in the field were not controlled. The boxes were placed in the same holes from which the sod blocks they contained had been removed. Field root box temperatures were 2 to 5° C higher than those in an undisturbed soil profile. Measurements were made at 2- to 4-day intervals throughout the 1974 growing season. In both field and phytotron, temperatures were recorded by means of thermocouples placed at 5 cm depth intervals.

Results

a) Field Root Elongation

Carex, Dupontia, and *Eriophorum* differed in their patterns of root elongation both with depth and over the course of the growing season (Table 1). These results are presented as means of all measurements on all boxes for each species, depth interval, and time period for the 1974 season. Results from the 1972 and 1973 seasons were inconclusive due to the relatively small number of root boxes available in those years, and to the fact that observations were not carried to the end of the season. Billings et al. (in press) noted a tendency toward higher elongation rates in all three species in the better-drained sites in 1972, but this was not apparent in 1974.

There were no differences in mean rate of root elongation with depth in *Dupontia.* Apparently, the factors limiting elongation in this species are constant through the soil profile. Observations were not made below 20 cm on this species in 1974 because roots were not observed growing below that depth. Measurements of *Dupontia* root elongation were made only of those roots which appeared at the root box face during the current year; *Dupontia* roots did not continue to elongate after their first year. The decline in rate of root elonga-

Table 1. Field root elongation rates of *Carex*, *Dupontia*, and *Eriophorum* in mm per 10 days. Each number is the mean, ± one standard deviation, of all observations in each 5 cm depth increment for each 10-day period through the 1974 season. Numbers in parentheses denote number of observations. n.d. indicates no data obtained. Time periods: 1=July 9–18, 2=July 19–28, 3=July 29-Aug. 7, 4=Aug. 8–17, 5=Aug. 18–27, 6=Aug. 28-Sept. 8

Species	Time period	Depth interval					
		0–5 cm	5–10 cm	10–15 cm	15–20 cm	20–25 cm	25–30 cm
Carex	1	n.d.	n.d.	2.0(1)	n.d.	n.d.	n.d.
	2	2.2± 1.1(7)	2.3±1.4(10)	2.3±1.5(8)	6.2±3.1(9)	4.4±3.0(5)	n.d.
	3	1.6± 1.3(11)	3.1±1.4(10)	2.9±1.7(14)	1.5±1.2(4)	3.9±2.8(18)	5.1±1.9(5)
	4	7.8±13.6(9)	1.6±1.2(27)	1.2±1.0(29)	0.3±0.6(8)	0.8±1.5(7)	2.9±2.0(2)
	5	7.3±14.4(9)	0.9±1.0(13)	3.3±6.2(30)	1.6±1.6(6)	0.0(3)	0.0(1)
	6	3.1±6.4(10)	0.4±0.6(16)	0.5±0.6(35)	0.4±0.4(12)	0.5±0.5(4)	1.3±0.1(2)
Dupontia	1	1.9±1.0(2)	n.d.	n.d.	n.d.	n.d.	n.d.
	2	2.0±1.4(46)	2.6±1.9(86)	1.6±1.3(24)	n.d.	n.d.	n.d.
	3	1.0±1.8(35)	1.1±1.8(128)	1.2±1.7(50)	1.1±1.4(6)	n.d.	n.d.
	4	0.3±0.7(144)	0.1±0.6(92)	0.0(6)	n.d.	n.d.	n.d.
	5	0.0(16)	0.1±0.5(104)	0.01±0.1(66)	0.0(5)	n.d.	n.d.
	6	0.0(16)	0.1±0.3(104)	0.0(64)	0.0(6)	n.d.	n.d.
Eriophorum	1	n.d.	2.1±2.4(2)	n.d.	n.d.	n.d.	n.d.
	2	2.8±2.0(7)	3.1±2.1(28)	4.4±2.4(48)	7.1±13.7(50)	6.6±0.4(3)	n.d.
	3	2.2±3.2(5)	4.4±2.3(13)	5.2±3.1(25)	4.2±3.2(39)	6.4±3.0(35)	6.4±2.1(4)
	4	0.7±1.5(11)	1.6±1.5(37)	4.7±2.7(8)	2.8±1.9(21)	3.4±2.7(19)	4.5±1.6(4)
	5	0.0(10)	0.4±0.7(17)	0.7±1.6(9)	1.5±2.2(8)	0.7±1.4(9)	5.7(1)
	6	0.1±0.3(9)	0.2±0.4(28)	0.0(8)	0.3±0.4(10)	0.1±0.2(10)	n.d.

tion in *Dupontia* during the season (Table 1) is a results of the slowing down and cessation of growth of large numbers of roots initiated from rhizome nodes beneath tillers in their first year aboveground (Shaver and Billings, 1975; Shaver, 1976). New roots rarely were found attached to tillers more than 1 year old. After about the first week of August, *Dupontia* roots stopped growing downward and began production of a large number of short (10 – 15 mm), fine lateral roots. Most roots also completed lateral production by the end of their first year.

Eriophorum roots elongated at their greatest rates at the bottom of the soil profile (Table 1), where soil temperatures were lowest (Fig. 1). The rate of *Eriophorum* root elongation also declined as the season progressed, although the decline was delayed somewhat in comparison to that in *Dupontia*, and there was some root growth into September (Table 1). Mean elongation rates at all depths were in general much higher than in *Dupontia*.

The root elongation pattern with season and depth in *Carex* was more complex than that of the other two species. There was a tendency for *Carex* roots to grow faster near the surface later in the season. Elongation rates at all depths were low during the final 10-day period of measurement. *Carex* roots grew at rates intermediate to those of *Dupontia* and *Eriophorum*.

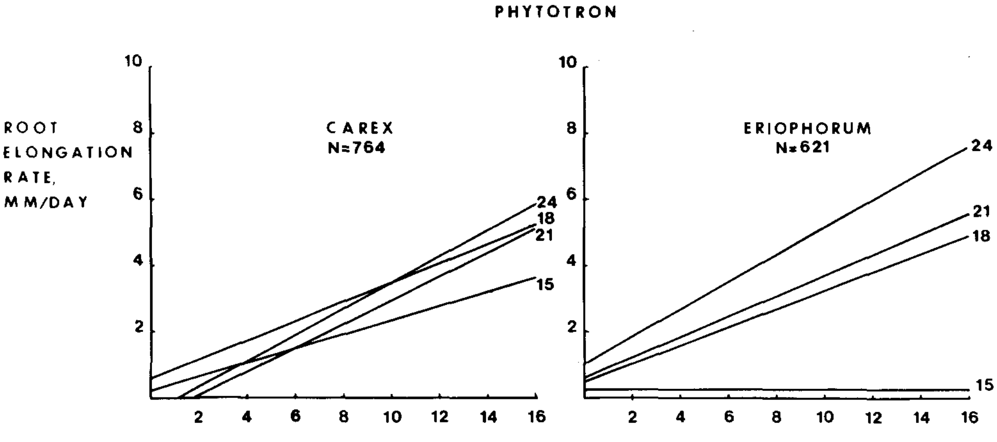

Fig. 2. Root elongation in mm per day of *Carex* and *Eriophorum* as a function of temperature and photoperiod in the phytotron experiment. Numbers beside regression lines denote daylength in hours. N = number of observations

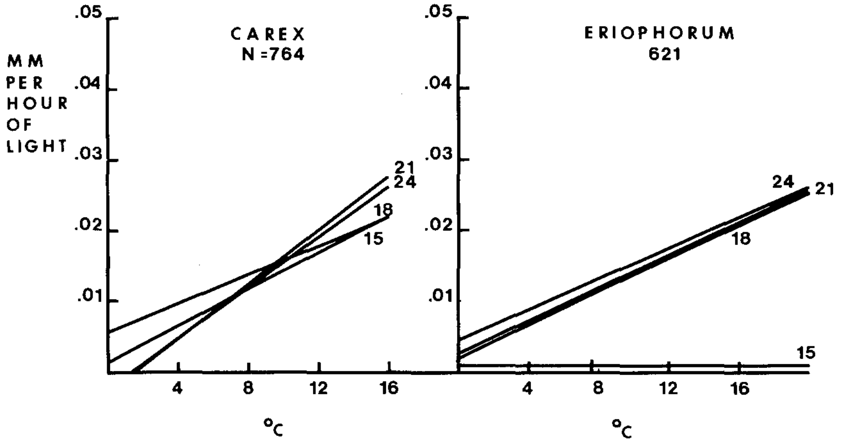

Fig. 3. Root elongation of *Carex* and *Eriophorum* in the phytotron experiment in mm per hour of light plotted against soil temperature. Numbers beside regression lines denote daylength in hours. N = number of observations

It was expected that root elongation in the field would be correlated with soil temperature, since Trent (1972) had previously demonstrated strong temperature dependence in his growth chamber studies. However, comparison of Figure 1 with Table 1 shows that *Dupontia* root elongation had little relationship with soil temperature, *Eriophorum* growth was inversely related to temperature, and *Carex* root growth was unpredictable with respect to temperature in the field. Soil temperature may be a factor in the lowering of root elongation rates in general as soil temperature decreased throughout the profile late in the season. Even so, there were occasional warm days in mid- to late season, as is shown in the data from August 17 (Fig. 1).

Table 2. Mean rates of root elongation in *Dupontia* under decreasing photoperiods in the phytotron (± 1 SE)

Photoperiod, hours	Elongation, mm per day	Elongation, mm per hour of light
24	2.09 ± 0.20	0.087 ± 0.005 ($n = 120$)
21	1.63 ± 0.32	0.078 ± 0.016 ($n = 24$)
18	2.35 ± 0.40	0.131 ± 0.022 ($n = 6$)
15	0.0	0.0

b) Phytotron Root Elongation

The range of temperatures through the soil profile in the phytotron was greater than the gradient of daily mean temperatures recorded in the field (Fig. 1). Temperatures were fairly constant, increasing slightly under the 18 and 15 h daylengths due to occasional freeze-up of the water bath and resulting inefficient cooling. There was no discernible diurnal temperature variation through the soil profile.

Results of the phytotron experiment are presented in Figures 2 and 3 and Table 2. *Dupontia* root elongation was not significantly correlated with temperature or depth, and the results have been calculated as simple means of all observations. The slopes of the regression lines for root growth measurements in *Carex* and *Eriophorum* are all significant to at least $P < 0.01$.

The effect of daylength on *Dupontia* and *Eriophorum* was strong: root elongation stopped at 15-h daylengths. *Carex* was much less affected, if at all. Differences between slopes of the regression lines for *Carex* could not be tested due to the non-homogeneity of the error mean squares about the regression lines but there is a continuous decrease in slope from 24–21 to 18–15 h.

The results for all three species under continuous light reflected the early season differences in elongation rate between species in the field. *Eriophorum* roots grew at the fastest rates in both field and phytotron; *Dupontia* was the slowest. Since the phytotron data also showed *Eriophorum* root growth to be temperature-related, it appears that *Eriophorum* roots are adapted to relatively rapid elongation at the very low temperatures at the top of permafrost where most of its root tips occur (Shaver and Billings, 1975). However, since the field results showed that any temperatures above 0° C do not limit growth in *Eriophorum* roots, this ability may be of importance in nature primarily in relation to nutrient uptake or some other factor.

The changes in root elongation rate with decreasing daylength in the phytotron were not simply the results of decreased amount of time available for photosynthesis. The fact that no root elongation took place under the 15 h daylength in *Dupontia* and *Eriophorum* is sufficient demonstration of an innately controlled shift in root elongation with daylength, although the receptor and physiological control mechanism have not been identified. All three species maintained a large amount of apparently healthy green leaves throughout the experiment, although there was some leaf senescence in *Eriophorum* under the 18 and 15 h regimes, and older *Carex* and *Dupontia* leaves became chlorotic at daylengths of 15 h.

The phytotron root elongation data may also be expressed on a mm per hour of light basis by dividing mm per day by the daylength. This transformation corrects for the decrease in daily photosynthesis in the 21, 18, and 15 h regimes, and is a more direct indicator of changes in allocation of photosynthate to roots than mm per day.

The transformation tends to reduce the differences between the 24, 21, and 18 h treatments in all three species (Fig. 3, Table 2). The results for *Eriophorum* are particularly striking: differences between the 24, 21, and 18 h regimes become very small and probably insignificant. Apparently in *Eriophorum,* the allocation of carbohydrates to root growth as a proportion of total daily photosynthate is not affected by daylengths greater than 18 h. Even so, the total amount of photosynthate available for root growth declines, resulting in lower root elongation on a mm per day basis (Fig. 3). Between 18 and 15 h, the supply of photosynthate to *Eriophorum* roots declines and root growth stops. The same cessation of root growth at daylengths of less than 18 h occurred in *Dupontia* (Table 2). Webb's (1976) results for birch seedlings showed similar dependence of root elongation on photosynthate supply.

Discussion

Comparison of the field and phytotron results demonstrates the difficulty of applying experimental results to field conditions. Trent (1972), using the same phytotron apparatus used in our work, found significant temperature-related root elongation rates in *Dupontia* as well as in *Carex* and *Eriophorum.* The relationships among species in his study were approximately the same as reported here for continuous light, although the measured elongation rates at all temperatures were considerably higher. Trent used a slightly higher growth chamber temperature (12° C) and applied more nutrients to his plants while maintaining soil moisture near field capacity. In our experiment, phytotron root boxes were water-saturated to more closely approximate field conditions.

It is clear that late season changes in root elongation in the dominant tundra graminoids are controlled by daylength in *Dupontia* and *Eriophorum.* Influence of decreasing daylength on *Carex* root growth appears to be weak and may or may not be important in natural situations. The importance of soil temperature above 0° C during the growing season as a factor limiting to root elongation apparently is a function of experimental conditions and may not be as significant as other environmental factors in the tundra itself. This is in agreement with an earlier observation by Billings et al. (in press). Since plants of all tundra species are generally tolerant of low temperatures during the growing season (Billings and Mooney, 1968), soil oxygen levels and nutrient availability, along with photoperiod, may be more limiting than temperature during the growing season and in initiating dormancy.

Photoperiodic control of root elongation may be of considerable importance in *Eriophorum*, which has an annual root system (Shaver and Billings, 1975). It should be of some selective value to *Eriophorum* plants to be able to stop root growth and start mobilization of carbohydrates and other compounds in the stembase before the soil begins to freeze and recovery becomes impossible. Recovery of nutrients by the stembase or rhizome at the end of the growing season from perennial root systems, such as those of *Dupontia* and *Carex*, is not so imperative as in *Eriophorum*. Photoperiodic controls of root elongation, or lack of them, in *Carex* and *Dupontia* are probably related to seasonal changes in partitioning of carbohydrates among roots, leaves, rhizomes, and inflorescences.

Additional information is needed on the nature of the photoperiodic signal initiating growth responses in tundra plants. Teeri (1974, 1976) has proposed that changes in spectral distribution of light at low sun angles, as well as low light intensity, may be involved in the induction of photoperiodic responses in plants which do not experience a true night except near the end of the growing season. For example, *Dupontia* root elongation begins to slow down remarkably in early August at Barrow (Table 1). Even though the sun first dips below the horizon at midnight, August 2, there is still a twilight at midnight for a week or more. This reduction in irradiance plus a possible shift in spectral quality may be the cue for stopping of root growth in both *Dupontia* and *Eriophorum* since soil temperatures are still well above freezing and not far below their seasonal maxima (Peterson and Billings, 1975).

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