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DEVELOPMENTAL AND TROPIC RESPONSES OF ZEA MAYS (L.)
AND ARABIDOPSIS THALIANA (L.) HEYNH. TO TEMPERATURE
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By

Marie-Claude Fortin

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ABSTRACT

DEVELOPMENTAL AND TROPIC RESPONSES OF *ZEA MAYS* (L.) AND *ARABIDOPSIS THALIANA* (L.) HEYNH. TO TEMPERATURE CONDITIONS SIMULATING CONSERVATION TILLAGE

By

Marie-Claude Fortin

Some aspects of *Zea mays* (L.) (corn) growth have been investigated under temperature conditions simulating the presence of crop residue covers. First, the effects of a straw mulch on the development and the agronomic characteristics (aboveground biomass, height, nitrogen concentration, nitrogen uptake, leaf area, grain and stover yields) of corn were measured in irrigated field experiments. Growth of residue-treated plants was similar or enhanced when compared to bare soil controls at similar stages of development. Subsequently, field experiments were designed to verify that the developmental delays observed with plants grown with residue covers could be accounted for by decreases in seed zone temperature under the residues. Time and thermal time between specific vegetative stages were measured for an oat straw mulch, an inert poplar mulch and a bare soil treatment. The results suggest that allelopathy may be an additional source of developmental delay and that its occurrence is weather-dependent. Finally, since mulch management practices can create horizontal temperature gradients and since corn root responses to such conditions are unknown, experiments under controlled conditions were designed to test if and how root direction of corn can be altered by thermal gradients

perpendicular to the gravity vector. Primary roots of corn grown on agar plates exhibited positive thermotropism when exposed to gradients of 0.5 to 4.2 C cm^{-1}. In order to characterize this phenomenon without the interaction of gravity, a wild-type and a gravitropism mutant of *Arabidopsis thaliana* Heynh. were used. The results show that the extent to which root thermotropism is exhibited varies widely with species, and in corn, is dependent on the gradient strength and the temperature of exposure.

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INTRODUCTION

The no-tillage and conservation tillage cropping methods were developed in the Mid-West for the prevention of land degradation from soil, water and wind erosion associated with the traditional ways of preparing soil for row crops. Adoption of these systems relied mostly on the fact that conservation tillage also provides economy of labor and energy, and reduces evapotranspiration. Along with these benefits come some important disadvantages such as problems with weed control and soil temperature (Phillips and Phillips, 1984).

In the northern agricultural regions of this continent, the consequences of altered soil thermal regimes have been extensively studied because of their impact on crop plants, particularly Zea mays (L.). The single most important factor modifying soil temperature regimes in conservation tillage environments is the amount of mulch left on the soil surface (Potter et al., 1985). Crop residues modify the radiant energy balance, resulting in the following effects: soil temperature under the residues can be lower than under a bare soil (Gupta et al., 1983); the amplitude of diurnal temperature variations is reduced, decreasing the vertical gradients through the soil profile (Van Doren and Allmaras, 1978); and horizontal temperature gradients are created with systems that leave mulch materials in bands between the row or over the row (Allmaras and Nelson, 1971).

This work attempts to develop an understanding of corn growth associated with some of these modifications of soil temperature induced by conservation tillage. The first study examines how some of the agronomic characteristics of corn grown with a residue cover compare with those of corn grown without residue cover when developmental differences are taken into account. The second study quantifies the extent to which developmental delays can be attributed to soil temperature. Finally, the third study explores if and how corn roots respond to horizontal temperature gradients.

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LITERATURE REVIEW

MODIFICATION OF THE SOIL ENVIRONMENT BY CROP RESIDUES

The soil temperature of residue-covered fields is lower than that of bare soil surfaces (Willis et al., 1957; van Wijk et al., 1959; Burrows and Larson, 1962; Moody et al., 1963; Lal, 1974; Van Doren and Allmaras, 1978; Wierenga et al., 1982). During the day, crop residues cause a substantial decrease in temperature down to at least 10 cm, while at night the soil temperature is close to that of bare soils (Unger, 1978). This thermal regime results primarily from two different physical effects: higher reflectance or albedo of residues (Baumgardner et al., 1985) and insulation from layered air pockets trapped in the dead plant material (Gupta et al., 1981). Only a few authors (Gupta et al., 1981; Gupta et al., 1984; Unger, 1988) have attempted to model soil temperature under residue covers because of the complicated nature of these soil temperature changes. Residue covers are not always layered uniformly across a field and their local placement can result in horizontal temperature gradients (Wierenga et al., 1982). This effect can be superimposed on other horizontal heat fluxes in the upper soil profile. These fluxes result from row cropping and can be far greater than the vertical gradients (Horton, 1984). They can result from the orientation of rows, especially in the case of raised beds or ridge tillage (Voorhees et al., 1981). They can also be a consequence of short range spatial variability of the soil physical conditions due to natural soil heterogeneity and tillage operations, mostly in the 0-14 cm depth. Thus, Cassel (1985) recommends that these considerations be taken in account in soil prediction models.

The presence of residues on the soil surface results in other changes of physical, chemical or biological nature and they concern mostly soil water content, nutrient availability, phytotoxicity, and pest problems. In general, there is increased soil water content under mulched conditions (Moody et al., 1963; Kladivko et al., 1986) since residues contribute to water conservation by decreasing run-off and evaporation and increasing snow trapping (Unger et al., 1988). Higher soil water content also contributes to reduce soil temperatures and interacts with weed control, which in systems devoid of plowing, relies heavily on herbicides (Lindwall and Anderson, 1981). Residues can also be a source of phytotoxin release during rainfall or microbial breakdown. Toxicity varies with the nature and persistence of the residue (Guenzi et al., 1967; McCalla and Norstadt, 1974; Barnes and Putnam, 1983; Yakle and Cruse, 1984; Lodhi et al., 1987). Finally, residues contribute favorably to nutrient cycling, especially during the first season (Legg et al., 1971) although residues with low N content can reduce N availability in the first years and need to be accompanied by an appropriate nutrient management program.

Among all these changes brought about by the presence of crop residues, the ones concerning soil temperature have the most direct effect on _Zea mays_ (L.) (corn) growth during the early vegetative development.

TEMPERATURE AND ZEA MAYS (L.) SHOOT GROWTH

Most of the studies on corn shoot growth involving residue covers have been designed with some form of soil temperature monitering. As a result, there are several reports of positive correlations between the average soil temperatures resulting from residue applications (or conservation tillage) and corn growth and development characteristics such as early dry matter weight (van Wijk et al., 1959; Allmaras et al., 1964), leaf number to the sixth leaf stage (Swan et al., 1987), and relative growth rates (Al-Darby and Lowery, 1987). Thus, a slower growth rate or lower values of these various growth characteristics of the treatments involving residues have been attributed to decreased soil temperatures. Deviation from this general rule is usually interpreted as an interaction of soil water with soil temperature (Swan et al., 1987). All of these studies have assumed that lower soil temperatures under residues were the causal factor for observed growth differences with a bare control. There is little evidence to verify that this assumption is totally true. A few studies have related leaf number to an index integrating time and temperature (Al-Darby and Lowery, 1987; Swan et al., 1987).

Research under controlled conditions has shown that temperature directly affects the shoot growth rate whether it is measured as time to emergence or xth leaf number (Walker, 1969;

Hesketh et al., 1969; Alessi and Power, 1971; Swan et al., 1981; Tollenaar and Hunter, 1983), estimated as dry weight (Walker, 1969), measured as leaf elongation during a very short period of time (Barlow and Boersma, 1972), or monitered as leaf appearance or leaf initiation rates (Tollenaar et al., 1979; Warrington and Kanemasu, 1983).

Despite this clear demonstration of the dependence of corn development on temperature, most agronomic research has only characterized corn growth under residue cover after specific periods of time on a day of year scale. As reviewed by Al-Darby and Lowery (1986), the effect of residues is almost invariable with the residue or conservation tillage treatments not faring as well as the bare or conventional tillage treatments, except for values of final grain or stover yields. The confounding of slower growth rates on such measurements is inevitable and has been avoided only in isolated cases in studies of dry weight and N upatke by Meisinger et al. (1985) and Timmons et al. (1986), respectively. Thus, there is a need to obtain more information on corn shoot growth once developmental differences due to residue covers are removed.

TEMPERATURE AND ZEA MAYS (L.) ROOT GROWTH

As with shoot growth, root growth of corn has been studied with respect to residue covers, mostly in relation to soil water and soil temperature. Both the practical aspects of root research on temperature effects under field conditions (Rykbost et al., 1975), and research under controlled conditions on elongation, growth, weight, nutrient uptake, and branching have generally been done at constant temperature (Beauchamp and Lathwell, 1967; Blacklow, 1972; Kleinedorst and Brouwer, 1972; Cooper, 1973; Brouwer, 1981; Mackay and Barber, 1984) with minima, maxima, optima temperatures and rates defined for specific temperatures. However, Allmaras and Nelson (1971) who have studied root weight and root growth indices as a function of soil water and temperature under natural conditions, have emphasized the importance of the influence of the row-interrow temperature differences in determining branching and elongation of corn roots. Unfortunately, there is little known about root responses to this inherent property of soils: temperature gradients. Beauchamp and Torrance (1969) have evaluated the temperature gradient that exists in young corn shoots exposed to different air and root temperatures but have not studied the roots. There are a few studies on the influence of temperature on the direction of root growth in corn. Mosher and Miller (1972) have observed the lack of response of corn roots to a temperature gradient applied opposite to or in the same direction as the gravity vector. Sheppard and Miller (1977) reported that the gravitropic response of corn seedlings is influenced by both a constant temperature of exposure and a diurnal cycle imposed on the whole seedling. Finally, Onderdonk and Ketcheson (1973) determined that it is the maximum of such cycles which influences the direction of root growth in corn. However, there is no report of how and if horizontal gradients affect root growth apart from old reports of thermotropism (change in direction of growth as a result of a thermal stimulus) (Hooker, 1914; Rose, 1929). This work is presently discredited because of rudimentary methods and conflicting results reported by different authors. Despite the lack of modern investigation on the subject, thermotropism is considered non-existent in roots. In recent sensory physiology reviews, roots were characterized as gravity-sensors only (Firn and Digby, 1980; Halstead and Dutcher, 1987). A notable exception is the review of Jackson and Barlow (1981) where the limited knowledge about the influence of temperature on the angle attained by the root as a result of gravitropism is recognized.

One of the difficulties associated with studying the effect of temperature gradients on root direction is that temperature has a general effect on enzyme activities and most cellular processes (Voorhees et al., 1981). Therefore the different temperatures on the two sides of a root exposed to a thermal gradient could possibly induce "passive" changes in root direction without any "active" sensing. Another problem is the inescapable effect of gravity in determining at least in part, the direction of root growth. Since a direct approach to this problem resides in the use of gravity-insensitive mutants and since such mutants of corn are not available, a solution to this problem may reside in the use of another species as a model system.

ARABIDOPSIS THALIANA (L.) HEYNH. AS A MODEL SYSTEM TO UNDERSTAND PLANT PHYSIOLOGY

Arabidopsis thaliana (L.) Heyhn. is a small, self-fertilizing crucifer weed used in genetic work for over 40 years (Meyerowitz and Pruitt, 1985) which is becoming the "*Drosophila*" of the plant world. Because of its small size, its short life cycle of five weeks, easy light and nutrient requirements, and abundant seed set, it is easily and quickly grown to maturity in small pots. These conditions make it well suited for genetic work and several mutants have been isolated and characterized: phenotypic mutants used as genetic markers; biochemical mutants with lesions affecting respiration, photosynthesis, amino acid pathways, phytohormones, starch and lipid metabolism; and gravitropism and phototropism mutants with altered hypocotyl and root responses (Caspar et al., 1985; Estelle and Somerville, 1986; Khurana and Poff, 1989; Bullen et al., 1989; Meyerowitz, 1989). Several types of gravitropism mutants of Arabidopsis have been defined within the population of strains determined to have altered gravitropism (Bullen et al., 1989). These types have been classified on the basis of a 1-g induced curvature by rotating the plants on their side. "Random" strains have curvature frequency distribution histograms similar to that of wild-types grown on a clinostat (Bullen et al., 1989). On a clinostat, plants are continuously rotating and changing their perception of the gravity stimulus, and fail to orient their roots or shoots to a unilateral gravity vector (Volkmann and Sievers, 1979). Thus, these "random" mutant strains fail to detect the omnipresent 1-g force and constitute a unique possibility for studying how root respond to environmental variables. They could permit a definite answer to the question of temperature gradients on root growth.

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CHAPTER 1

DISTINCTION BETWEEN DEVELOPMENTAL AND GROWTH EFFECTS OF CROP RESIDUES ON ZEA MAYS (L.)

Experiments comparing Zea mays (L.) (corn) production under residue-covered and bare soil conditions (Willis et al., 1957; Burrows and Larson, 1962; Moody et al., 1963) and under conservation and conventional tillage (Griffith et al., 1973; Mock and Erbach, 1977; Timmons et al., 1986; Al-Darby and Lowery, 1986, 1987) have reported lower soil temperatures, delayed emergence, shorter plants and lower aboveground dry weights during the vegetative period, different whole plant nitrogen concentrations, and delayed silking. In general, the results have been summarized as residue-induced slower development and depressed growth of corn, and have been attributed to lower soil temperatures.

The effect of temperature on the development of corn has clearly been shown both in the field (Mederski and Jones, 1963; Watts, 1973; Swan et al., 1987), and under controlled conditions, from leaf initiation and/or appearance measurements (Beauchamp and Lathwell, 1967; Tollenaar et al., 1979; Warrington and Kanemasu, 1983) and number of days to tassel emergence observations (Bonaparte, 1975). Soil temperature effect on corn growth was investigated by Walker (1969) who showed that shoot dry weight and total leaf length were well correlated, and had a similar soil temperature optimum which was different from that of leaf initiation rate. Beauchamp and Lathwell (1967) also reported different effects of soil temperature on leaf development and on plant dry weight for corn grown until the sixth leaf stage. These studies indicate that leaf initiation and leaf growth should be studied independently with respect to temperature.

Since residue covers can have a dramatic effect on soil temperature (VanDoren and Allmaras, 1978), and therefore on leaf development rates, height and biomass measurements can become a function of the developmental stage early in the season. However, most tillage studies reporting plant height and aboveground biomass have measured growth parameters at rather arbitrary points in time with little consideration for developmental differences. Also, these studies often did not take emergence delays into account in the interpretation of later plant development measurements such as tasselling, silking or maturity dates. Therefore, there is a need in agronomic studies of tillage to distinguish between the effects of residues on growth (increase in size of an organ or a plant part) and the effects of residues on development (rate of progression through the life cycle), (Hall, 1950).

The objective of this research was to study the effects of plant residues on growth and development of corn during the vegetative period, at selective reproductive stages, and on yield and grain water content at the end of the life cycle. This study was designed to exclude the confounding effects of delayed emergence on later development stages and of development delay on growth characteristics, and minimized water deficit differences between treatments through irrigation. This paper demonstrates the importance of considering developmental effects when assessing growth and the impact of such an approach on the interpretation of corn performance data.

MATERIALS AND METHODS

Field experiments were conducted in 1987 and 1988 at the Michigan State University Research Farm, East Lansing, Michigan (42 42'N, 84 28'W), on a Conover loam (mixed, mesic, Udollic Ochraqualf) cropped to continuous no-till corn since 1984.

Two treatments consisting of a bare no-till left uncovered or having 100% of the plots'surface covered with straw residues applied at emergence were arranged in a randomized complete block design with four replications. Corn residues from the previous year were removed prior to establishment of the treatments. Corn was planted at 64,500 plants ha^{-1} on 7 May 1987 (hybrid 'Pioneer Brand 3737'), and on 11 May 1988 (hybrid 'Pioneer Brand 3744') on an adjacent site. Starter fertilizer was applied through the planter at a rate of 11-45-45 kg ha^{-1} (N-P-K) and was followed by a broadcast N application of 168 kg ha^{-1} as ammonium nitrate. In 1987, wheat (Triticum aestivum L.) "cv. Frankenmuth" and oat (Avena sativa L.) "cv. Heritage" straw was applied three days prior to 50% emergence at a rate of 5.6 Mg ha^{-1} in 1987 . In 1988, oat straw "cv. Heritage" was applied one day prior to 50% emergence at a rate of 4.9 Mg ha^{-1}. In 1987, ten consecutive plants in each plot were marked at the beginning of the growing season and observed during vegetative growth for dates at which 50% of the plants reached V8, V12 and VT stages of development (Ritchie and Hanway, 1982). On these dates, ten plants per plot were harvested; they were washed, oven-dried to determine the aboveground biomass, and ground for Kjeldahl analysis of whole plant N concentration.

In 1988, ten plants were marked for determination of the day when 50% of the plants reached each of V3 through V16, and 75% of the plants reached R1 (silking). Ten plants were harvested in each plot whenever a treatment reached V3, V6, V9, V12 and R1 stages; height (leaves extended) was measured as well as aboveground biomass and N concentration. In 1988, the leaf area of the fourth, fifth and sixth leaves of V6 plants and leaf area index at R3 (milking) were determined on ten plants per plot using an electronic leaf area meter.

In both years, soil temperatures were measured hourly at the seeding depth (2.5 cm) in each treatment of one of the replicates. The temperature readings of four copper-constantan thermocouples connected in series to a data logger were recorded for each treatment. Air temperature, rainfall, irrigation and solar radiation were recorded on site. Overhead irrigation was supplied both years. Soil water potential was monitored regularly using tensiometers at 15 cm depth, and irrigation was applied whenever the soil water potential of a treatment reached -0.05 MPa.

Analyses of variance were performed and differences between means were tested using the least significant difference test (LSD) at an alpha level of 0.05.

RESULTS AND DISCUSSION

The 1987 and 1988 growing seasons were both warm and relatively dry, especially 1988 with a total of 68.6 mm of rainfall from the day of planting to the day where all plots reached 75% silking. The average soil temperatures at the 2.5 cm seeding depth in 1988 were lower under the residue cover than under the bare soil. This was due to lower daily maxima (Figure 1.1), a finding consistent with reports by Willis et al. (1957), Burrows and Larson (1962) and Moody et al. (1963). Periodic equipment failure in 1987 prevents plotting of the data on a continuous basis.

Plant Development

Prior to the addition of straw residues, the bare soil and residue treatments had synchronized development until emergence since 50% emergence was reached on all plots 11 days after planting i.e. 18 May for 1987 and 22 May for 1988. In both years, the subsequent developmental stages were attained at dates significantly later for the residue treatment than for the bare treatment (Table 1.1). In 1987, 3.8, 2.7 and 4.5 more days were required to reach the V8, V12, and VT stages, respectively for an average of 3.7 days delay until tasselling. In 1988, the residue treatment was delayed 3.7 days by V3 and 7.4 days by V4, maintaining an average of 7.7 days delay until silking (Table 1.1). The rate of corn development is determined primarily by temperature, more specifically of the shoot apical meristem (Beauchamp and Lathwell, 1967). It is known that the shoot apical meristem is strongly affected by soil temperatures while it remains under or at the surface of the soil (Beauchamp and Torrance, 1969; Watts, 1973) i.e. until the V6 stage (Ritchie and Hanway, 1982). Accordingly, the 1988 data (Table 1.1) indicate that the developmental delay was fully manifested by V4. The average soil temperature maxima recorded prior to V4 were 24.8 and 21.3 C for the bare and the residue treatments, respectively. The delayed plants did not catch up past the V6 stage, when the apical meristems of plants in both treatments were exposed to air temperatures. Swan et al. (1987) made a similar observation with corn grown under two tillage systems and four levels of surface residue.

Finally, the water content of the grain at harvest was significantly higher for the residue treatment in both years, an indication of delay in maturity (Table 1.1). Burrows and Larson (1962) reported emergence delays with corn residue treatments varying from 4.5 to 17.9 Mg ha^{-1} while Willis et al. (1957) reported a 6-day delay at silking for a 5.6 Mg ha^{-1} oat straw residue treatment compared to a bare soil control. Reduced tillage treatments have also been reported to be delayed at silking and/or maturity (Mock and Erbach, 1977; Timmons et al. 1986; Al-Darby and Lowery, 1986; Swan et al. 1987).

In both years, the extent of the delay (Table 1.1), the straw material and its application rates varied. A mixture of wheat and oat straw was applied in 1987 at 5.6 Mg ha^{-1} while oat straw was applied at 4.9 Mg ha^{-1} in 1988. However, there was a clear retardation of development each year that cannot be attributed to delayed emergence since the residue was applied around 50% emergence. Therefore, an accurate assessment of crop residue effects on corn growth requires that comparison of growth parameters be made at similar developmental stages in order to remove apparent growth effects due to differences in development. The interpretation of results analyzed in this way must also take into account that with the residue treatment the developmental stages were delayed and therefore, attained under different weather conditions than the bare soil control.

Aboveground biomass

In 1987, there was no significant difference between the two treatments for dry weight of aboveground biomass when the plants were at V8, but the residue treatment had significantly more biomass than the bare treatment at V12 and VT (Figure 1.2). Table 1.2 shows no major difference by V12 in solar radiation or average daily maximum air temperature. By VT, the residue treatment had received 8 mm or 3.4% more precipitation than the bare treatment. Although the total amounts are nearly equal, their distribution between emergence and V12 was different (Table 1.2). In any case, the residue treatment did not affect adversely the dry weight of corn in 1987 during the vegetative period from V8 to VT.

The 1988 aboveground biomass data (Figure 1.2) include earlier samplings than in 1987. The differences between treatments were not significant at V6, V9, and V12. The residue treatment had significantly more biomass at V3 and less biomass at R1 than the bare control. It appears that in 1988, the aboveground dry weight accumulation of corn was not affected in a consistent manner by the residue treatment during the vegetative period. Table 1.2 shows that from V12 to R1, the residue plants received 39% less precipitation than the bare plants which may help explain the significant difference at R1. From emergence to V3, the residue treatment had 10% more precipitation, similar solar radiation and average daily maximum air temperature, and a lower average maximum soil temperature than the bare treatment (21 versus 25 C). Lower soil temperatures between emergence and V3 did not inhibit growth although the reasons for higher biomass in the residue treatment are unclear. Beauchamp and Lathwell (1967) showed that dry weights at stages V2 to V6 were higher at root zone temperatures lower than 25 C. This implies that the dry weight differences between treatments may have depended on early season soil temperature differences and later, at R1, when the shoot meristems were subjected to air temperature, on the differences in environment-developmental stage interaction brought about by dissimilar development rates. Very few reports of corn dry weights during the growing season have been presented on a developmental stage basis and these studies involve tillage rather than residues treatments.

Our results agree with those of Meisinger et al. (1985) who measured corn dry weight at V11-V12 and found no significant difference between minimum tillage and moldboard plow treatments. Timmons et al. (1986) measured lower dry weight per unit area with no-till as compared to a fall plow system at V4 and R1, but the differences were attributed to unequal rates of emergence and percentages of emergence.

Most of the previous research has presented biomass data either at one point in time or on a calendar time scale. The 1988 results of Figure 1.2 are presented on a calendar time scale in Figure 1.3. The aboveground biomass of the bare treatment is higher than the residue treatment throughout the vegetative period. However, Figure 1.2 indicates that these differences are developmental in nature. Finally, when one or both treatments attained the silking stage (last two samplings) (Figure 1.3), there was no significant difference between the two treatments. In this form, our results concur with the many reports in the literature on the effects of temperature, reduced tillage or residue cover depressing dry weights of corn during the vegetative period (van Wijk et al., 1959; Burrows and Larson, 1962; Mederski and Jones, 1963; Mock and Erbach, 1977; Al-Darby and Lowery, 1986), but leads to a conclusion completely different from that derived from Figure 1.2.

Whole plant N concentration and uptake

In 1988, whole plant N concentration at V3, V6, V12, and R1 (Figure 1.4A) show a significant difference only at V3 when the bare treatment was higher than the residue treatment. However, the values of both treatments are above 3%, and within the sufficiency range. Timmons et al. (1986) reported no consistent effect of tillage on N concentration for no-till and fall plow treatments at V4, V18, R1 and R6 (physiological maturity). However, Meisinger et al. (1985) did find significantly lower N concentrations in no-till than on plowed corn at the V11-V12 stage in two of three years studied.

On a calendar time scale, the bare treatment whole plant N concentrations were highest very early in the season, (Figure 1.5A). From then on, there was no significant difference between the treatments until the 38th day after emergence i.e. when the bare plants had 9 leaves and the residue-treated plants had 7 leaves. Later, the difference in development shows up as the plants with a greater number of leaves and older leaves (bare treatment) have a significantly lower N concentration. Moody et al. (1963) also measured lower N in unmulched corn in the first part of the growing season. When both treatments have terminated leaf growth (last sampling), there is no more difference (Figure 1.5A), as reported by Burrows and Larson (1962).

There is no significant difference in N uptake of the two treatments at V3, V6, V9 and V12 (Figure 1.4B). On a calendar basis, these same data indicate that until both treatments reach the 55th day after emergence, the residue treatment is significantly lower than the bare treatment at most sampling dates (Figure 1.5B). The residue treatment's consistently lower N uptake in the set of data plotted on a calendar time (Figure 1.5B) is not evident in Figure 1.4B, and suggests that in our study, this effect is mostly development-related. These results agree with Meisinger et al. (1985) who did not find N uptake differences between minimum tillage and conventional tillage at V11-V12 unless no N was applied as fertilizer. However, Timmons et al. (1986) in a similar tillage study did find differences in N uptake at V4 and V18, with a 179 kg ha^{-1} application of anhydrous ammonia before planting.

Plant Height

The plant height (leaves extended) of the residue treatment was significantly higher at V3 and V6, significantly lower at V12, and similar to the bare treatment at V9 and R1 (Table 1.3). On a calendar basis, the plants of the residue treatment were significantly smaller throughout most of the vegetative period (Table 1.3) as reported by Burrows and Larson (1962) and Moody et al. (1963), except very early in the season and when treatments are either at or past silking (last sampling). Again, the conclusions drawn from sampling on arbitrary dates implies depressed growth while Table 1.3 indicates that the faster developing plants (bare treatment) can be shorter than or similar in height to the residue-treated plants when compared at equal stages of development. Mock and Erbach (1977) gave an indication of such a tendancy when they presented juvenile plant heights taken at a July date, along with leaf number, with the dry weights increasing with the leaf numbers. In our experiment, environmental conditions must account in part for the observed differences: from emergence to V6, a combination of lower soil temperatures and 36% more precipitation for the residue treatment produced taller plants than in the bare treatment (Table 1.2).

From the aboveground biomass, height, and nitrogen concentration data presented above, it is clear that while the response curve over time of a parameter appears interesting, its interpretation needs to be coupled with data on development. One way to accomplish this is to plot the parameter as a function of time and leaf number. For example, the plant height data is presented in Figure 1.6 in such a form. From Figure 1.6 it can be seen that the height difference observed 55 days after emergence also corresponds to a three leaf difference in development - or that the V6 to V8 plants of the residue treatment were taller than the V6-V8 bare plants although delayed by six to seven days - or that in both treatments, a plant of ten collared leaves attained a height of 150 cm.

Leaf Area

Leaf area of the fourth, fifth and sixth leaf of V6 plants and leaf area index (LAI) of R3 plants are shown in Table 1.4. All differences were significant at V6 with higher leaf areas for the residue treatment. Recently, Al-Darby and Lowery (1987) reported that in general, leaf area values of four tillage treatments ranked as the cumulative soil-based degree-days when measurements were made weekly during the vegetative stage. Their results suggest that measurements based on calendar days assess developmental differences. However, their results do not permit one to distinguish growth from developmental effects of tillage.

The leaf area results at V6 (Table 1.4) agree with the dry weight and height data presented above that the growth of corn prior to V6 was more favorable with the residue treatment than with the bare treatment in 1988. At R3, when leaf growth was terminated, there was no significant leaf area index difference between treatments, a pattern similar to dry weights and heights.

Stover and Grain Yields

There was no significant differences in grain yield between treatments in both years (Table 1.4). This has been reported earlier with residue or tillage treatments (Willis et al., 1957; Moody et al., 1963; Griffith et al., 1973; Jones et al., 1968; Van Doren et al., 1976; Al-Darby and Lowery, 1986), except in experiments where plant density (Mock and Erbach, 1977) or drainage conditions (Griffith et al., 1973) or length of the growing season (Swan et al., 1987) were limiting. The stover yield varied with years in this study. There was no significant difference between treatments in 1988, but the residue treatment was significantly higher than the bare treatment in 1987 (Table 1.4). The grain to stover ratio varies accordingly, emphasizing again the fact that overall vegetative growth of the corn plants with residues cover is not depressed. Jones et al. (1968) came to a similar conclusion in a 6-year study comparing vegetative yields of no-tillage to those of conventional tillage.

Under irrigated conditions, during a 2-year study, residue cover of a no-till soil produced significant differences in development of corn plants but no consistently significant differences in above-ground biomass from V6 during the rest of the vegetative stage and in grain yield at the end of the season, when compared to the bare control. In 1988, a higher frequency of sampling showed that there was a retardation of development and an enhancement of growth during the period when the apical meristem was below ground. Presentation of the 1988 biomass, N concentration and uptake, and height data on a calendar day basis rather than on a growth stage basis overlooked delayed development effects and can lead to opposite conclusions concerning the general growth of the plants. It is suggested that one must distinguish effects on development from those on growth in order to gain a better understanding of the crop's physiology in the complex ecosystem of a field situation. Moreover, accounting for growth stages also permits more precise inferences about the weather data and improves the interpretation of results.

Table 1.1. Number of days (after emergence) to reach various developmental stages[+] (D.S.) and grain water content at harvest for corn grown on bare and residue-covered soil.

	Year													
	1987				1988									
	D.S.			Grain Water	D.S.									Grain Water
Treatments	V8	V12	VT		V3	V4	V5	V6	V8	V12	V16	VT	R1	
	days			%	days									%
Bare	33.4	45.0	56.0	16.3	10.8	14.8	21.5	25.2	32.8	47.5	56.5	58.2	60.5	22.8
Residue	37.2	47.7	60.5	18.2	14.5	22.2	28.0	31.2	43.0	54.7	65.0	66.2	68.0	25.1
LSD (0.05)	2.0	2.6	2.8	1.6	0.9	0.9	0.9	2.2	2.7	0.8	1.6	1.3	2.0	1.6
Difference	3.8	2.7	4.5		3.7	7.4	6.5	6.0	10.2	7.2	8.5	8.0	7.5	
Ave. difference[++]		3.7							7.7					

[+] As defined by Ritchie and Hanway (1982).

[++] Average of underlined differences.

Table 1.2. Total precipitation (rainfall plus irrigation), solar radiation, maximum daily air temperature, maximum daily soil temperature during various developmental stages[+] (D.S.) of corn in 1987 and 1988.

		Precipitation		Average Solar Radiation		Average Maximum Daily Air temperature		Average Maximum Daily Soil Temperature	
Year	D.S. Intervals	Bare	Residue	Bare	Residue	Bare	Residue	Bare	Residue
		mm		$MJm^{-2}d^{-1}$		°C			
1987	EM[++]-V8	106.4	158.4	22.47	22.05	27.8	28.3	missing	missing
	V8-V12	63.0	11.0	19.46	20.44	27.6	27.4	N/A	N/A
	V12-VT	61.4	69.4	22.55	20.77	30.2	28.6	N/A	N/A
1988	EM[+]-V3	38.0	42.0	26.63	26.89	27.9	27.4	25.1	21.2
	V3-V6	23.0	41.2	28.41	25.00	29.0	32.0	25.7	23.6
	V6-V9	66.6	76.1	26.83	23.72	32.8	32.2	N/A	N/A
	V9-V12	31.7	44.4	26.84	25.54	31.9	36.4	N/A	N/A
	V12-R1	90.4	55.0	21.20	19.20	33.5	30.8	N/A	N/A

[+] as defined by Ritchie and Hanway (1982)
[++] EM:emergence
N/A: non-applicable

Table 1.3. Height (leaves extended) of corn grown on bare and residue-covered soil from emergence to silking.

	Developmental Stages[+]					Days after emergence									
Treatments	V3	V6	V9	V12	R1	11	14	25	31	38	45	48	55	60	68
Bare	22.8	60.0	129.4	184.6	244.7	22.8	28.3	60.0	88.0	129.4	162.0	184.6	203.7	245.0	242.3
Residue	27.7	70.0	122.4	170.6	237.0	24.2	27.7	42.0	70.0	94.3	122.4	150.1	170.6	201.6	237.0
LSD(0.05)	2.0	2.8	8.8	8.4	10.6	2.3	4.0	6.8	4.3	10.4	17.4	20.2	10.0	16.1	14.5

[+] as defined by Ritchie and Hanway (1982).

Table 1.4. 1988 fourth, fifth and sixth leaf areas at V6+, leaf area index (LAI) at R3+ and 1987 and 1988 stover yield, grain yield and grain to stover ratio of corn grown on bare and residue-covered soil.

	1987			1988						
Treatments	Stover Yield	Grain Yield	Grain to Stover Ratio	V6 4th leaf Area	V6 5th leaf Area	V6 6th leaf Area	R3 LAI	Stover Yield	Grain Yield	Grain to Stover Ratio
	$Mg\ ha^{-1}$			cm^2				$Mg\ ha^{-1}$		
Bare	6.27	10.19	1.62	37.5	72.8	126.6	3.96	4.83	9.04	1.87
Residue	8.47	10.53	1.24	57.2	104.2	178.3	3.84	5.83	8.74	1.50
LSD (.05)	2.15	0.92	0.40	13.2	25.8	41.3	0.88	1.70	0.82	0.38

+as defined by Ritchie and Hanway (1982).

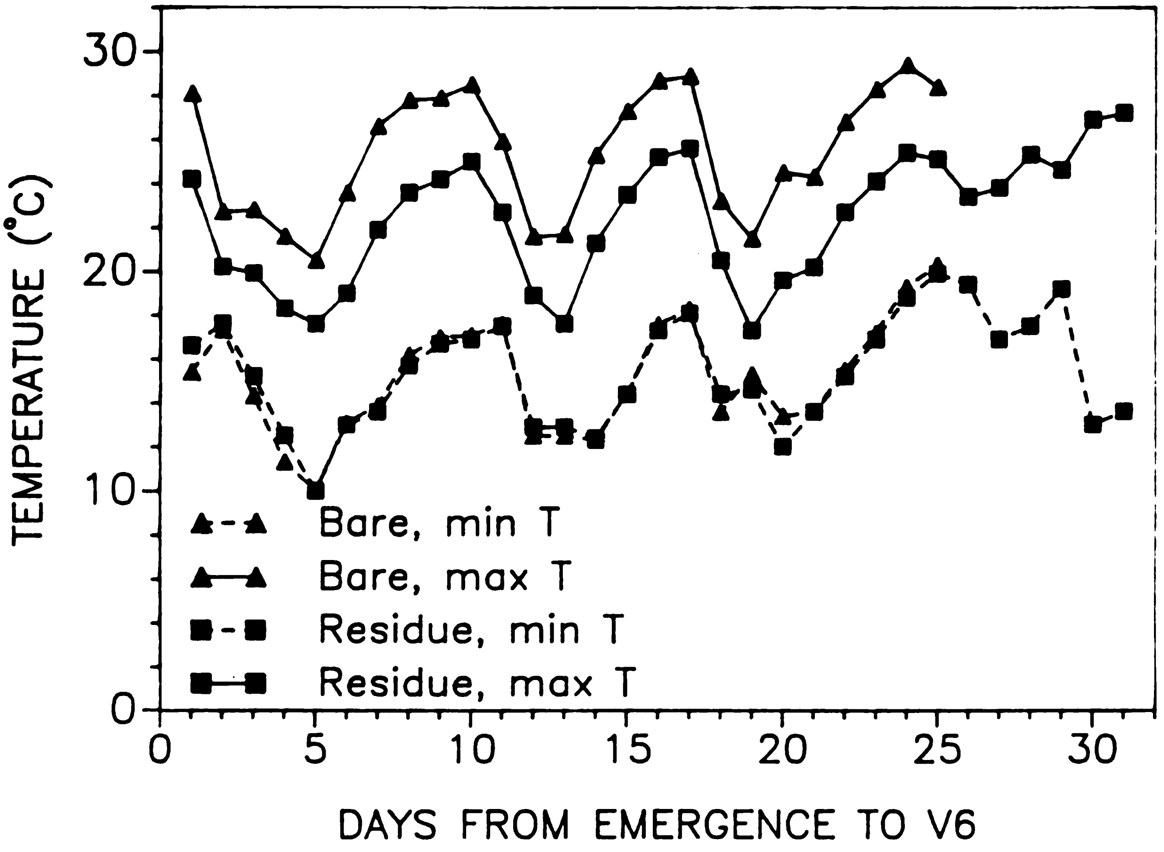

Figure 1.1. Daily minimum and maximum soil temperature at the 2.5 cm depth from emergence to V6, in 1988 at the Michigan State University Research Farm, East Lansing, MI.

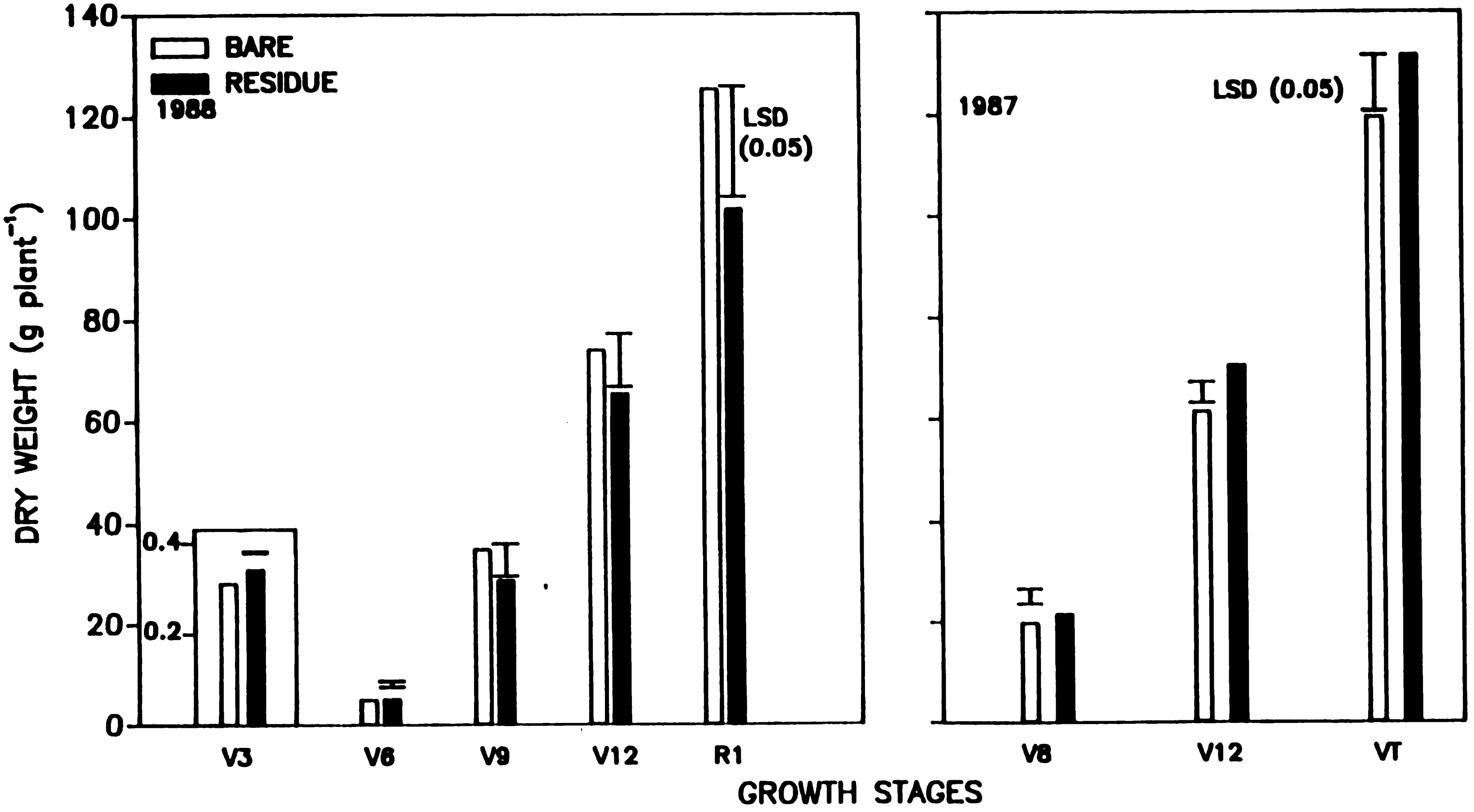

Figure 1.2. Dry weight of corn aboveground biomass at various stages of development in 1987 and 1988.

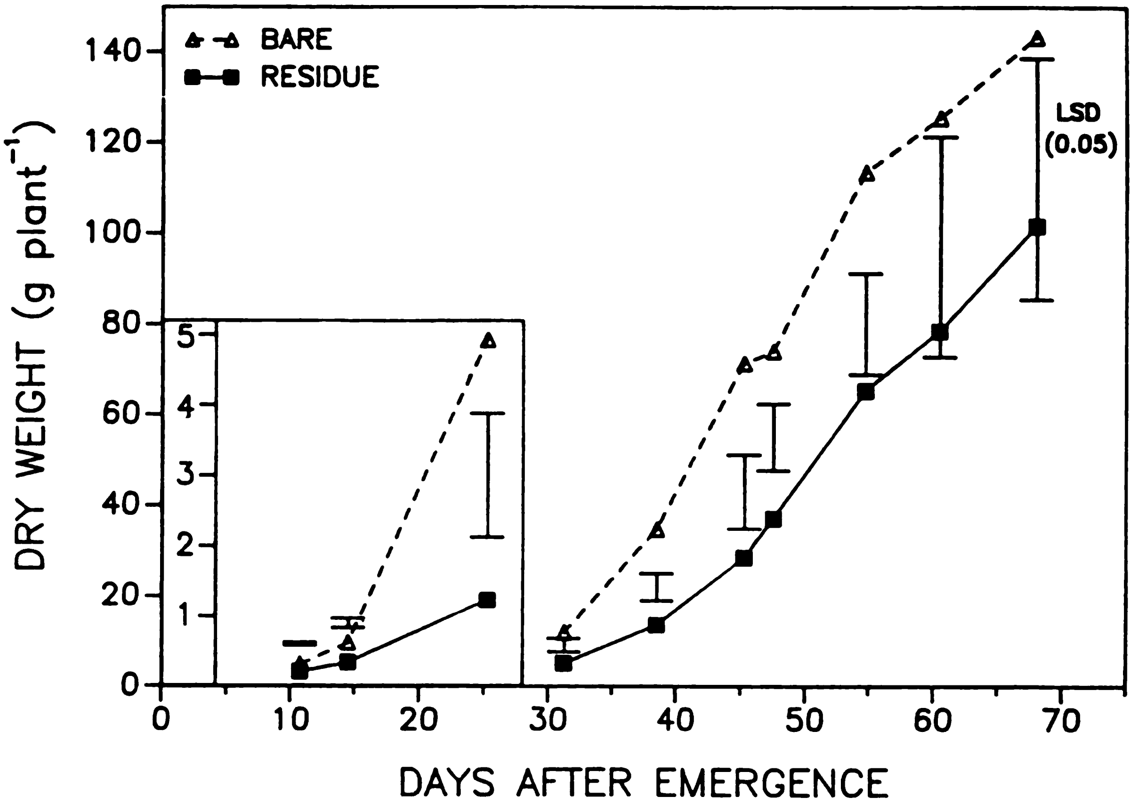

Figure 1.3. Dry weight of corn aboveground biomass at various dates during the vegetative period until 75% silking in 1988.

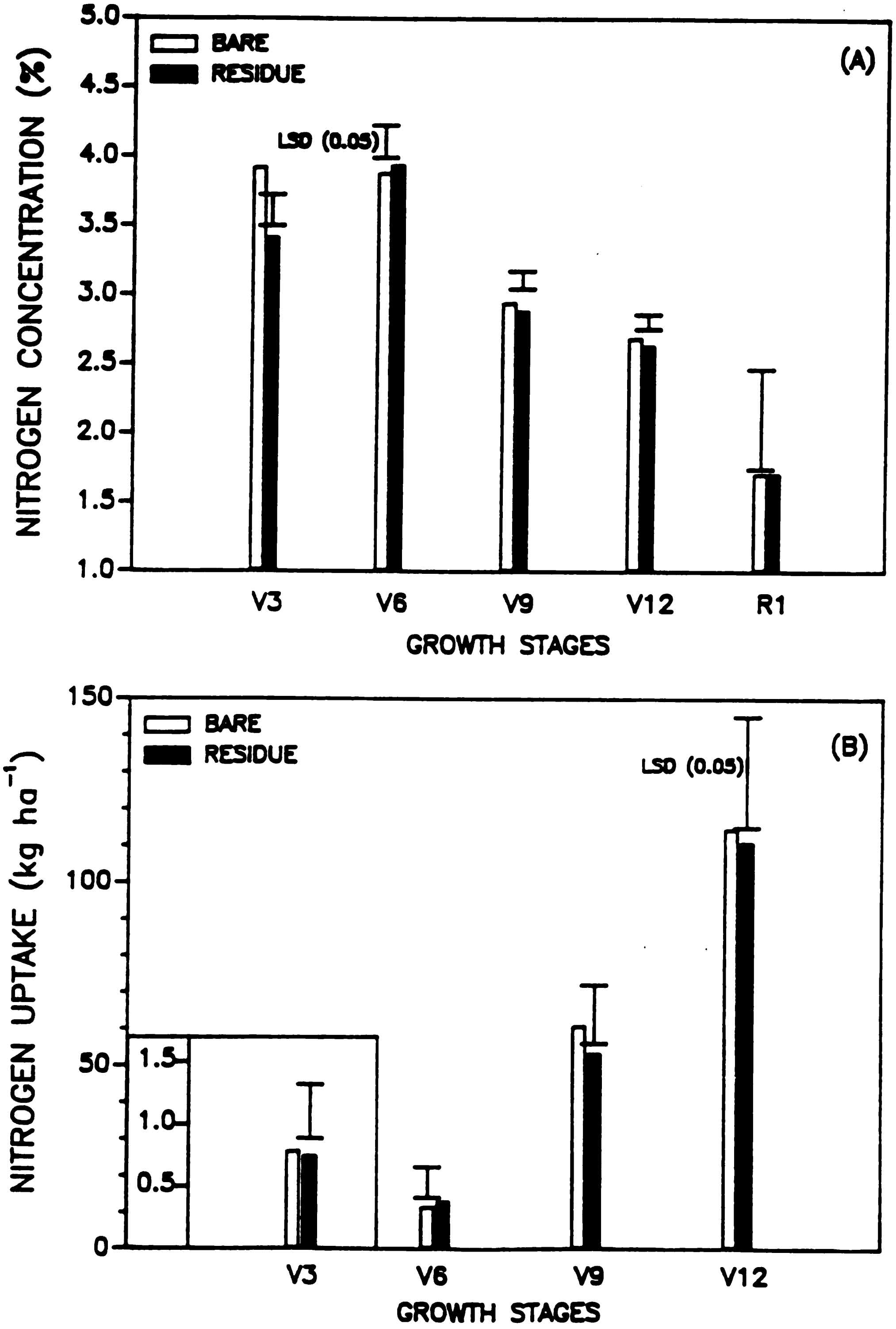

Figure 1.4. Whole plant N concentration (A), and N uptake (B) at developmental stages V3, V6, V9, V12 and R1 in 1988.

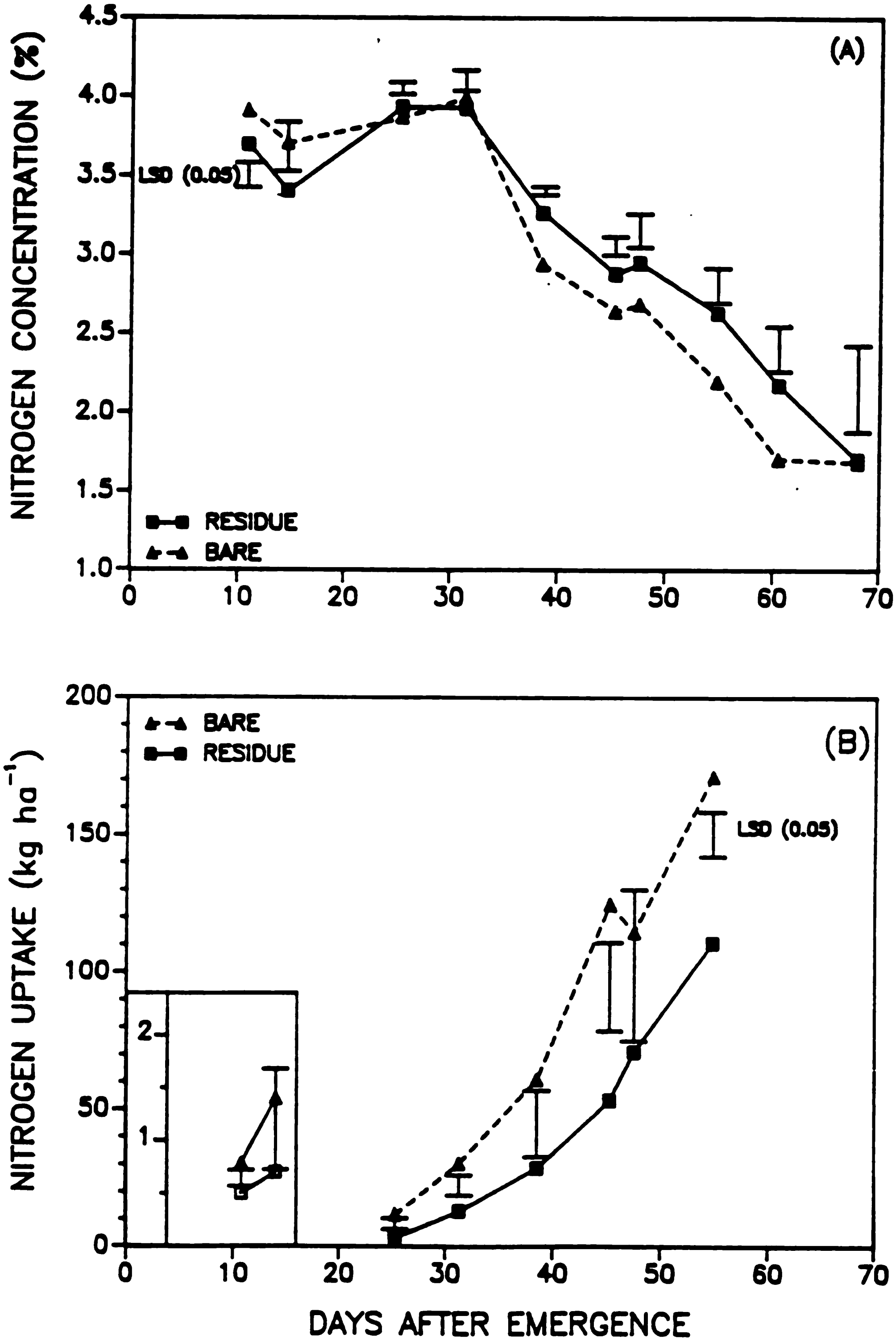

Figure 1.5. Whole plant N concentration at various dates during the vegetative period until 75% silking (A), and nitrogen uptake until V12 (B) in 1988.

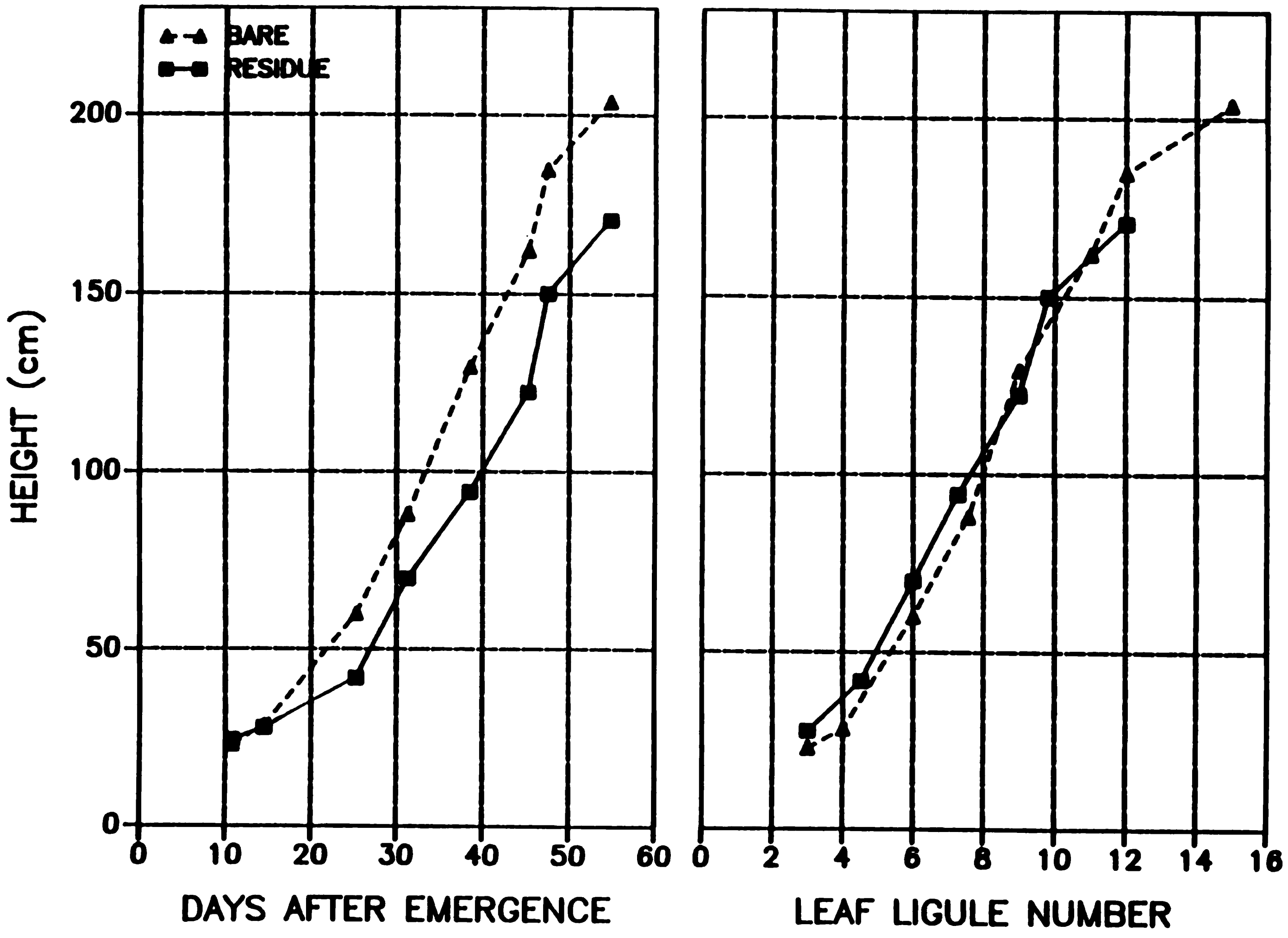

Figure 1.6. Corn height (leaves extended) at various dates and as a function of increasing leaf ligule number during the vegetative period in 1988.

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CHAPTER 2

TIMING AND NATURE OF *AVENA SATIVA* (L.) STRAW MULCH RETARDATION OF *ZEA MAYS* (L.) VEGETATIVE DEVELOPMENT

Many studies have emphasized how *Zea mays* (L.) (corn) vegetative development is primarily dependent on temperature. Leaf appearance rates have been described as a linear function of the mean daily temperature when corn is grown at constant temperature (Warrington and Kanemasu, 1983) and, as a curvilinear function when corn is grown under differential day/night temperature regimes (Tollenaar et al., 1979; Warrington and Kanemasu, 1983) but with regions close to linear between 12 to 15 C and 26 to 28 C, and with a maximum around 30-32 C. These studies support the use of thermal time as an index to predict stages of development. Indeed, several variations on the original thermal index of growing degree-days (GDD) have been successfully used to predict flowering and maturity times (Coelho and Dale, 1980).

Although it has been demonstrated that corn leaf development responds to soil temperatures (Walker, 1969) until the sixth leaf stage (Beauchamp and Lathwell, 1967), most models or prediction equations use air temperature as the basis for the thermal indices since it is more readily available than soil temperature and since bare soil temperature at seeding depth is correlated with air temperature (Alessi and Power, 1971). However, tillage practices leaving crop residues on the soil surface cause significant decreases in soil temperature (Van Doren and Allmaras, 1978; Gupta et al., 1984) accompanied by significant delays in corn development when compared to conventional tillage (Griffith et al., 1973; Mock and Erbach, 1977; Al-Darby and Lowery, 1987; Swan et al., 1987). Residues are assumed to delay corn development via their effect on soil temperature. By decreasing the soil temperature, residues are thought to decrease the rate of cell division in the shoot apical meristem during the period it is below the soil surface, which is described to last until V6 by Ritchie and Hanway (1982). However, a thorough analysis of a mulch's effect on corn leaf development has been lacking.

In addition to the fact that crop residue mulches decrease the average daily temperature mainly by lowering the daily maximum attained during daytime (Van Doren and Allmaras, 1978), crop residue mulches reduce growth in several species (Lodhi et al., 1987) through leaching or microbial production of allelopathic chemicals. *Avena sativa* (L.) (oat) stems have been shown to decrease root and shoot lengths of corn seedlings in germination bioassays (Guenzi et al., 1967) and numerous phytotoxic substances have been associated with various crop residues (McCalla and Norstadt, 1974). Potential chemical effects would increase the difficulty of modelling corn phenology in conservation tillage situations.

In chapter 1, it was reported that corn development was delayed as a result of oat straw mulching. Studies on allelopathy led us to question whether or not our observations were derived entirely from thermal effects on meristematic tissues. In order to gain a better understanding of early corn development under mulched soils, the objectives of this study were to: 1) characterize the effect of oat straw and a non-degradable mulch on corn development from emergence to V12, with an emphasis on the period from emergence to V6, over two different growth seasons on the same soil; 2) verify that thermal time accounts for all developmental differences in corn between the mulches and a bare soil control and 3) use established modelling equations to predict developmental dates of our field experiments. This research was done using a non-degradable mulch to test for allelopathic potential of oat straw residues. Irrigation was used in order to prevent soil moisture stress at any time during the vegetative stages and possible confounding of the temperature effects. Finally, mulches were applied at emergence in order to distinguish residue effects on leaf development from that on germination and emergence.

MATERIALS AND METHODS

Field experiments were conducted in 1988 and 1989 at the Michigan State University Research Farm, East Lansing, Michigan (42 42'N, 84 28'W), on a Conover loam (mixed, mesic, Udollic Ochraqualf) cropped to continuous no-till corn since 1984. In 1988, three surface residue treatments were arranged in a randomized complete block design: bare; 100% surface covered with oat "cv. Heritage" straw; 100% surface covered with Populus spp. (poplar) excelsior (American Excelsior Co., Westland, MI). The mulches were applied after emergence, on the day of the second leaf tip emergence (LTE2). A second experiment in 1988 compared two treatments consisting of a bare soil and a soil with 100% of its surface covered with "cv. Heritage" oat straw on the day 50% of the plots' plants reached V4.

In 1989, four surface residue treatments were arranged in a randomized complete block design: 1) bare 2) 100% surface covered with oat straw "cv. Heritage" applied at LTE2, 3) 100% surface covered with oat straw "cv. Heritage" applied at V4 and 4) 100% surface covered with poplar excelsior applied at LTE2.

In all cases, corn residues from the previous year were removed prior to planting and establishment of treatments. Corn was planted at 66,000 plants ha^{-1} (hybrid 'Pioneer Brand 3744') on 11 May 1988 and on 3 May 1989. Starter fertilizer was applied through the planter at a rate of 11-45-45 kg ha^{-1} (N-P-K) and was followed by a broadcast application of 168 kg N ha^{-1} and 151 kg N ha^{-1} ammonium nitrate in 1988 and 1989, respectively. In 1988, the oat and poplar straw were applied at 4.9 and 7.4 Mg ha^{-1}, respectively to achieve 100% surface cover. In 1989, the rates were 5.6 and 8.7 Mg ha^{-1} for oat and poplar, respectively.

Ten consecutive plants in each plot were marked at the beginning of each growing season and observed during vegetative growth for dates at which 50% of the plants reached stages LTE2, and V3 to V12 in both 1988 and 1989. Leaf tip emergence of leaves 2 to 10 were also recorded in 1989. Soil temperatures were measured hourly at the seeding depth (2.5 cm) in each treatment of one of the replicates of each experiment. The temperature readings of four (1988) or five (1989) copper-constantan thermocouples connected in series to a datalogger were recorded on site. Thermal time was calculated from either air temperature or soil temperatures as:

$$\text{Degree-days} = 0.5(\text{Min} + \text{Max}) - 10$$

where Min is the daily temperature minimum and greater than 10 C and where Max is the daily temperature maximum and smaller than 30 C. Overhead irrigation was supplied both years. Soil water potential was monitered regularly using tensiometers at 15 cm depth, and irrigation was applied whenever the soil water potential of a treatment reached - 0.05 MPa. Analyses of variances were performed and differences between means were tested using the least significant difference test (LSD) at an alpha level of 0.05.

RESULTS AND DISCUSSION

The 1988 growing season was characterized by constant hot and dry weather with a total of 50 mm of rainfall from the day of mulch application (second leaf tip emergence, LTE2) to the day all plots reached V12, and required water applied in 10 irrigations to maintain soil water potential above -0.05 MPa at 15 cm depth during this period. During this same period in 1989, there was a total of

297 mm of rainfall, one irrigation required and lower temperatures than in 1988 (Figure 2.1). The oat and poplar straw applied at LTE2 decreased the maximum soil temperature at the seed zone depth by an average of 3.3 C in 1988 and 3.9 C in 1989 for the period between LTE2 and V6 stages but they did not affect the daily minimum soil temperature (Table 2.1). As a result, during this period, soil-based degree-days at the seed zone accumulated more slowly under the mulches than under bare soil (Figure 2.2). Similarly with a conservation tillage experiment, Al-Darby and Lowery (1987) reported slower accumulation of degree-days (based on seed zone temperature) under no-till and chisel plow than under conventional moldboard treatments. In both years, the air temperature-based degree-days was intermediate to the bare soil and mulched soils-based degree-days (Figure 2.2). Consequently, the development of corn was delayed by the two types of mulches in 1988 and 1989 (Figure 2.3) in accordance with the expectation that soil temperature is the main determinant of development during early growth when soil water content is not limiting. More specifically, in 1988, the number of days to reach growth stages V3 to V12 were significantly higher for the oat and poplar mulches than for the bare control. In 1988, the V3 stage was attained 6.0 and 3.4 days later than the bare treatment by corn grown with the oat straw and poplar mulches, respectively (Figure 2.3). At V4, 8.3 and 6.0 extra days were required for the oat straw and poplar treatments, respectively. From V4 to V12, the oat straw mulch retarded development by an average of 7.8 days while the poplar retarded

development by an average of 5.0 days.

In 1989, the number of days required to reach V3 to V12 was also significantly higher for the mulches than for the bare control. Corn attained the V3 stage 5.0 and 3.8 days later than the bare treatment, and the V5 stage, 7.5 and 6.0 days later than the bare treatment for the oat straw and poplar mulches, respectively. From V5 to V12, the oat straw mulch and the poplar mulch retarded development by an average of 6.1 and 5.2 days, respectively (Figure 2.3).

Swan et al. (1987) calculated that the delay associated with 70% surface cover following planting in no-till was equivalent to using a corn hybrid with maturity of 95 rather than 105 days in Southern Minnesota. Indeed, it appears that in both a dry and hot (1988) and cool and humid (1989) early vegetative period, the retarding effect of mulches culminates around V4 (1988) or V5 (1989) and that no further retardation is accumulated throughout the rest of the vegetative period (Figure 2.3) as reported earlier in chapter 1, and as shown by Swan et al. (1987) with varying amounts of residue cover. There could be two explanations why the delay culminated at V4 and V5 when in theory, the apical meristem emerges at V6. First, although it is generally assumed that the apical meristem of corn remains below ground until V6, it is possible that there is some variation among genotypes. However, dissection of the corn plants during both growing seasons revealed that the apical meristem of corn 'Pioneer Brand 3744' was below ground at V3, V4 and V5 and that the meristem tip reached the soil surface a few days prior to or past V6. Second, this pattern of retarded development could be understood by comparing the soil temperature at the seed zone between the treatments on a developmental time scale (Table 2.2). The data presented in this manner (Table 2.2), indicate that in 1988, soil maxima temperature differences between the bare treatment and the two mulches occurred mainly between the periods LTE2-V3 and V3-V4 (with a minimum difference of 3.4 and 2.6 C, respectively) and in 1989, between LTE2-V3 and V4-V5 (with a minimum difference of 2.2 and 3.9 C, respectively). These periods coincide with the periods during which delay is accumulated (Figure 2.3) and suggest why the effect was not extended to V6. In addition, this explains why years such as 1988 and 1989 differ in the period of time during which mulches retarded corn development while curves for thermal time accumulation for those years are similar (Figure 2.2).

While soil temperature fluctuations clearly influence the timing of corn development, the question remains as to whether thermal time accounts entirely for the observed delays or whether additional factors are involved. We addressed this question through the analysis of variance of the thermal time required during the period LTE2 to V6 and by comparison of thermal time values estimated from CERES-MAIZE, a corn phenology model (Jones and Kiniry, 1986) with our six treatment-years sets of data.

Under controlled conditions, Warrington and Kanemasu (1983) showed that thermal time required for a corn plant to reach a specific number of leaves (defined through collar emergences) is constant until V12 in the absence of moisture or nutrient stress. Air temperature-based thermal time is not expected to give an accurate value of thermal time under mulched conditions until the apical meristem reaches the soil surface. This has been verified to be at the sixth leaf stage as mentioned earlier. Therefore, when soil-based thermal time, calculated from soil temperatures measured at the 2.5 cm seeding depth is examined, no significant effect of treatments on the number of degree-days required for the period between the application of mulches and V6 is expected if soil temperature is the only factor involved in developmental delay.

However, soil temperature-based thermal time is only equal among treatments for the periods between the V4-V5 and V5-V6 intervals in 1988 and 1989 (Table 2.3). During the 1988 LTE2-V3 and V3-V4 periods and the 1989 LTE2-V3 period, the poplar treatment does not differ from the bare treatment in total amount of soil-based degree-days. It simply accumulates them slower (Figure 2.2), resulting in a delayed development on a calendar-based time scale (Figure 2.3). During these same periods, the oat straw treatment is significantly different from the bare and the poplar treatments, requiring 35, 29% and 8% more soil based degree-days than the bare treatment, respectively. This indicates that the plants treated with oat straw were delayed prior to V4 in 1988 and prior to V3 in 1989 by a factor other than soil temperature. Since poplar is resistant to decomposition and has been used as a control mulch cover for allellopathic studies (Barnes and Putnam, 1983), these results strongly suggest that the delayed development of corn grown with oat residues may be a combination of decreased soil temperature maxima and adverse chemical effects due to oat straw decomposition. On the contrary, during the 1989 V3-V4 period, the bare control is significantly different from the two mulch treatments applied at LTE2. Since the oat and poplar do not differ from each other, the thermal unit differences with the bare control must be attributed to the presence of a mulch.

Swan et al. (1987) reported fewer soil-based degree-days from planting to sixth leaf stage as percent in-row cover of residues increased. This does not agree with our results but since some dry conditions after planting were acknowledged, their results could have relected uneven emergence times. In fact, Al-Darby and Lowery (1987) attributed their finding of lower seed zone degree-days for corn emergence in no-till versus conventional tillage to higher soil water content in the seed zone with no-till.

An adaptation of a phenology equation of a subroutine of the CERES-MAIZE model (Jones and Kiniry, 1986) was used to estimate how the contribution of soil temperature differences accounted for the delay in corn development. The original CERES-MAIZE linear equation provided a means of predicting the number of degree-days to be accumulated by the plant for the full extension of the last leaf using 38.9 degree-days per phyllocron after LTE2. Adaptation of this equation in order to predict the number of degree-days to be accumulated until the full extension of the 3rd (V3), 4th (V4), 5th (V5) and 6th (V6) leaf from LTE2 required the degree-days necessary for the period between each leaf tip emergence and formation of the collar (70, 95, 111, 118 degree-days, respectively). These values were obtained from field observations of hybrid 'Pioneer Brand 3744' since Muldoon et al. (1984) showed that there existed differences among hybrids in rates of collar appearances. Using these equations as a base for prediction, Figure 2.4 compares the measured and predicted degree-days values for appearance of collar of leaves 3 to 6. Since CERES-MAIZE's phenology predictors are based on temperature and photoperiod relationships, any other factor delaying development will result in an underestimation of thermal time by the model. While the model accurately predicts the number of degree-days of most of the treatments over the 2 years especially at V3 and V6, it clearly underestimates the oat treatment in 1988. The model does not account for some of the delay, which is most conspicuous by V3 (Figure 2.4).

The fact that the 1989 oat treatment did not affect corn development in the same proportion as in 1988 indicates that this is a weather-dependent phenomenon since the experimental protocol was similar in both years. The 1988 and 1989 periods of LTE2-V4 of the oat treatment differ in average maximum soil temperature, 21.6 C (1988) and 17.1 C (1989) and in precipitation, 120 mm (1988) and 184 mm (1989). Therefore, it could be that high precipitation or lower soil temperatures or a combination of both will not lead to unexplained developmental delays in contrast with warmer and drier conditions.

Post-V6 development was described earlier (Figure 2.3). There is no significant difference in air temperature-based degree-days (Table 2.3) among treatments in both years, indicating that the delays of Figure 2.3 are due to a carryover of the early season mulching retardation effects.

Finally, when oat mulches were applied at V4 rather than at LTE2, the mulch treatment failed to show any significant difference in number of days required to reach various developmental stages from V5 to V12 in 1988 (Table 2.4). In 1989, the oat straw applied at V4 required significantly more time (0.8 days) than the bare treatment from V5 to V6 (Table 2.4). This delay is carried on to V8 but the difference is not significant by V12. Soil-based thermal time for the V4-V6 interval for the V4-applied oat mulch and the bare treatment is not significantly different (Table 2.3), indicating that the developmental delay is entirely due to slightly lower soil temperature effects (Table 2.2). This confirms the previous finding from the thermal time analysis of application of mulches at LTE2 that the retardation in corn development is due to the presence of a mulch prior to the V4 stage and that post-V4 effects are due to soil temperature differences only.

The data from our study show that complete residue cover on a no-till loam soil resulted in over a 3 C decrease in maxima soil temperature during the period of application (LTE2) to V6 and delays of 5 to 7.5 days in vegetative development of corn. The delays took place during the leaf stage intervals when the difference in average maxima temperatures of the seed zone between the bare control and the mulch treatments were greater than 2.2 C. The soil temperature differences are dependent on weather conditions but no increase in delay was noted in both years starting at V5 when soil maxima temperature (at the seed zone) differences between the mulch treatment and the bare control are 2 C or less. Quantitative analysis of the development delay in terms of soil temperature-based thermal time indicated that the delay observed with the poplar mulch is regulated by temperature. However, other factors contributed to the delay in corn development when oat straw was added to the soil surface in 1988. The discrepancy between the inert mulch and the oat straw effects on thermal times and between the oat straw effects over years, suggest that allelopathy may be the source of unexplained delay and that its occurrence is weather-dependent. These conclusions imply that corn phenology modelling efforts for conservation tillage should be directed towards the early developmental stages, considering possible chemical effects of crop residues retarding leaf development and predicting how soil water content affects the warming trends of the seed zone.

Table 2.1. Average daily maximum and minimum seed zone temperatures from the day of mulch application (LTE2[+]) to V6[++].

	1988			1989		
	Bare	Oat	Poplar	Bare	Oat	Poplar
	°C					
MAXIMUM	25.5	22.5	21.9	23.2	19.6	19.0
MINIMUM	15.3	15.5	15.6	15.4	15.0	15.3

[+] Second leaf tip emergence.
[++] As defined by Ritchie and Hanway (1982).

Table 2.2. Average daily maximum seed zone temperature for various periods of development for a bare soil and mulch treatments applied at LTE2[+] or V4[++].

	1988			1989			
	LTE2			LTE2			V4
Period[++]	Bare	Oat	Poplar	Bare	Oat	Poplar	Oat
	°C						
LTE2-V3	25.1	21.7	20.0	18.5	16.3	16.3	18.3
V3-V4	24.0	21.4	19.8	19.5	19.2	18.7	19.4
V4-V5	25.2	24.4	23.5	20.7	16.8	16.6	19.1
V5-V6	27.8	27.7	25.8	18.1	20.1	18.6	17.3

[+] LTE2:Second leaf tip emergence
[++] V stages as defined by Ritchie and Hanway (1982)

Table 2.3. Seed zone thermal time for the LTE2[+]-V6[++] period and air temperature-based thermal time for the V6-V12 development interval for a bare treatment and an oat straw mulch and poplar excelsior mulch treatments applied at LTE2 or V4[++].

	1988				1989				
	LTE2			LSD	LTE2			V4	LSD
Periods[++]	Bare	Oat	Poplar	(0.05)	Bare	Oat	Poplar	Oat	(0.05)
	degree-days								
LTE2-V3	108.4	139.9	111.2	8.4	101.8	108.4	100.2	100.1	5.1
V3-V4	41.6	58.8	48.2	10.3	57.6	46.0	44.8	56.2	8.3
V4-V5	60.4	51.6	59.2	ns	46.3	54.4	50.9	45.4	ns
V5-V6	58.7	49.9	48.5	ns	58.9	60.6	55.0	58.8	ns
V6-V8	110.5	104.7	127.5	ns	101.7	103.8	102.6	99.6	ns
V8-V12	150.1	157.9	143.0	ns	157.1	161.2	163.1	153.9	ns

[+] Second leaf tip emergence day.

[++] V stages as defined by Ritchie and Hanway (1982)

Table 2.4. Days required between various developmental stages[+] for corn grown on bare soil and soil covered with oat straw mulch applied at V4.

	Year											
	1988						1989					
Treatments	LTE2[++]-V3	V3-V4	V4-V5	V5-V6	V6-V8	V8-V12	LTE2[++]-V3	V3-V4	V4-V5	V5-V6	V6-V8	V8-V12
Bare	11.2	4.5	5.7	4.8	10.3	14.9	12.0	6.0	4.5	7.2	8.2	14.25
Oat	11.5	4.2	7.2	5.5	10.3	13.3	12.0	6.0	5.0	8.0	9.2	14.0
LSD (0.05)	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.6	0.8	ns

[+] As defined by Ritchie and Hanway (1982).

[++] Second leaf tip emergence.

[*] Significant at the 0.05 level.

ns, non-significant

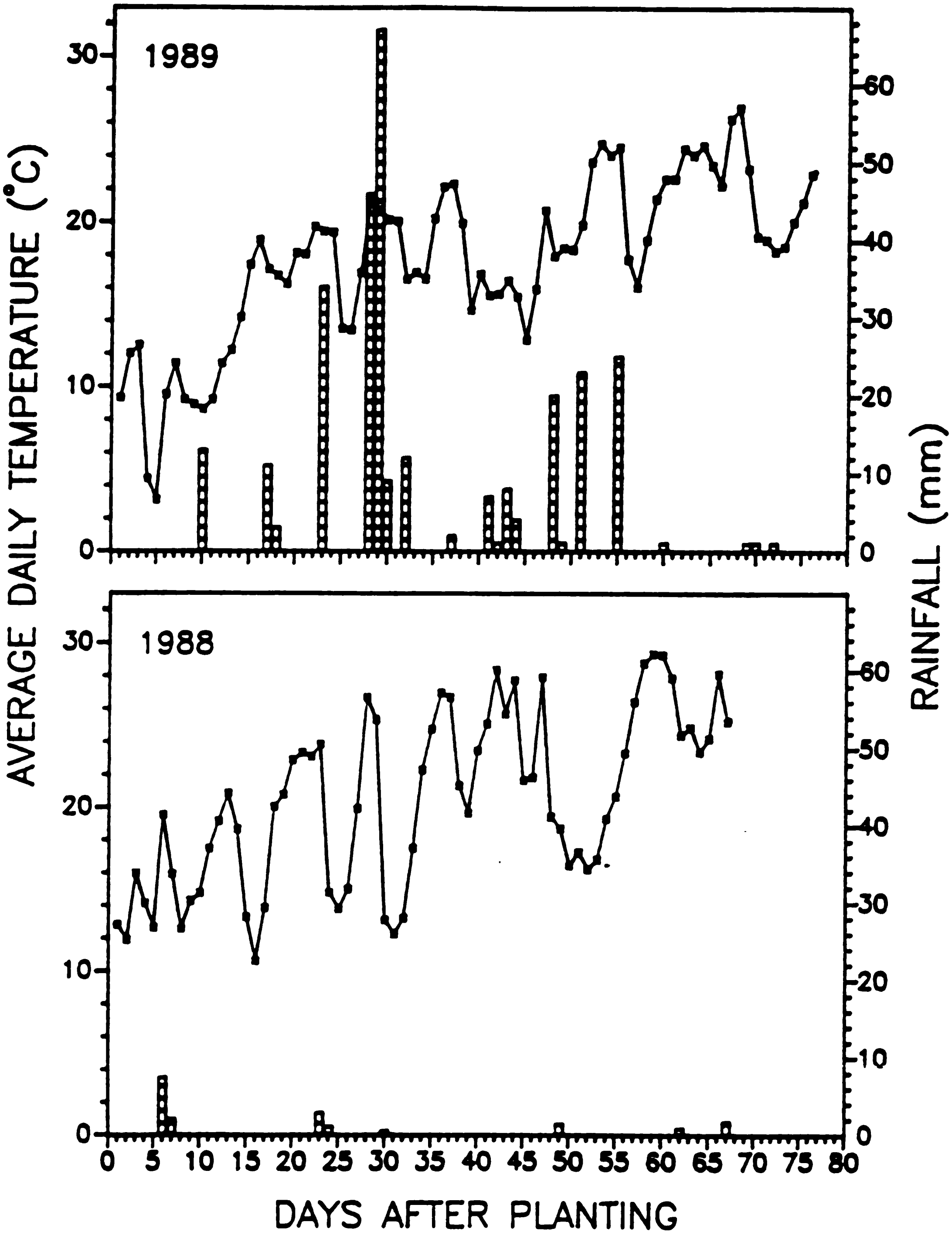

Figure 2.1. Daily average air temperature and rainfall from planting to the date all treatments reached V12 at the Michigan State University Research Farm, East Lansing, MI

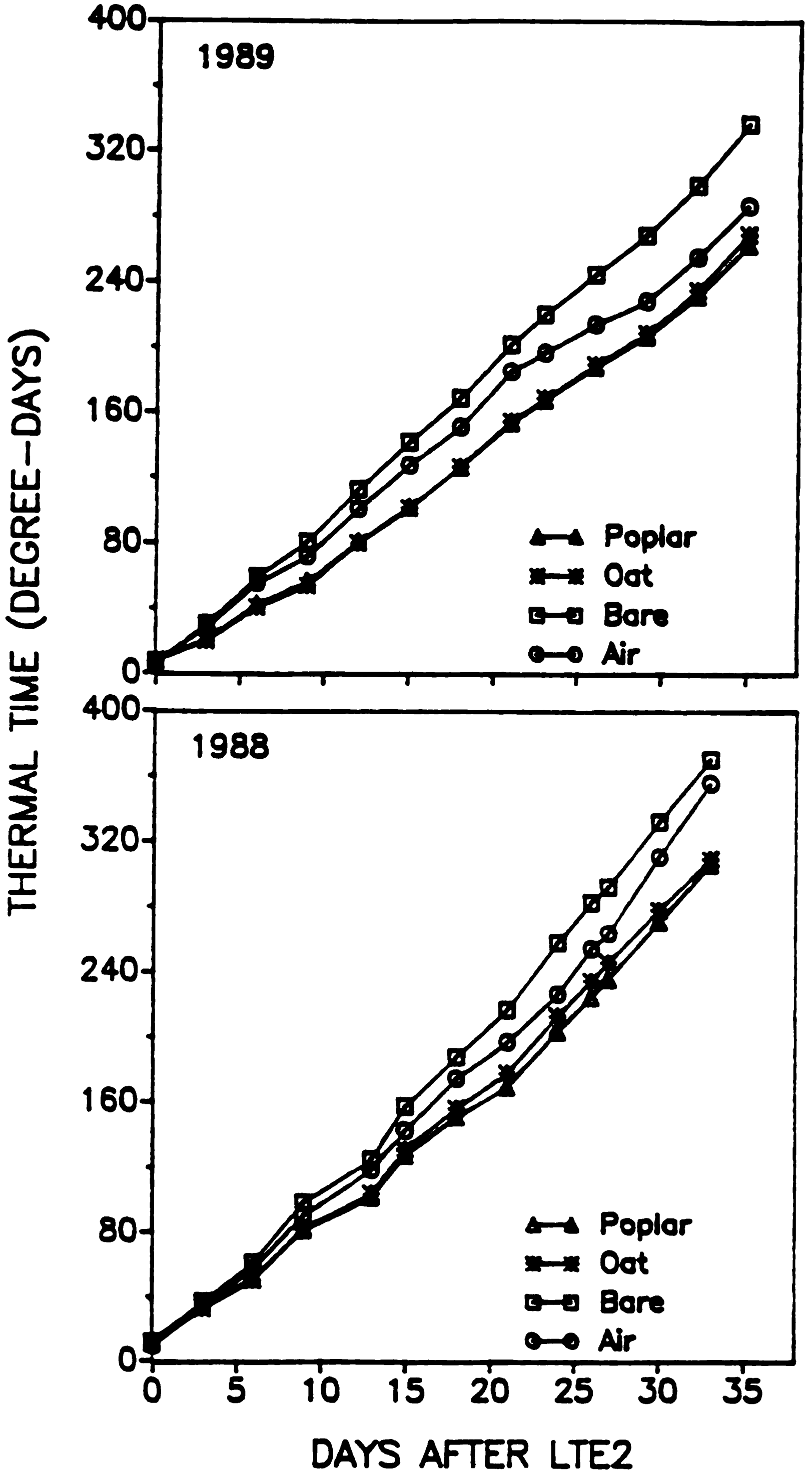

Figure 2.2. Seed zone temperature degree-day and air temperature degree-day accumulation from the day of mulch application (LTE2) to the day all plots reached V6.

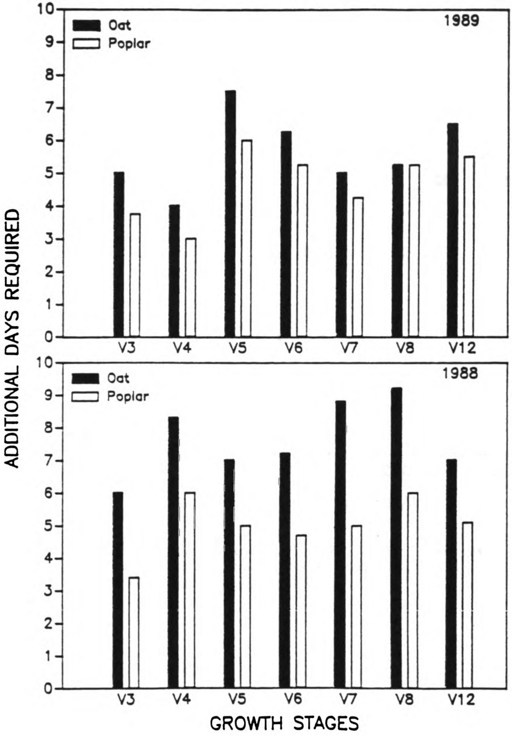

Figure 2.3. Additional number of days required by corn grown with an oat straw mulch and a poplar excelsior mulch to reach some vegetative developmental stages as compared to a bare soil treatment.

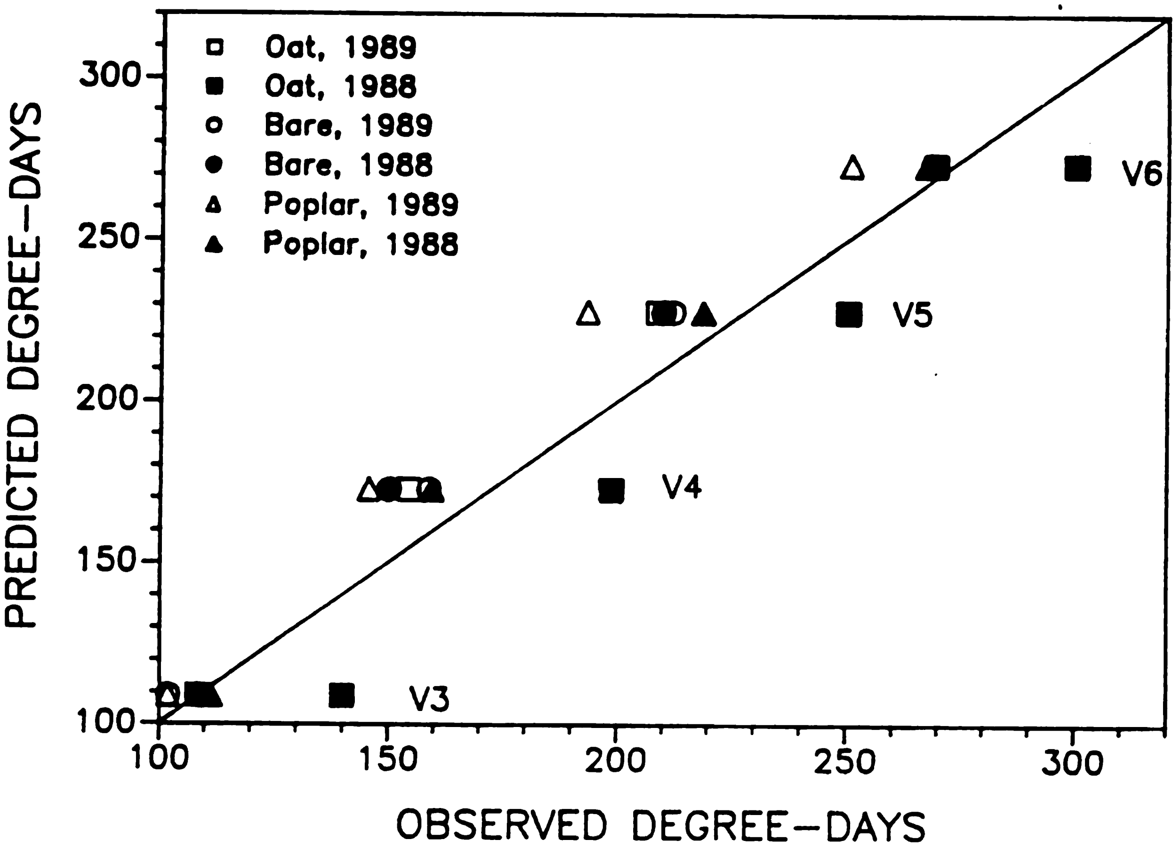

Figure 2.4. Observed thermal time to V3, V4, V5 and V6 versus predicted thermal time from an adaptation of a CERES-MAIZE phenology equation.

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CHAPTER 3

THERMOTROPISM BY SEEDLINGS OF ZEA MAYS (L.) AND ARABIDOPSIS THALIANA (L.) HEYHN.

Thermosensing is well documented in a variety of microorganisms such as *Escherichia coli* (Maeda et al., 1976; Maeda and Imae, 1979), *Dictyostelium discoideum* (Poff and Skokut, 1977; Whitaker and Poff, 1980; Fontana and Poff, 1984) and in the nematode, *Caenorhabditis elegans* (Hedgecock and Russell, 1975). All these organisms exhibit thermotaxis or the ability to respond to thermal gradients by changing the direction of their movements. On the other hand, thermal gradient sensing in plants has not been well documented. Thermotropism, which is the directed orientation of a plant organ in response to a temperature gradient, was only reported in the late nineteeth century and early twentieth century literature.

Hooker (1914) writes that Barthelemy executed the first experiments on root thermotropism with bulbs of hyacinth growing in water in 1884. In 1885, Wortmann presented data suggesting root thermotropism in *Ervum lens*, *Pisum sativum* and *Zea mays* (Hooker, 1914). In these experiments and those of several later workers, the methods and measurements were crude, and the results conflicting (Rose, 1929), discrediting this early sensory physiology work. For example, while Klecker in 1891 cast doubts on the validity of the work of Barthelemy and of Wortmann on root thermotropism because of the lack of control of moisture in their experiments, he failed to demonstrate that moisture gradients could influence root direction. Later, Hooker (1914) attempted to disprove the existence of root thermotropism by showing the absence of response to thermal gradients when roots were grown in agar, free of exposure to moisture gradients. Meanwhile, Eckerson (1914) and Collander (1918) presented more evidence for, and Sierp in 1926, presented evidence against root thermotropism. Finally, Rose (1929) reviewing the literature did not take any position. In modern reviews of root sensory responses, the topic of root orientation in a thermal gradient is ignored because it is assumed that these early reports of thermotropism were due to artifacts.

However, roots do have tropic responses to gravity and mechanical pressure (Feldman, 1984) and their curvature can be affected by unilateral application of certain cations (Hasenstein, 1988). Thermal effects on root growth, branching and metabolism at specific constant temperatures have been well studied subjects (Walker, 1970; Cooper, 1973). However, the question of root orientation within a temperature gradient is still unanswered mainly because most of the approaches to study the effects of temperature on roots consisted of subjecting the entire root system or the parts under study to constant controlled temperatures. However, compensation in one half of the root system for unfavourable temperatures in the other half has been demonstrated using the split-root technique (Brouwer, 1981). Minorsky (1989) reviewed a series of experiments on cooling plants to temperature above their chilling injury threshold. Onderdonk and Ketcheson (1973) reported that the angle of corn root growth is influenced by both constant and cyclic temperatures. Mosher and Miller (1972) found no response when they studied the orientation of maize roots grown in an undefined thermal gradient applied opposite to or in the same direction as the gravity vector.

Thus, the objectives of this work were to examine if Zea mays (L.) primary roots respond to a thermal gradient applied perpendicular to the gravity vector. Thermal gradients were found to influence the direction of root growth. Since this was the case, Arabidopsis thaliana (L.) Heynh., ecotype Estland was chosen for further work because it offered the possibility of using mutants with gravity-insensitive roots and shoots to examine how thermal gradients interact with gravity in determining the direction of root growth. However, the Arabidopsis wild-type was found to have a small response to temperature gradients and the use of a gravitropism mutant did not enhance the response.

MATERIALS AND METHODS

Seeds of Arabidopsis thaliana, ecotype Estland were sterilized and planted on 1% (w/v) agar plates supplemented with 1 mol m^{-3} KNO_3 and 1% sucrose. The plates were sealed and incubated under light with the surface of the agar oriented vertically until 60%

germination i.e. 26 hours at 26 C or 30 hours at 16 C. The plates were then treated for 72 hours in darkness with the same vertical orientation in one of two ways: 1) transferred to a thermogradient plate set to a gradient of 4.2 C cm^{-1} (Poff and Skokut, 1977), with the seeds in the petri dish at the position of 21 C within the gradient; 2) transferred to a similar plate at 21 C without a temperature gradient, as a control. In a second experiment, the MG-32 mutant strain of *Arabidopsis thaliana*, ecotype Estland with altered root and hypocotyl gravitropism (Bullen et al., 1989) was subsequently used as described above. An average of 700 plants were used in each experiment.

Seeds of *Zea mays*, hybrid 'Pioneer 3744' were sterilized and soaked in sterile deionized water for 26 hours to stimulate germination. The seeds were then placed in the holes of thin perforated plexiglass strips embedded in 1% (w/v) agar plates supplemented with 1 mol m^{-3} KNO_3 and 1% sucrose. The plexiglass strips kept the corn seeds in place in the vertically oriented plates during the experiment. The plates were sealed and incubated under low light for 26 hours at 26 C, allowing the radicle to grow past the strip through the perforations to the agar. Then, the plates were screened for seedlings with radicles of 1 to 2 cm long. These plates were either placed on a thermal gradient or at constant temperature for 24 hours in darkness as described above for *Arabidopsis*. Further experiments with corn involved the same procedure as described above but with different gradient and temperatures of exposure within the gradient. A minimum of 60 plants was used in each individual experiment with corn.

A solid aluminum block in which two channels were bored lengthwise was used to create a thermogradient plate by allowing each of two constant temperature water baths set at different temperatures to continuously circulate water within one side of the block (Poff and Skokut, 1977). The temperature gradient established across the block spanned the temperature from that of one bath to that of the other. A similar apparatus was used for the constant temperature control using only one circulating water bath channeling water to the two sides of the block, establishing a constant temperature across it. The aluminum block was insulated with a minimum of 9 cm of styrofoam and embedded in a commercial cooler. Three thermocouples were installed permanently on each aluminum block and read regularly using a programmable datalogger. The temperature on the surface of the agar was estimated through linear regression to the temperature on the aluminum block with a coefficient of determination of 0.99. The temperatures were maintained within ± 0.1 C for 72 hours and within ± 0.3 C for the entire period of the experiments. At the end of the treatments, the petri dishes were placed in a photographic enlarger and the shadowgraph of the seedlings was traced.

The length and the final direction of the corn primary roots were measured. The final direction was determined relative to the direction after the 24-hour pre-treatment period i.e. the angle of deviation (θ) from the original direction projection (Figure 3.1), using a protractor. Positive and negative angles indicate angles towards the warm side and the cold side of the petri dish, respectively.

The growth of Arabidopsis roots and hypocotyls was characterized with an angle of direction and a measure of curvature since the gravitropism mutant's shoots and roots are not only growing but curving in all directions. The direction of the Arabidopsis hypocotyls and roots was determined as an angle between 180° and -180° where 0° indicates a hypocotyl growing up or a root growing down in a perfect vertical orientation, and a negative angle indicates growth towards the cold side of the petri dishes while a positive angle indicates growth towards the warm side. In order to detect any change in the frequency of curvature of the hypocotyls or the roots of Arabidopsis, the "wiggliness" criterion was used. Wiggliness is defined as the the average rate of change of the slope of a curve (Rosenfeld, 1984). These data, as well as length were determined with a Vicom Image Analyzer computer programmed to digitize a video image of the hypocotyl or root shadowgraphs, break the image into segments of 10 pixels, record the coordinates of each segment and calculate the above mentioned parameters.

Analyses of variance were performed to determine if the treatments were significantly different from each other. The treatments in the experiments with Arabidopsis were arranged in a split plot with the large experimental units as the germination temperatures in a completely randomized design and the small units as the gradient treatment and the control. The experiments with corn included a gradient treatment and its control, arranged in a completely randomized design.

RESULTS AND DISCUSSION

Zea mays root:

The first screening of corn roots was done at 21 C within a gradient of 4.2 C cm^{-1}. The mean orientation of the roots within the gradient was 47° from the vertical towards the warm side and was significantly different from the control which was 0.4° from the vertical. The magnitude of the response was such that subsequent experiments involving four other exposure temperatures were set up. The orientation of corn primary roots in the 4.2 C cm^{-1} gradient were also significantly different from their respective controls at 9.0, 14.7, 21.0 and 26.4 C but not at 32.1 C (Figure 3.2). Since corn primary roots grew faster at 32 C than at any other temperatures (Figure 3.3), the absence of response cannot be accounted for by a unfavorable growth rate. As indicated by the positive sign of the angles difference in Figure 3.2, in all cases where the responses were significantly different from the control, the root tip orientation was towards the warm side.

A similar set of experiments at a gradient of 2.2 C cm^{-1} showed an absence of response at 26.8 C cm^{-1} and responses towards the warm side, significantly different from the control at temperatures 14.7 to 24.0 C (Figure 3.2). A third and fourth set of experiments at temperatures of 14.7 and 21 C within gradients of 1.4 and 0.5 C cm^{-1} also gave significant re-orientation of the primary roots towards the warm side of the dish (Figure 3.2). The re-orientation angles at 14.7 and 21 C within the various gradient strengths described above were re-plotted as a function of stimulus strength (gradient) (Figure 3.4). The extent of the re-orientation of corn roots increases with the stimulus strength. The re-orientation also varies with the temperature of exposure: it is larger at 14.7 than at 21 C (Figure 3.4). Based on these observations tropic responses of corn roots to thermal gradients indeed exist.

However, it is difficult to establish when a response to a thermal gradient is truly sensory as opposed to being a non-specific consequence of a differential effect of temperature on each side of the root. If the latter were the case, we should expect two types of responses: first, the most favorable temperatures for elongation growth should also be the temperatures with the highest curvature responses; second, the side of the root exposed to the most favorable temperature in terms of elongation should grow faster and as a consequence, the root should curve towards the opposite or cooler side. However, we observed the lowest curvatures at the temperatures of 26.4 and 32.1 C (Figure 3.2) which are the thermal conditions where elongation growth was the highest (Figure 3.3). Moreover, there exists a higher response at 14.7 than at 21 C, while the roots grew significantly less at 14.7 than 21 C (Figures 3.3, 3.4). Finally, while elongation growth is relatively independent of temperature in the 26-32 C range (Figure 3.3), the curvature is not, as shown by the different responses at 26.4 and 32.1, at the 4.2 C cm^{-1} gradient and, the different responses at 26.4 C in gradients of 2.2 and 4.2 C cm^{-1}. Finally, all the significant curvatures are towards the warm side of the dish (positive sign of the angle), implying that the colder side of the roots grew faster, although the highest temperatures of exposure are clearly favoring growth in this experiment (Figure 3.3). Thus, it is very unlikely that the observed change in root direction is a passive consequence of the gradient across the root. Although the plates were sealed and roots grew at 100% humidity, the temperature gradient across the roots creates a moisture gradient since saturation vapor pressure increases with temperature. This is of concern since Jaffe et al. (1985) showed that a root gravitropic mutant of pea could sense moisture gradients and re-orient its roots towards high humidity zones. However, the curvatures at 14.7 C were much higher than at 32.1 C in the highest gradient (4.2 C cm^{-1}) (Figure 3.2), but yet the vapor pressure at 32.1 C is twice that at 14.7 C (Fritschen and Gay, 1979); also, the 32.1 C temperature of exposure at 4.2 C cm^{-1} gave a response similar to that of 26.1 C at 2.2 C cm^{-1}, while under a hydrotropism situation, it would be expected that the highest temperature at the highest gradient would show a higher response. Therefore, the curves of Figure 3.2, would be expected to increase with temperature rather than decrease. Based on these observations, it can be argued that hydrotropism is of little consequence in our experiments.

Further characterization of this phenomenon is needed. For example, it remains to be seen if the degree of root re-orientation varies with pre-treatment temperatures and if orientation towards cold temperature can exist as it has been shown with different thermotactic systems such as *Paramecium tetraurelia* (Henessey and Nelson, 1979), *E. coli* (Maeda et al., 1976), and *Dictyostelium discoideum* (Whitaker and Poff, 1980). Some similarities with microbial systems exist since the temperatures at which *Dictyostelium* becomes insensitive to a thermal gradient decrease as the stimulus strength decreases (Whitaker and Poff, 1980). This trend is also true for corn (Figure 3.2). As well, the response of *Dictyostelium* increases with gradient strength (Fontana and Poff, 1984) which has been noted with corn too (Figure 3.4).

Finally, it is interesting to note that the temperatures at which corn did not have a response to the thermal gradients correspond to the optimal temperature for corn root growth (Cooper, 1973). Meanwhile, the range of temperatures where maximal responses were measured, corresponds to spring and early summer seed zone temperatures typical of the northern regions where corn is grown. Under circumstances where horizontal temperature gradients would exist (non-uniform placement of residues, row cropping, raised beds, ridge tillage), root thermotropism could be of adaptive value.

Arabidopsis thaliana root:

The question remains whether thermotropism interacts with gravitropism such that the curvature is the result of a vector sum of 2 forces orthogonal to each other. Since this question cannot be answered directly with corn, Arabidopsis was used in another series of experiments since shoot and root gravitropism mutants are available. However, a preliminary test of Arabidopsis wild-type at 21 C in the strong gradient of 4.2 Ccm^{-1} resulted in a low curvature response. In order to enhance the response, two pre-treatment germination temperatures, 5 C above and below the treatment 21 C temperature were used for both the wild-type and the mutant strain, characterized as randomly orienting its hypocotyl and root in a 1-g environment (Bullen et al., 1989). The underlying hypotheses for such treatments were that the response could depend on the temperature to which the plant was growing prior to the thermal gradient treatment and/or that gravitropism may have been "masking" the response to the treatment.

For both the wild-type and the gravitropism mutant, there was no significant interaction between the germination temperature and the gradient treatments. Thus, the two sets of treatments will be discussed separately.

The root direction of both genotypes showed different responses to the thermal gradient. The wild-type roots were more horizontal within the gradient than with the control. The wild-type control was 5° away from the vertical towards the cold side while the plants in the gradient treatment were 18° away from the vertical towards the cold side (Table 3.1). The direction of the mutant roots within the gradient was not significantly different than that of the control mutant roots (Table 3.1). It appears that in the wild type genotype, the plants subjected to the gradient were about 13° more horizontal than their controls, suggesting that there is a significantly different orientation of the roots towards the cold side in Arabidopsis. The wiggliness of the roots exposed to the gradient was significantly higher (higher rate of change of curvature) than that of the controls in the wild type and also in the mutant plants (Table 3.1). The root lengths of the two genotypes were higher for the control plants than for the plants on the gradient. This growth rate difference may be a result of the plants within the gradient growing more directly towards the cold side of the gradient, at least in the case of the wild-type. There is a difference in the extent to which both genotypes express their root orientation in the gradient relative to their respective controls. Since there is evidence that the mutant strain is the result of a single recessive nuclear mutation (B. Bullen, personal communication), it can be implied that Arabidopsis root behavior in the gradient is not independent of gravity sensing. The root direction and wiggliness of both genotypes were not affected by the germination temperatures (Table 3.2).

Arabidopsis thaliana hypocotyl:

The small size of the Arabidopsis seed permitted the measurement of the hypocotyl direction, length and wiggliness in addition to the root measurements. There was no significant interaction between the germination temperature and the gradient treatments for both genotypes.

The hypocotyl direction was not affected by the gradient treatment for either the wild-type or the mutant (Table 3.3). However, the wiggliness was significantly higher in the gradient (Table 3.3). As for the roots, the hypocotyls of mutant plants have a higher wiggliness than the wild-type, which is an expected consequence from the curving phenotype of a gravitropism mutant.

The germination temperatures had no effect on the hypocotyl direction of either genotypes or on wild-type wiggliness but the mutant plants exhibited higher wiggliness with the 16 C germination temperature than the 26 C (Table 3.4).

In summary, the wild-type root showed a higher curving frequency (wiggliness) and is more horizontal by 13° when grown at 21 C in a 4.2 Ccm^{-1} than at constant 21 C. The wild-type hypocotyl did not exhibit any change in direction but did have a higher curving frequency in the gradient. The pre-treatment temperatures did not have any effect apart from diminishing the growth rate of the plants. Therefore, if thermosensing exists in Arabidopsis, it is probably more prevalent in roots than hypocotyls. In general, the use of the mutant genotype did not enhance the responses (in terms of direction and wiggliness) to the thermal gradient. Thus, it cannot be argued that it is gravity that limits the response of Arabidopsis to a gradient as high as 4.2 C cm^{-1}. In fact, there was an absence of mutant root responses (direction) to the thermal gradient while there was a significant one in the wild-type. This absence of mutant response to thermal gradients could be attributed to the mutation and, assuming that thermotropism exists to a limited extent in Arabidopsis, the absence of response in the mutant for both thermal gradients and gravity suggests that thermotropism and gravitropism share part of the same signal transduction pathway. On the other hand, in general, the frequency of curvature (wiggliness) of roots and hypocotyls was affected to the same degree by the thermal gradients for the wild-type and the mutant. Thus, there was no interaction of gravity sensing and thermal gradients for the wiggliness criterion.

It must be concluded that our hypotheses that that germination temperature could affect the response and that use of the mutant would lead to an enhanced response were not correct. Since the root of Arabidopsis has the potential of being only sligthly thermotropic, Arabidopsis should not be considered as a model system with which we can better understand the thermotropic responses observed in corn.

The differences observed between the two species in these experiments emphasizes the fact that root thermotropism is expressed under certain sets of conditions and not under others. Arabidopsis ecotype Estland, could be screened for thermal gradient responses at other temperatures than at 21 C but its practical range of growth temperatures is limited (16 to 32 C). Meanwhile corn responses can be characterized under a broader range (9 to 40 C) (Cooper, 1973). There could be a correlation between the extent of the range of growth temperature and the extent of root thermotropism in a number of species. Further characterization of a number of species would be necessary before such a conclusion could be drawn.

Table 3.1 Effect of a 4.2 C cm^{-1} temperature gradient on root length, direction and wiggliness of a wild-type (WT) and gravitropism mutant (GM) of Arabidopsis thaliana (L.) Heynh.

	Length (cm)		Direction (°)		Wiggliness	
Treatment	W.T.	G.M.	W.T.	G.M.	W.T.	G.M.
Gradient	2.1	2.8	-18	-1	11.8	14.0
Control	2.8	2.4	-5	6	6.3	10.3
Lsd (0.05)	0.2	0.1	6	ns	1.2	1.3

ns: non-significant

Table 3.2 Effect of germination temperature on root length, direction and wiggliness of a wild-type (WT) and gravitropism mutant (GM) of Arabidopsis thaliana (L.) Heynh.

	Length (cm)		Direction (°)		Wiggliness	
Treatment	W.T.	G.M.	W.T.	G.M.	W.T.	G.M.
16 C	1.8	1.2	-10	5	8.4	10.3
26 C	3.1	2.7	-7	3	7.6	10.8
Lsd (0.05)	1.0	0.5	ns	ns	ns	ns

ns: non-significant

Table 3.3 **Effect of a 4.2 C cm^{-1} temperature gradient on shoot length, direction and wiggliness of a wild-type (WT) and gravitropism mutant (GM) of *Arabidopsis thaliana* (L.) Heynh.**

	Length (cm)		Direction (°)		Wiggliness	
Treatment	W.T.	G.M.	W.T.	G.M.	W.T.	G.M.
Gradient	3.1	2.1	0	-4	7.7	10.5
Control	3.3	2.4	3	6	5.0	9.1
Lsd (0.05)	0.1	0.1	ns	ns	0.6	1.2

ns: non-significant

Table 3.4 Effect of germination temperature on shoot length, direction and wiggliness of a wild-type (WT) and gravitropism mutant (GM) of *Arabidopsis thaliana* (L.) Heynh.

	Length (cm)		Direction (°)		Wiggliness	
Treatment	W.T.	G.M.	W.T.	G.M.	W.T.	G.M.
16 C	2.3	1.2	1	3	6.6	12.2
26 C	3.8	2.8	3	3	5.3	8.3
Lsd (0.05)	0.9	0.8	ns	ns	ns	2.3

ns: non-significant

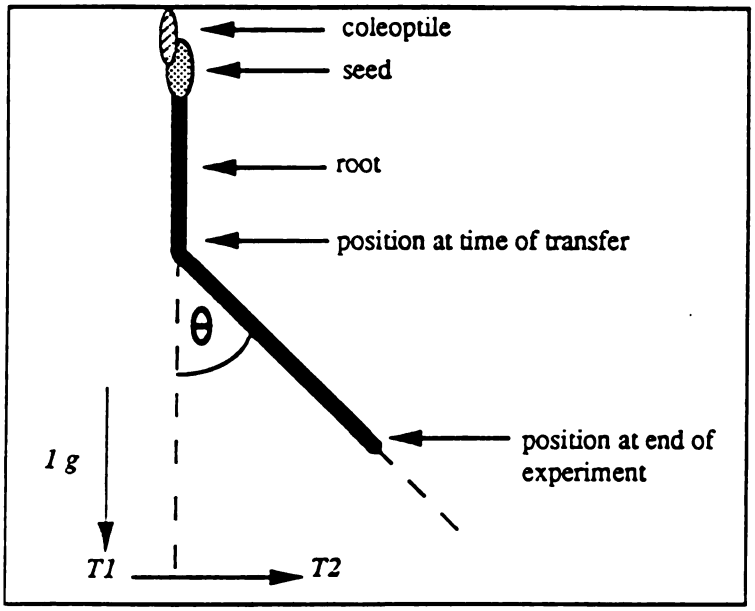

Figure 3.1. Diagram of the angle of deviation (θ) of a corn primary root curving after the transfer of the seedling to a thermogradient plate. The positions of the root tip at the time of transfer and at the end of the experiment are marked.

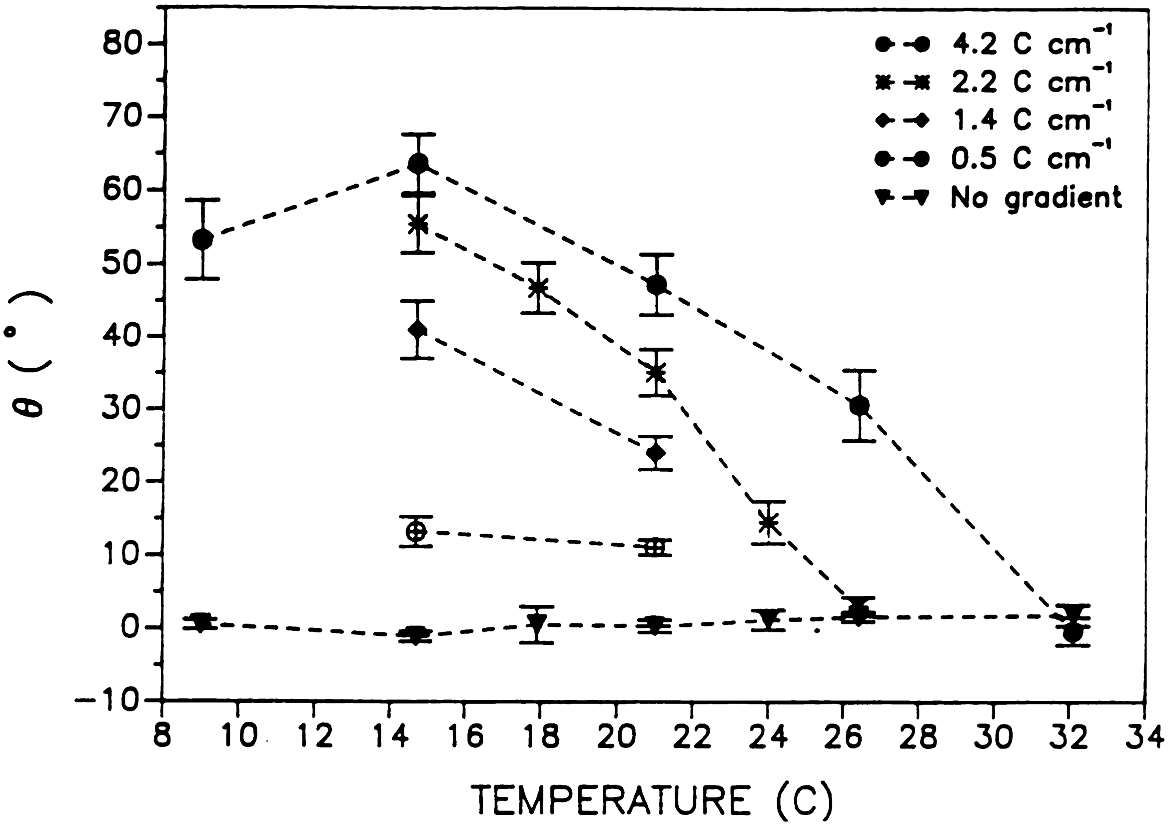

Figure 3.2. Angle of deviation of the primary root of corn exposed to various temperatures within four gradients.

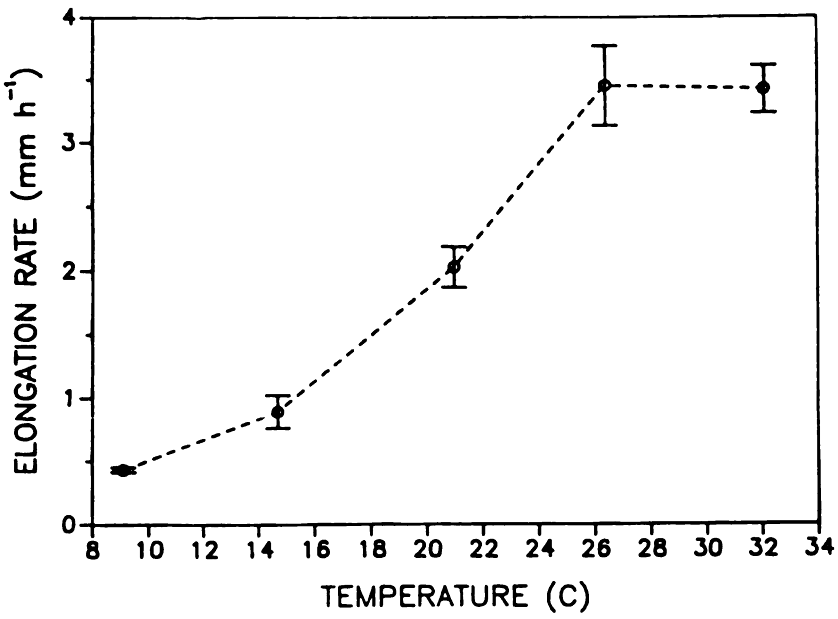

Figure 3.3. Elongation growth of corn primary roots grown for 24 hours in darkness in insulated aluminum plates at constant temperatures.

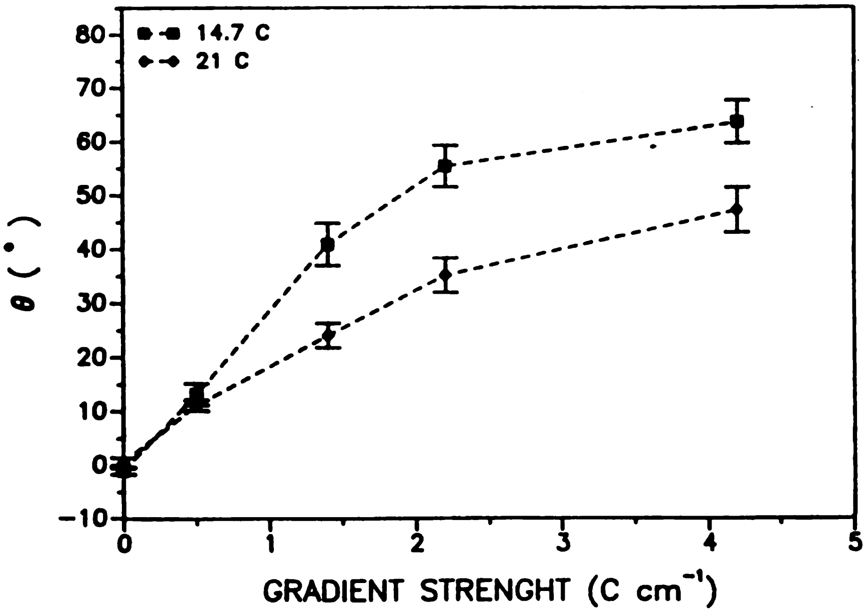

Figure 3.4. **Angle of deviation of the primary root of corn exposed to 14.7 C and 21 C within four gradients.**

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CONCLUSIONS

Studying conservation tillage influences on plant growth is a complex task. It is usually done in comparison to conventional tillage which involves an inversion of the upper soil layers leaving a bare soil surface. Conservation tillage alters soil properties and involves the presence of a residue cover. In this work, efforts focused on selected aspects relating to the temperature effects of residue covers while moisture was controlled to a point where it would not be a significant factor in any of the following experiments.

The first two studies investigated crop residue effects on growth and development during the emergence to flowering period in addition to some final yield measurements. First, it was shown that under irrigated and uniform emergence conditions, the agronomic characteristics of corn grown with a residue cover are mostly a consequence of developmental differences when compared with a bare control. Although the practical importance of delayed maturity associated with the presence of residues cannot be ignored, to grasp the difference between residue effects on development from residue effects on growth was critical for a better understanding of the growth of the corn crop. This approach is unique in the literature of tillage influences on corn. Although these experiments under uniform emergence and adequate soil moisture allowed better definition of corn responses during vegetative development, future research should examine other areas that were not addressed. Conservation tillage is known to create problems with uniformity of emergence and the exact conditions for this phenomenon need to be defined. Growth at the cellular level depends on division and expansion. Both processes are impaired with a lack of available soil moisture. This is a common situation during a normal growing season and yet, its effect on the timing of the coleoptile and subsequent leaf emergences is not well documented.

Second, it was also demonstrated that the effect of low temperatures on corn with residue covers may be coupled to allelopathic effects. The developmental delays of the oat mulch treatment was shown not to be due entirely to seed zone temperature, in one of two years. Such chemical effect is not incorporated in growth models and could result in errors predicting corn development. An interesting continuation of this study would be to study the effect of the same oat straw on fall-seeded crops growing under warmer conditions than spring-planted corn. Allelopathy potential and weather pattern interactions must also be defined if modelling of such effects are to take place.

Finally, the last part of this work dealt with corn primary roots. In the very early stages of growth, the environment plays a critical role because the plant has limited resources to emerge. The effect of horizontal thermal gradients could be critical and may be beneficial if plants responded to them. Thermosensing could be of adaptive advantage and contibute to determine the date and uniformity of emergence. In fact, corn roots responded to thermal gradients by re-orienting their original constant temperature-grown vertical direction. A sensory response was demonstrated to be most likely and we obtained the first modern evidence that root thermotropism exists. The resulting angles of root growth were significant in determining a direction of growth different from the vertical. The thermotropic responses of corn roots need to be characterized so that testable hypotheses on the sensing system can be formulated. The description of the system and its comparison with already defined microbial temperature sensing systems constitutes an exciting research avenue. In addition, the interaction with gravitropism needs to be explored. Finally, root thermotropism needs to be assessed in natural growing conditions in order to determine if its importance warrants the modification of management practices for field crops.