Effect of Planting Date and Nitrogen Fertility on Appearance and Senescence of Sugarbeet Leaves

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ABSTRACT

Seasonal leaf production and senescence in sugarbeet (*Beta vulgaris*) were studied in a field experiment conducted at the Colorado State University Agronomy Research Center in 1977. Three levels of N fertilizer (0, 100, and 300 lb N/A) and two planting dates (April 22 and May 27) were imposed to study numbers of green, senescent, and total leaves; leaf appearance rate (LAR); and leaf death rate (LDR). Weekly observations on 120 previously designated plants were conducted to follow leaf production and senescence during the growing season. Growth equations were developed, using regression least squares, to express production and senescence of leaves over a growing season.

Maximum number of green leaves on the plant was reached on September 7 for both planting dates although separated by 36 days. Changes in leaf numbers with varying N and time indicate that sugarbeets planted later approach optimum top growth more rapidly when the level of available N is increased. Later planting of sugarbeets with recommended or higher levels of available N caused the plant to respond with an increased rate of leaf production (LAR) which compensates, in part, for the later planting but at the expense of reducing sucrose storage in the root. Increasing the level of N fertility did not affect the LDR until the number of green leaves already on the plant were taken into account.

Harvest of the plants at the end of the season showed that increasing the level of N fertility increased the yield of the root at the expense of the sucrose concentration. Later planting significantly reduced root yield, and the high N rate (300 lb/A) reduced the sucrose content.

Additional Key Words: Leaf appearance, leaf senescence, nitrogen, sucrose accumulation, planting date, fertilizer rate

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In sugarbeets the primary site of photosynthetic activity is the leaf, while the sink for photosynthate is in the root. Many studies in the past have focused on the relationship of leaf area development, dry matter accumulation, sucrose accumulation, and final root yields to cultural practices and environmental parameters (Cole, 1975; Golus and Schmehl, 1973; Houba, 1973; Milford and Watson, 1971; Storer, et al., 1973). It was noted in an early study (Watson, 1952) that as leaf size decreased and leaf number increased, both sucrose content of the root and total dry matter tended to increase. Increase in leaf number was found to depend on both leaf production rate and leaf life-span (Watson, 1952).

In sugarbeet field studies conducted in Colorado, the number of living leaves per plant was found to increase to a maximum number of approximately 30 leaves per plant about the first of September, then declined until harvest (Follett, et al., 1970; Storer, et al., 1970). In England, a sugarbeet field study (Watson, 1947) showed that later planting dates resulted in fewer leaves per plant. Stout (1961) in his review of the literature for N relationships in sugarbeets presented a basic assumption that high levels of N fertilizer stimulate the growth of new leaves, inferring not only an increase in size and weight, but also an increase in the total number of leaves living at any one time.

Humphries and Wheeler (1963) in their literature review found many factors influencing leaf senescence, some environmental, such as water supply, daylength, and light, and some internal and not yet well understood. They found senescence was accelerated by a decline in available nutrients; ample N as well as P deficiency delayed senescence. A field study in the Netherlands (Houba, 1973), found that losses of sugarbeet leaves by senescence were so high they could not be ignored. Loomis and Nevins (1963), however, grew sugarbeets in nutrient solutions and found that the N level had no effect on leaf senescence.

Leaf appearance rate (LAR) or the number of new leaves appearing on a plant during a specified period of time has been found to range from two (Humphries and French, 1969) to 4 to 5 leaves per week (Loomis and Nevins, 1963) in controlled environments. A maximum LAR, under pot culture, of almost 5 leaves per week was reached after 8 to 10 leaves had unfolded in a California study (Fick, et al., 1975). In a field study in California it was found that prior to full cover the lower the plant density the higher the LAR (Clark and Loomis, 1978). As full cover was achieved the LARs for the various plant densities converged to a common level which were generally not significantly different from each other for the rest of the season.

Leaf death rate (LDR), the number of leaves which become senescent on the plant during a specified period of time, has not been studied extensively. In pot or solution culture of sugarbeet, the importance of studying the rate of leaf senescence has been alluded to by many researchers (Loach, 1970; Loomis and Nevins, 1963; Terry, 1968). A field study in England (Humphries and French, 1969) measured LDRs of 0.11 to 1.26 leaves per plant per week over the growing season of May 3 to September 30. In the Netherlands (Houba, 1973) a field study emphasized the importance of obtaining data on LDR but assumed an LDR of 1.5 leaves per plant per week for all N treatments. This research was initiated to characterize the influence of planting date and N fertility on the number of green leaves, cumulative number of senescent leaves, total leaf production, and the rate of appearance and senescence of sugarbeet leaves under field conditions.

MATERIALS AND METHODS

This study was conducted on the Colorado State University Agronomy Research Center as a companion experiment to that reported by Lee, et al., 1987.

A split-plot experimental design was used with two dates of planting as the main plots (April 22 and May 12) and three levels of N fertilization as the subplots (no N, control; 100; and 300 lb N/A). At the time of the second date of planting, the surface soil was dry, and there was no germination until after irrigation on May 27. For the data analysis of this study the May 27 irrigation date was designated as the second planting date. The six treatments (three N levels and two planting dates) were replicated four times to give 24 plots. The plants were hand thinned to about a 10-in spacing in late May and mid-June, for the early and late planting dates, respectively. Soil properties and cultural practices are described by Lee, et al., 1987.

After thinning, a set of five consecutive plants was selected in the third row of each plot, and 15 feet from the end of the plot. Each set of five plants represented one replication of a treatment to give a total of 120 observation plants. Weekly, starting June 5 for the early planting and June 29 for late planting, each new leaf on the observation plants was tagged and numbered. When the leaf died (senesced), the blade and petiole were removed, the date was recorded, and the dry weight was measured. Leaf senescence for this study was determined as the point when the chlorophyll disappeared but before the leaf lost biomass by disintegration. The total number of green leaves on each date was recorded and a cumulative total of leaves (green plus senescent) produced to that date. At the end of the season the 120 plants were harvested. Dry weights for each leaf were obtained, as well as the condition of the leaf at harvest, i.e., senescent, frosted, or green.

Statistical Analysis

The time required to label new leaves, remove senescent leaves, and count living leaves on the 120 plants was up to seven days. Since it was not possible to observe all plants on a given day, data for the number of green leaves on each date and cumulative number of senescent leaves and total leaf production were each fitted to second degree polynomial regression equations which provided parameter values to estimate values of the previously mentioned growth attributes for any day during the growing season.

The variation in observation dates between and within treatments required a multistep statistical analysis of the field data. Second degree polynomial regression equations were developed for each treatment and replication to express changes over the growing season for each of the variables. Since the independent variable was time, the equations were solved for a common date. Therefore, statistical analyses were performed on estimates of response and not on primary data.

Leaf appearance rate (LAR)

The leaf appearance rate, LAR, or the number of new leaves appearing on a plant during a specified period of time can be determined by two methods. In the first method the most recently emerged but fully developed leaf is tagged at the beginning of the week and at the end of the week the number of new leaves is recorded (Clark and Loomis, 1978; Loomis and Nevins, 1963). This method requires a precise time schedule of leaf counting to obtain the LAR on weekly basis.

An alternative method of determining LAR used for tomatoes (Hussey, 1963), wheat (Syme, 1974), and sunflowers (Marc and Palmer, 1976) is not dependent on a precise data collection time schedule, and thus, was used in this research. The growth equations previously calculated to express total leaf production during the growing season were used to study the rate of leaf appearance. Since equations for number of green leaves represented only the number of living leaves at each observation, LAR would be in error due to leaf loss from senescence. Therefore, green and senescent leaves were summed to calculate the LAR for any specific time. The LAR was obtained by taking the derivative of the growth curve for total leaf production (TLP).

$$\text{TLP} = a + bt + ct^2 \qquad (1)$$

Parameters a, b, c, were estimated for each curve by least squares and the LAR is

$$\text{LAR} = \frac{d\text{TLP}}{dt} = b + 2ct. \qquad (2)$$

Since TLP is a continuous function, LAR was calculated for specific days, t, corresponding to harvest dates of the companion study (Lee, et al., 1987).

Leaf death rate (LDR)

Similar to the development of LAR the leaf death rate (LDR) reflects the rate that leaves are senescencing over the growing season. Analogous to LAR, LDR can also be obtained by two methods. One is a weekly count of the number of senescent leaves. In the other method, and the one used in this study, LDR was determined by taking the derivative of the equation for the cumulative number of senescent leaves (CSL).

$$CSL = a + bt + ct^2 \tag{3}$$

$$LDR = \frac{d(CSL)}{dt} = b + 2ct \tag{4}$$

Parameters a, b, c were estimated for each curve by least squares. Since this is a continuous function, LDR may be calculated for any day once the parameters are established.

RESULTS AND DISCUSSIONS

Although the focus of this study was on leaf production and senescence, a review of the final yield and quality parameters reported in the companion study (Lee, et al., 1987) is needed to assist in the interpretation of these results. Root yield was significantly affected both by the planting date and N fertilization. Beets planted April 22 averaged 24.6 T/A, while the beets planted May 27 averaged 15.0 T/A. Increasing levels of N fertilizer resulted in a hyperbolic yield response. When averaged for planting date, the control N treatment (N_0) produced 15.4 T/A compared to 21.6 T/A for 100 lb N/A (N_1) and 22.5 T/A for 300 lb N/A (N_3). These yields were very good for the Fort Collins area and indicate that there was an excellent production environment for the experiment. Planting date had little differential effect on sucrose content or purity of roots at any of the N levels. Increasing N fertilizer levels decreased both sucrose and purity (N_0: 19.2% sucrose and 98.0% purity; N_1: 18.5% and 97.3%; and N_3: 17.0% and 95.2%). Based on the preplant soil analysis, the recommended N fertilizer rate for the field, was 100 lb per A. This level of N fertilizer (N_1) was found to maximize both gross and recoverable sucrose production for either planting date.

Seasonal leaf production and senescence

The main effect of planting date (D) and harvest date (H) and the interactions D x H and nitrogen (N) x H were the principal sources of variance for the number of green leaves, cumulative number of senescent leaves, and the total number of leaves (Table 1). Relationships among green, senescent and total leaves for the previously recommended N level (N_1) using the fitted equations are shown in Figure 1a and 1b for the April 22 and May 27 plantings, respectively. The vertical dashed line designates the date when the number of green leaves reached a maximum as indicated by the horizontal dashed line.

Table 1. Significance of the principal sources of variance for the number of green leaves, cumulative number of senescent leaves, total leaf production, leaf appearance rate (LAR), and leaf death rate (LDR).

Source of Variation	df	Number of Green Leaves	Cumulative Number of Senescent Leaves	Total Leaf Production	LAR	LDR
Planting Date (D)	1	*	**	*	NS	NS
Block (Rep)	3	NS	NS	NS	NS	NS
Error (a)	3					
Nitrogen (N)	2	NS	NS	NS	NS	NS
D x N	2	NS	NS	NS	NS	NS
Error (b)	12					
Harvest (H)	7	**	**	**	**	**
D x H	7	**	NS	**	**	*
N x H	14	*	*	**	**	NS
D x N x H	14	NS	NS	NS	**	NS
Error (c)	126					

** Significant at 1% level of probability
* Significant at 5% level of probability
NS = Not significant

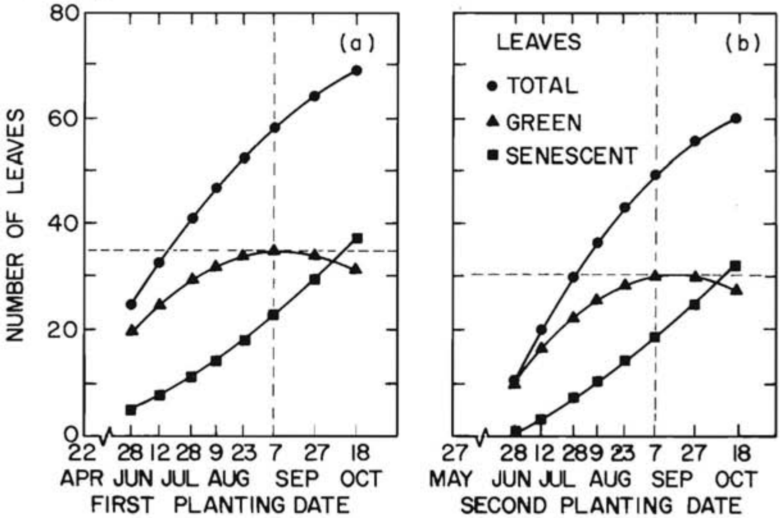

Figure 1. The number of green, senescent and total leaves over the growing season at each planting date for the 100 lb N rate, (a) April 22 planting, (b) May 27 planting. Dates of respective green leaf maxima are indicated by vertical dashed lines.

For the April 22 planting, (Figure 1a) the maximum was September 7 with an average of 35 green leaves per plant. After September 7 the number decreased until final harvest. In contrast, the number of senescent leaves continued to accumulate throughout the season at an increasing rate. Total leaf production increased throughout the season, but at a decreasing rate as the season progressed. In other field studies conducted in Colorado (Follett, et al., 1970; Storer et al., 1970), a similar seasonal relationship for the number of green leaves was observed. They found that the number of green leaves per plant increased to a maximum of approximately 30 leaves per plant about the first of September, then declined until harvest or with a heavy frost. Seasonal studies of leaf loss from senescence have not been characterized although the need of such a study has been indicated by several researchers (Houba, 1973; Humphries and Wheeler, 1963; Humphries and French, 1969).

The average green, senescent and total leaf production for the May 27 planting is illustrated in Figure 1b. The results are similar to the first planting. The number of green leaves per plant reached a maximum on the same date as the earlier planting but at a lower value (30.5 leaves per plant), even though the planting dates were separated by 36 days.

The effect of N rate (data averaged over two planting dates) on the number of green leaves during the growing season is shown in Figure 2. After July 12, the number of green leaves per plant for the 300 lb N rate was greater on each date than the other two N rates. The maximum number of green leaves per plant on September 7 was 35.8, 32.8, and 29.9 for the high, medium and zero rates of N, respectively (Figure 2). The effect of N rate on the cumulative number of senescent leaves did not become apparent until late in the season (Figure 3). There were no differences among harvest dates before September 27, but after this date, the N_3 treatment had lost more leaves per plant (29.3) than the control treatment (24.7). The N_1 treatment, with 28.1 leaves lost per plant, was not different from the N_3 or the control. By the end of the season, both N_3 and N_1 had lost more leaves per plant, 37.1 and 36.0 respectively, than the control which lost 31.5 leaves per plant.

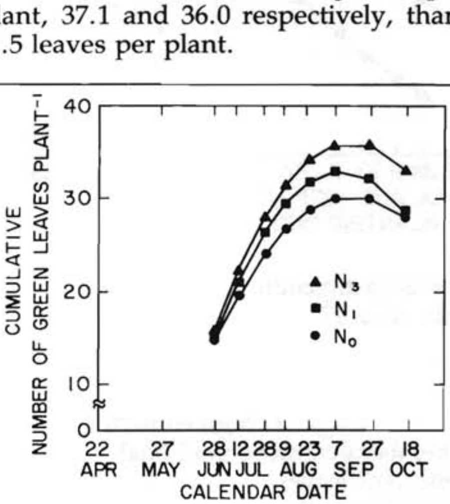

Figure 2. The effect of nitrogen rate and harvest date on number of green leaves at various calendar dates (average of two planting dates).

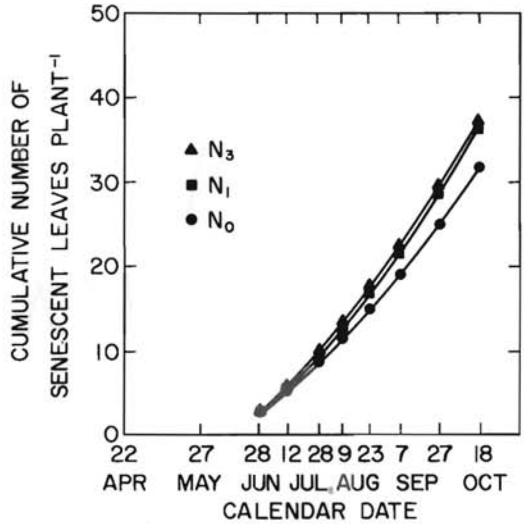

Figure 3. The effect of nitrogen rate and harvest date on the cumulative number of senescent leaves at various calendar dates (average of two planting dates).

In the companion study, Lee, et al. (1987) reported that the LAI increased and was sustained longer when the rate of N was increased. When the maximum number of green leaves for September 7 was 35.8, 32.8 and 29.9 for the N_3, N_1 and N_0 rates respectively (Figure 2), the corresponding LAI were 2.8, 2.1 and 1.4 (Lee, et al., 1987). This relationship between leaf number and leaf area shows that as N becomes limiting, the size of the newly formed leaves is reduced. Conversely, as the N fertilizer was decreased, as shown earlier, the sucrose storage in the roots was increased. Thus, as the level of N fertilizer increases, the sucrose produced by photosynthesis is channeled into leaf production which increases the size of the canopy while concurrently decreasingly the sucrose stored in the root.

The effect of N fertility on senescence of leaves can be understood when the above analysis of the number of green leaves and LAI are related to light penetration into the canopy. Total solar radiation pattern for the 1977 growing season, illustrated in Figure 4, showed that during the later half of August a week of cloudy weather reduced incident solar radiation to 300 ly/day. Reduction in available incident radiation causes light to become limiting within the canopy as the rate of N fertilizer increases. As the number of leaves on a sugarbeet plant increases, lower leaves do not receive sufficient light to exceed the light compensation point. Thus light-deficient leaves can not be supported and begin to senesce.

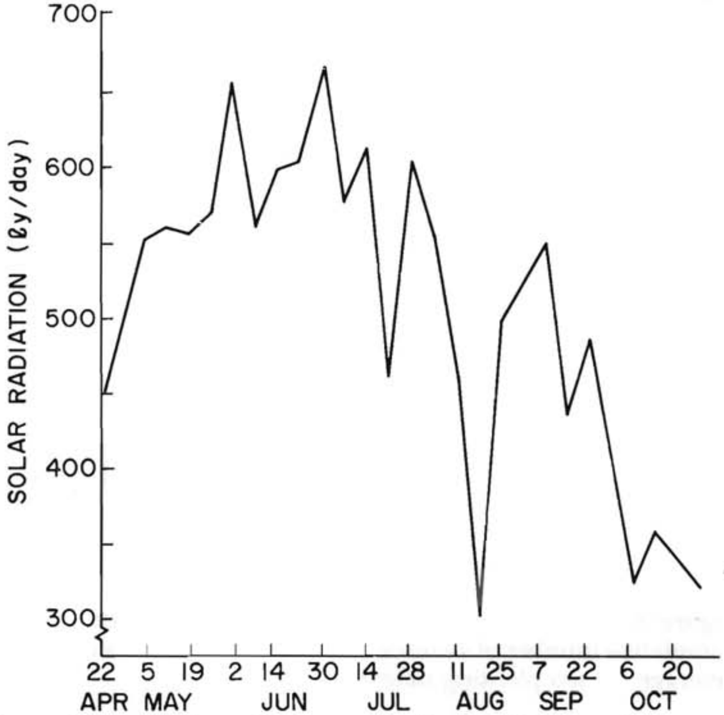

Figure 4. Total solar radiation profile for the 1977 growing season at Fort Collins, Colorado.

Rate of leaf appearance and senescence

Leaf appearance rate (LAR) was calculated as the derivative of second degree polynomial growth curves of total leaf production (sum of cumulative number of senescent leaves and number of green leaves). Mathematically, using a second degree polynomial for a growth curve means that the resulting equation for the seasonal LAR would be a straight line (LAR vs. time) as illustrated in equations (1) and (2). Solving these linear equations for the harvest dates used in the companion study (Lee, et al., 1987) provided estimates of parameter values for statistical analyses. A split plot analysis of variance of the data (Table 1 and Lee, 1980) showed that the main effects of planting date and N were not significant at the 5% level while the seasonal effect of harvest date, and the two way interactions of D x H and N x H, and the three way interaction of D x N x H were highly significant. Table 2 summarizes the three way interaction data and the Tukey's HSD test for the appropriate mean separations.

The LAR in mid-June ranged from 4.7 new leaves per plant per week for the N_3 treatment planted April 22 to 6.6 for the same treatment planted May 27. The number of green leaves for the N_3D_1 treatment on June 14 was 14.8 while the N_3D_2 treatment had 10.2 green leaves on June 28. As the season progressed the number of green leaves for the N_3D_1 treatment increased to 36.4 leaves by September 7 while the LAR decreased to 2.6 new leaves per plant per week. For the later planting the N_3 treatment on September 7 had 35.2 green leaves and a LAR of 2.9 new leaves per plant per week. By October 18 the LAR for the N_3D_1 had decreased to 1.5 new leaves per plant per week compared to 1.1 for the later planting at the maximum N rate. The number of green leaves on the plants were 33.3 and 32.5, respectively, on October 18. In other studies, the maximum LAR ranged from 2 (Humphries and French, 1969) to 4-5 (Loomis and Nevins, 1963) leaves per week in controlled environments. In a pot culture experiment (Fick et al., 1975) a maximum LAR of almost 5 leaves per week was reached after 8-10 new leaves had unfolded.

Table 2. Leaf appearance rate (LAR) per week for the significant D x N x H interaction (Table 1) on specific calendar dates.

	June		July		August		September		October	
Nitrogen	14	28	14	28	9	23	7	27	18	Mean
D1 April 22 planting										
N_0	4.2	3.9	3.6	3.2	2.9	2.6	2.2	1.7	1.2	2.8
N_1	4.7	4.3	3.9	3.5	3.2	2.8	2.4	1.9	1.3	3.1
N_3	4.7	4.4	4.0	3.6	3.3	3.0	2.6	2.0	1.5	3.1
Mean	4.5	4.2	3.8	3.4	3.1	2.8	2.4	1.9	1.3	3.0
D2 May 27 planting										
N_0	4.3	4.0	3.6	3.3	3.0	2.7	2.3	1.9	1.4	2.9
N_1	6.0	5.4	4.9	4.3	3.7	3.1	2.5	1.7	0.8	3.6
N_3	6.6	6.0	5.4	4.7	4.1	3.5	2.9	2.0	1.1	4.0
Mean	5.6	5.1	4.6	4.1	3.6	3.1	2.6	1.9	1.1	3.5

Tukey's HSD: Planting date and harvest date	**0.05**	**0.01**
Planting date (D)	NS	NS
Harvest date (H)	0.37	0.43
Interaction (D x H)	0.6	0.7
Tukey's HSD: Nitrogen and harvest date	**0.05**	**0.01**
Nitrogen (N)	NS	NS
Harvest date (H)	0.37	0.43
Interaction (N x H)	0.7	0.8

Plotting D x N x H interaction for LAR shows a difference in seasonal trend for the N_3D_2 and N_1D_2 treatments when compared to the other four treatments (Figure 5). Since the data are linear, the slopes of the lines were used to test the hypothesis that there exists a difference among slopes. No significant difference was found among the slopes of the N_0D_1, N_0D_2, N_1D_1, and N_3D_1 treatments or between the slopes of the N_1D_2 and N_3D_2 treatments, but the slopes of the latter two treatments decreased at significantly greater rate than those for the other four treatments. Examination of the data for planting date at each N level shows the two-way interaction effect. When N was limiting, (N_0), planting date had little differential effect on LAR during the season. For both the 100 and 300 lb N rates the LAR for the May 27 planting was greater than for the April 22 planting early in the season, and the slopes of these lines (N_1D_2, N_3D_2) were steeper than the April planting at the same N levels. Also, the rate of decline in LAR, although higher in June, was greater for the later planting when N was applied. The LAR for the 300 lb N rate for the May planting was greater than the LAR for the N_1D_2 treatment throughout the season. For the April planting the LAR was about the same for the two N treatments throughout the season. These results seem to indicate that available N may be more important for inducing a more rapid leaf formation for later rather than for early plantings. This study indicates that, when beets are planted later in the season with optimal or higher levels of available N, plants respond with increased rate of leaf production which compensates, in part, for later planting. The cost of increased leaf production is at the expense of reduced sucrose storage in the root (Lee, et al., 1987).

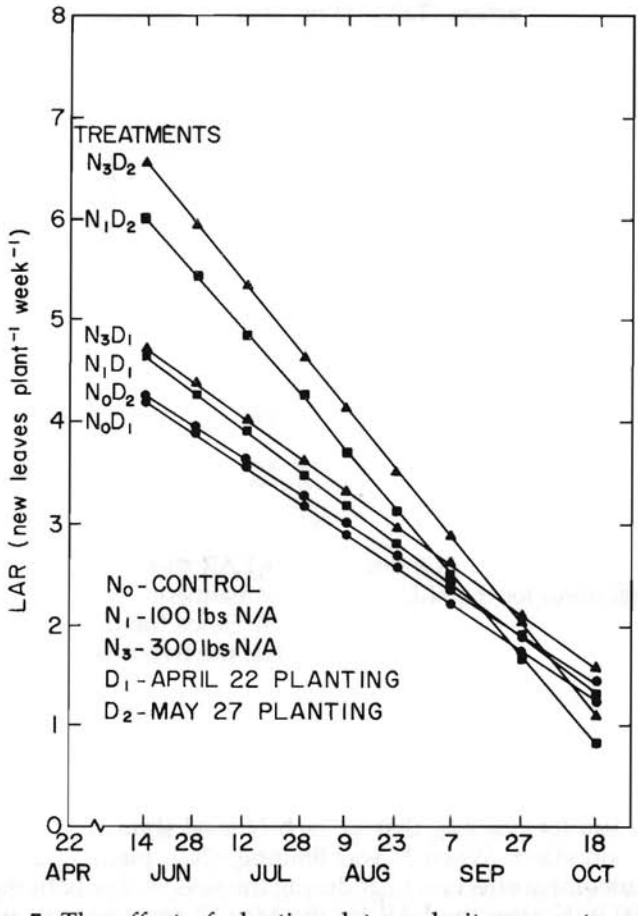

Figure 5. The effect of planting date and nitrogen rate on LAR at specific calendar dates (D x N X H interaction).

Leaf death rate (LDR), similar to LAR, was calculated as the derivative of second degree polynomial equations for the cumulative number of senescent leaves as illustrated in equations (3) and (4). The resulting curve for LDR is a linear function of time. Solving these linear equations for specific harvest dates provided estimate values for the analysis of variance (Table 1).

Harvest date (H) and D x H interaction were the only significant effects (Table 3). Neither planting date (D), nor N, nor the N x H and D x N x H interactions affected the leaf death rate. During the early part of the season the plants were losing 1.5 leaves per plant per week from senescence compared to the 2.5 leaves per plant per week in October. Humphries and French (1969), in England, measured LDRs of 0.11 in May to 1.26 leaves per plant per week by late September. Houba (1973) in the Netherlands assumed a constant average LDR of 1.5 leaves per plant per week for the growing season. These values (Houba, 1973; Humphries and French, 1969) of LDR are considerably below those obtained in our experiment for Colorado field conditions.

Table 3. Leaf death rate (LDR) per week on selected calendar dates.

Planting	June		July		August		September		October	
Date (D)	14	28	12	28	9	23	7	27	18	Mean
April 22	1.2	1.3	1.5	1.7	1.9	2.0	2.2	2.5	2.7	1.9
May 27	1.4	1.6	1.7	1.8	1.9	2.0	2.1	2.3	2.4	1.9
Mean	1.3	1.4	1.6	1.7	1.9	2.0	2.2	2.4	2.6	1.9

Tukey's HSD: Planting date and harvest date	0.05	0.01
Planting date (D)	NS	NS
Harvest date (H)	0.2	0.3
Interaction (D x H)	0.4	NS

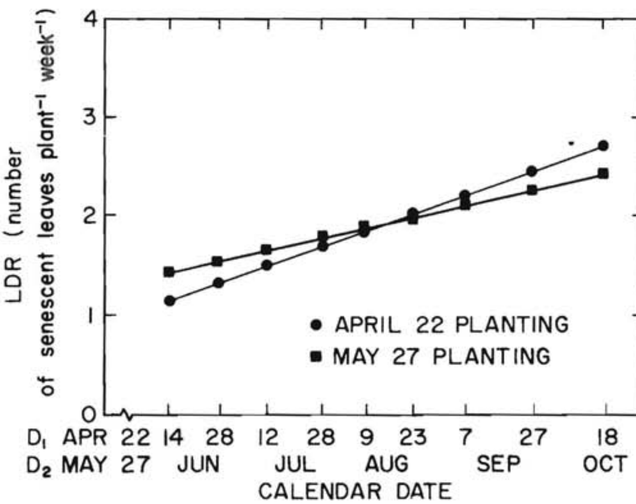

Figure 6. The effect of planting date over the growing season on the leaf death rate (LDR) with time expressed as calendar dates (averaged over three nitrogen rates).

The significance of D x H interaction is illustrated in Figure 6. The slope of the LDR for the early planting increased at a greater rate than that for the later planting. The rate of leaf senescence for the April planting was less than for the May planting until mid-August, then the rate of senescence was greater for the April planting. Nitrogen fertilizer had little effect on the rate of leaf senescence, although increasing the N fertility increased the cumulative number of senescent leaves over the growing season.

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