Effect of Soil Temperature on Rate of Barley Development and Nutrition


ABSTRACT

Results from this experiment indicate that for barley plants harvested at equal stages of morphological development, low soil temperatures per se are not detrimental to growth. Barley was grown to maturity in a growth room at soil temperatures of 9, 15.5, and 22°C with either 9 or 44 ppm fertilizer phosphorus. At a given stage of plant development, dry matter production and N and P uptake were usually lowest at a soil temperature of 22°C. Dry weights, grain yields, and nutrient uptake at 9°C usually equalled or exceeded those at 15.5°C— the soil temperature considered optimum for barley production. At 9°C growth was very slow until the barley developed to the 4-leaf stage, but thereafter approximated the growth rate at higher soil temperatures. Nutrient uptake and water use data suggest that the slow initial growth rate at 9°C may be due to restricted nutrient translocation from roots to tops, rather than to reduced rate of uptake of water or nutrients. Soil temperatures affected both the growth rate and water use rate, resulting in only a small effect of soil temperature on total water used to reach a given growth stage.

Additional index words: Plant morphology, Plant nutrition, Translocation, Top/root ratio.

Within the past decade the volume of published literature concerning the effects of soil temperature upon plant growth has multiplied several times (7). Although soil temperature experiments are conducted for various purposes, the techniques used are surprisingly uniform. Typically, a test crop is grown in a light-temperature-controlled plant growth chamber, or a greenhouse, at several soil temperatures for a certain length of time—usually 1 to 50 days. During this period the plants may be monitored for various morphological or physiological changes; then the plant material is usually harvested and analyzed for various chemical constituents. Afterwards interpretations of the effects of soil temperature upon numerous plant growth processes are made.

The use of such techniques has resulted in a number of publications implying that low soil temperatures severely restrict plant growth and nutrition (5, 7). However, a few publications show that reduced soil temperatures generally reduce the rate of morphological development of a plant (4, 7, 10, 11). Consequently, in experiments in which plants of equal calendar age are compared, the effects of soil temperature on plant growth and nutrition are confounded by differences in physiological and morphological maturity. This confounding has often led to the erroneous conclusion that below-optimum soil temperatures severely retard plant growth. This conclusion frequently is drawn in experiments confined to germination or seedling periods, or in certain biochemical studies involving short time periods (7).

The purpose of the research reported here was to obtain quantitative data on the effects of controlled soil temperatures upon spring barley growth and nutrition as measured on plants equal in morphological development. A phosphorus variable was included to determine how these effects were conditioned by nutrient availability.
METHODS

No. 10 cans were filled with Parshall fine sandy loam (2810 g per can can oven-dry equivalent) to which the following fertilizer elements were added as inorganic salts: 120 ppm P (NH₄NO₃), 50 ppm K, 5.6 ppm Mg, 0.07 ppm B, 0.3 ppm Mn, 5.6 ppm Zn, 0.08 ppm Cu, 0.007 ppm Mo, and 2.5 ppm Fe. In addition, concentrated superphosphate was mixed with the soil at two rates -- 9 and 44 ppm P. The cans of soil were placed in constant temperature water baths (12) at 9, 15.5, and 22C (± 0.5) in a plant growth chamber maintained at an air temperature of 22C.

Nine seedlings of spring barley (Hordeum vulgare L., var. Sacramento), grown in washed sand at 15C to the 2-leaf stage, were transplanted into each can of soil. Five days later, stands were thinned to eight plants per can. The soil surface of each can was covered with shredded aluminum foil to a depth of 2 cm to reduce temperature gradients at the soil surface. Soil water content was maintained above 50% of the available waterholding capacity by daily (twice daily in later stages of growth) weighing and watering of each can. Light intensity at 15 cm above the cans was about 12,000 lux for a 16-hour day. Relative humidity normally varied between 30 and 50%. All treatments were replicated three times in a split-block design with soil temperatures as main plots.

Notes were taken weekly on plant height, color, and morphological development. Plant material was cut at the soil surface and roots washed free of soil whenever half of the plants for a given treatment were at the 3-leaf, 4-leaf, tillered, headed, soft dough, and mature stages of plant development. Specific criteria used in defining these stages of development were: (1) 3-leaf = third leaf 1/2 length of preceding leaf; (2) 4-leaf = fourth leaf 1/2 length of preceding leaf; (3) tillered = no increase in number of tillers for 3 days; (4) headed = flowering with pollen shedding; (5) soft dough = kernel doughy when opened; and (6) mature = all hulls and awns yellow. On the Feeke scale (8), these samplings correspond approximately to stages 1.5, 2.0, 4.5, 10.5; 11.2, and 11.4, respectively. Leaf area was measured from tracings of leaves, and plant material (tiller and roots) was oven-dried (70C), weighed, ground, and analyzed for total N and P.

To reduce border effects and variability, all cans in each soil temperature tank were rotated daily. Also, voids in the tanks created by the harvest and removal of plant material at each plant sampling date were filled with plants growing in similarly fertilized cans of soil. These replacement plants were grown in the greenhouse at 9C, and were equal in age to the plants harvested.

RESULTS

Dry Matter Production

Dry weights of barley tops and roots are shown in Fig. 1. The effects of both time (calendar day) and stage of morphological development upon dry weights are illustrated. The latter comparison may be made by comparing dry weights at equal stages of development, as indicated by the same numbers on the graphs — for example, all plants at tillering are indicated by 3. For any given number of days after transplanting, dry weights of tops were least for barley grown at the 9C soil temperature. Greatest top growth occurred at the 22C soil temperature for the first few weeks after transplanting and at 15.5C thereafter. Greatest root growth prior to any given day generally occurred at the 15.5C soil temperature. Root weights for the 22C soil temperature failed to show a rapid rate of increase as was observed for tops. Higher P rates generally increased dry weights.

When dry weights are compared at equal stages of morphological development, a completely different picture emerges. Prior to heading, top growth of barley at 9C was equal to that at the other two soil temperatures. At heading top growth was greatest at 15.5C, but by maturity top growth at 9C was greater than that at 22C and approximately equal to that at 15.5C. Changes in root growth followed much the same pattern. The increase in both top and root growth at 9C was approximately linear with time from the 4-leaf stage to maturity. At 15.5C soil temperature, growth ceased after the soft dough stage for both tops and roots. At 22C little or no growth occurred after heading.

Dry weight of barley grown at the 9C soil temperature increased only slightly in the 22 days from transplanting to the 4-leaf stage. At 22C, only 10 days were required for barley to develop to the 4-leaf stage. Development from the 4-leaf stage to maturity, however, required 70 days at 9C, and 69 days at 22C soil temperatures. Consequently, it appears that a period of adjustment was required for the barley plant to initiate rapid growth and development. This period of adjustment was shorter at the higher soil temperatures. However, once this period was over, growth rates for the different soil temperatures were very similar. This indicates that low soil temperatures did not greatly alter growth processes after this period of adjustment.

Morphological Development

Some quantitative effects of the treatments under study upon morphological development are shown by data in Table 1. The number of culms per plant at the tillering stage was significantly increased by the higher P level, and was least for the 9C soil temperature. The number of flag leaves per plant (10.1 on the Feeke scale) was greatest for the 9C treatment, and was increased by higher P. However, many tillers senesced and failed to produce mature heads. Mature heads per plant were significantly greater at the 9C soil temperature, and were increased only slightly (not significantly) by higher P levels. The weight of...
mature grain produced per plant was increased by the higher P level, and was lowest at the 22C soil temperature. Grain production was similar at 9 and 15.5C soil temperatures. Plants grown at the 15.5C soil temperature were normal in color, appearance, and development. Barley grown at 22C soil temperatures appeared normal until about the flag-leaf stage of growth. Shortly thereafter leaves became necrotic much more rapidly than for other treatments. Plants grown at 9C had normal green leaves, many of which they retained to maturity.

Water Use

Water use data as a function of both dry weight and leaf area are given in Table 2. These are essentially transpiration data, since evaporation from uncropped cans of similarly treated soil was usually less than 10 ml per day. Water use per gram dry matter of tops was generally highest at the 22C soil temperature until soft dough. The time-weighted average water use per g dry weight from transplanting to maturity also was highest at 22C. Water use per g dry weight was generally reduced by the higher P rate. On a unit leaf area basis, water use was lowest at 15.5C soil temperature until after heading. The validity of such calculations after heading is questionable since green leaf area was diminishing rapidly while the transpiring surface of the stem and head was increasing. Total quantity of water used per plant from transplanting to harvest was increased slightly by increased soil temperature, as well as by the higher P rate.

Plant N

Percent total N in barley tops and roots is shown as a function of time in Fig. 2. Maximum percent total N in tops occurred at the 4-leaf stage for all treatments. Since morphological development was much slower at the 9C soil temperature, rate of increase in percent total N from the 2-leaf to the 4-leaf stages was least for the 9C treatment. After the 4-leaf stage, neither soil temperature nor P fertilization had a great effect on percent total N in tops at a given stage of growth.

Percent total N in roots reached a maximum during the 4-leaf to tillering period. At the 3- and 4-leaf stages, percent total N in roots was markedly less at 22C than at lower soil temperatures. In fact, at 22C total N in roots actually declined to values as low as 0.07% between transplanting (2-leaf) and the 3-leaf stage 7 days later.

Total N uptake curves in Fig. 3 resemble those for dry weight in Fig. 1. At most stages of growth, soil temperature did not greatly influence total N uptake by barley tops. Major exceptions to this statement were higher total N uptake at heading for the 22C soil temperature with P, and at maturity for the 9C soil temperature without P. Total N uptake rate after heading was greatest at the 9C soil temperature. Like dry weights, the rate of total N uptake for the 9C soil temperature was markedly lower before the 4-leaf stage. Thereafter, rate of total N uptake was not closely related to soil temperature. On a calendar-day basis, however, total N uptake of tops was always lowest at 9C for at least the first 60 days.

Total N uptake in roots was near maximum at the heading stage for all treatments. Total N in roots was lowest for the 22C soil temperature at the 3-leaf and 4-leaf stages. In fact, total N content for 22C with high P was only 0.2 mg N/can at the 3-leaf stage. After heading, total N in roots was often slightly higher at 9C than at warmer temperatures. On a calendar basis, total N uptake in roots generally decreased in the order of 15.5C, 22C, and 9C soil temperatures between about the 15th and 55th days.
NaHCO₃-soluble P content of the soil at each sampling date is listed in Table 4. Soluble P was greatly increased by higher P rates, and decreased with time. However, soil temperature had little or no effect upon P solubility at a given stage of growth. Thus, the difference in plant growth and development due to temperature cannot be attributed in any part to a difference in P availability. The rate of decline in P solubility corresponded very closely to stage of plant development in spite of the time differential involved for the various temperature treatments.

**DISCUSSION**

The data presented in the preceding section suggest that low soil temperatures affect plant growth and development primarily by reducing growth rates (10). Given sufficient time, it appears that barley grown at low soil temperatures will develop normally, and will attain its growth potential as dictated by environmental and genetic factors. Assuming plants grown at 15.5°C to be “normal” in development, plants grown at 9°C exhibited reduced growth before the 4-leaf stage and greater growth during the soft dough to mature stages. In general, the higher the soil temperature, the greater the growth activity during early stages of growth and the lesser the activity during later stages. High soil temperatures appear to hasten the aging process within the plant. This is in agreement with the conclusions of Geronimo and Beevers (3).

Had the data given in this paper been analyzed on a time scale, rather than as a function of stage of growth, the results and their interpretations might be quite different. For instance, after 10 days of growth, the data indicate that growth rates were maximum for 22°C soil temperatures, and that the 9°C temperature had a very adverse effect upon growth. At 40 days the 15.5°C soil temperature appears optimum for barley. Had the experiment been terminated at 70 days, the conclusion would probably have been that the 9°C temperature was very detrimental to growth. However, comparisons made at definite stages of plant development, in contrast to those made after a specified number of calendar days, indicate that high soil temperatures per se are generally more detrimental to barley growth than are low soil temperatures. Consequently, the conclusions drawn from a soil temperature experiment are conditioned to a considerable extent by the harvest schedules followed. A major argument in favor of harvesting by stage of growth, of course, is that most plants produced for economic purposes are harvested according to stage of growth.

In terms of practical application, more than the direct effects of soil temperature upon plant growth processes may be involved. It appears that the direct effect of reduced soil temperatures on plant growth is merely a reduction in growth rate, with only a slight or no reduction in potential yield. For field-grown crops, however, reduced growth rate could result in increased exposure to frost, disease, insects, and hail, as well as increased exposure to midsummer drought during the critical period of grain formation and filling. In the Great Plains, however, these disadvantages of low soil temperatures may be offset by a corresponding reduction in rate of evapotranspira-

---

**Table 3. Percent total P and total P uptake by barley tops and roots.**

<table>
<thead>
<tr>
<th>Soil temp, °C</th>
<th>Pert, F, ppm</th>
<th>3-leaf</th>
<th>4-leaf</th>
<th>Tiller</th>
<th>Head</th>
<th>Dough</th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>0.0204, 0.0201</td>
<td>0.0275, 0.0213</td>
<td>0.190, 0.197</td>
<td>0.199, 0.197</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.5</td>
<td>0.0326, 0.0229</td>
<td>0.0205, 0.0153</td>
<td>0.122, 0.144</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>0.0297, 0.0215</td>
<td>0.0265, 0.0209</td>
<td>0.197, 0.225</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Percent total P, roots</td>
<td>0.19</td>
<td>0.32</td>
<td>0.33</td>
<td>0.35</td>
<td>0.36</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>0.0204, 0.0201</td>
<td>0.0275, 0.0213</td>
<td>0.190, 0.197</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.5</td>
<td>0.0326, 0.0229</td>
<td>0.0205, 0.0153</td>
<td>0.122, 0.144</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>0.0297, 0.0215</td>
<td>0.0265, 0.0209</td>
<td>0.197, 0.225</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**Table 4. NaHCO₃-soluble P in soils after harvest of barley at various stages of plant growth.**

<table>
<thead>
<tr>
<th>Soil temp, °C</th>
<th>Pert, F, ppm</th>
<th>3-leaf</th>
<th>4-leaf</th>
<th>Tiller</th>
<th>Head</th>
<th>Dough</th>
<th>Mature</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>0.0204, 0.0201</td>
<td>0.0275, 0.0213</td>
<td>0.190, 0.197</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15.5</td>
<td>0.0326, 0.0229</td>
<td>0.0205, 0.0153</td>
<td>0.122, 0.144</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>0.0297, 0.0215</td>
<td>0.0265, 0.0209</td>
<td>0.197, 0.225</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

**Plant P**

Percent total P and total P uptake in barley tops and roots are given in Table 3. In general, P content and uptake varied in a manner similar to N content and uptake; therefore, the data are not shown on a time scale. Percent total P in tops at 9°C was greatest during the 4-leaf to tillering interval; at higher temperatures maximum values occurred at the 3-leaf stage. From tillering to maturity, percent total P in tops was greatest at 9°C. Percent total P was highest in roots at the 4-leaf stage for all temperatures. From tillering to maturity, percent total P in roots was greater for the 9°C treatment than for higher soil temperatures.

Total P uptake by tops increased until maturity for all treatments. Total P uptake between heading and maturity was greatest at the 9°C soil temperature than at higher temperatures. A similar trend was noted for dry weights. At the 3-leaf stage, total P uptake by tops was least for the 9°C treatment. Total P uptake in roots at 15.5 and 22°C was maximum at or even before the heading stage, but at 9°C increased until at least the dough stage. Total P content in roots was generally lowest for the 22°C soil temperature at all stages of growth; however, this effect was most pronounced during earlier growth stages.
tion, thereby delaying the advent of water stress. Consequently, with a given level of soil water, yields of small grains in semiarid regions may be highest in years of below-normal temperature (1, 6).

Kramer (5) advanced the theory that reduced growth rates at low soil temperatures resulted from restricted root absorption of soil water. This theory has since been developed by other investigators, showing that plant water deficits increased as plants were subjected to lower soil temperatures. Although no water deficit measurements were attempted in this experiment, water use rates until heading were reduced by lower soil temperatures (rates can be calculated by dividing the water use data in Table 2 by the respective time interval between growth stages). This of course occurred because low soil temperatures slowed the rate of plant development. However, the water use data from this experiment indicate that while low soil temperatures do reduce rates of water use, they have much less effect upon the quantity of water transpired between given stages of growth.

The fact that reduced soil temperatures reduce both water use rate and growth rate, resulting in little reduction in total water use, lessens the validity of the argument that plant growth at low soil temperature is restricted by the rate of water entry into the plant. It is unfortunate that in most studies on this subject, water use rates were measured only for a few hours or days, and no accounting was made of total water use. Consequently, the conclusions arrived at from such experiments agree with those arrived at from short-term measurements of dry matter accumulation rates — namely that suboptimum soil temperatures per se adversely affect plant growth. However, the data presented in this paper do not support this conclusion.

In reviewing the data presented here on dry matter production and nutrient uptake, several other facts stand out. All data indicate that at the 3-leaf stage, growth and nutrient uptake by barley tops were greatly stimulated by increased soil temperature. Growth and nutrient content of roots during early growth stages were generally lowest at the highest soil temperatures. These observations might be interpreted to indicate that the higher soil temperatures stimulated top growth at the expense of root development. However, since total nutrient uptake was not greatly affected by soil temperature, it appears that the lag period in growth that occurred at 9°C during early development could not be attributed to differential rates of nutrient absorption by roots. Rather, the data indicate that this lag period was associated with a reduced rate of nutrient transfer from roots to tops at low temperatures. However, the data presented do not reveal the cause for this reduced transfer rate — whether it was due to lack of sugar, lack of ATP, or other factors.

Boatwright and Haas (2), in a field experiment, measured little P uptake by spring wheat after the soft dough stage. In the cool year of 1958, however, Power et al. (9) measured significant P uptake after the soft dough stage. The results from such field experiments agree with the results of the experiment reported here in that greater growth and P uptake during maturity would be expected in the cooler year. These observations may have consequence in regulating the practice of swathing small grain for harvest. Generally, small grains are considered physiologically mature and can be swathed as soon as the water content of the grain is reduced to about 35%. Since it appears that at low soil temperatures growth processes continue to maturity, it may be that early swathing is detrimental to grain yield and quality in cool years.

LITERATURE CITED