TILLERING AND CARBOHYDRATE CONTENT OF ORCHARDGRASS AS INFLUENCED BY ENVIRONMENTAL FACTORS

by

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INTRODUCTION

The development of new tillers in grasses is important for several reasons. Growth rates of grasses and survival during periods of stress are apparently related to the number of tillers and the physiological age or stage of development. The aggressiveness of orchardgrass toward other species and its persistence is, no doubt, attributable to the sum of responses of all tillers and their physiological conditions. Tillering rate and physiological status, as related to lateral spread and erect growth, apparently influences plant succession, recovery after grazing or cutting, and dry matter production. Thus, information on the interrelationship of environmental factors and tillering would aid in establishing management principles.

The regrowth rate of defoliated perennial grasses when other environmental factors are favorable, have been associated with high leaf areas with near maximum light interception and high carbohydrate reserves in the stubble or roots. Stored carbohydrates in the basal part of perennial grasses have been associated with survival and regrowth under periods of stress. There is surprisingly little information on the relationship between tillering (production of new shoots) and carbohydrate content of perennial cool season grasses. Thus, morphological and physiological studies on the reaction of grass to various environmental factors should provide helpful information in evaluating species and new varieties for local climatic conditions.

A series of experiments was conducted in the field, greenhouse, and controlled environment chambers to study the effect of natural and imposed environmental factors on growth, tillering, and water soluble carbohydrates of orchardgrass.

LITERATURE REVIEW

The Effect of Environmental Factors on Tillering and Growth

Many investigators have found that variation in environmental factors, such as light or temperature, resulted in differences in composition morphology, and yield of forage plants (3,4,8,9,20).

Light. The response of tillering to either light intensity or duration has been demonstrated by several workers. Margadant (18) found that tillering of perennial ryegrass increased with increasing light intensity. Mitchell (21) subjected S23 and short rotation ryegrasses to light of 700 and 2000 F.C. intensity for ten hours daily. Tillering at equal leaf appearance age was increased four fold by raising light intensity from 700 to 2000 F.C. He concluded that quantity of light energy available appeared to be the chief determinant of the number of tillers formed.

A further analysis of the effect of light intensity on tillering of herbaceous species has been reported by Hoshino et al. (14). They noted that tiller numbers per plant declined continuously as light intensity was decreased from 100% to 5% of natural light. Ryle (28) reported that tillering of S48 timothy was reduced by shading. Patel and Cooper (26) concluded from studies on the effect of seasonal changes on tiller production in ryegrass, timothy, and meadow fiscue that tillering is linearly related to light energy received per day, although differences among species occurred. Mitchell (22) examined the effect of shading on tillering of S23 ryegrass. He found that a reduction in light intensity from 65% to 25% daylight decreased the rate of tillering and caused a reduction in the development of axillary buds.

Mitchell and Coles (23) compared ryegrass plants grown in full light with plants under two shading treatments. These treatments were: 1) general shading of the whole plant to 30% of daylight with muslin screens, and 2) base shading in which green muslin was wrapped on a wire frame around the base of the plant to simulate light conditions in a pasture. Graduation from slight shade at the top to dense shade at ground level was achieved by increasing the layers of muslin at the base. The effect of general shading and base shading in reducing the rate of tillering were similar, and it was concluded that tiller formation by shaded plants was dependent on the quantity of light energy absorbed by the whole plant rather than the intensity of light at the base of the plant. Both treatments reduced dry weight production and altered tillering and leaf growth. When base shaded plants were transferred to full daylight, the rate of tillering increased immediately to a rate equal to that of plants not previously shaded. Mitchell stressed that the rate and pattern of tissue formation is dependent on current rather than previous light conditions.

The influence of the length of photoperiod on tillering of herbage plants has been investigated. Watkins (36) found that reducing natural daylength to 8.5 hours in brome grass (Bromus inerimis) encouraged tiller production. Reducing the light period from 19 to 11 hours increased tiller production in Kentucky bluegrass (Poa Pratensis) without causing inflorescences to form, Peterson and Loomis (27). Templeton et al. (32), working with tall fescue, found that tillering was significantly increased in short days under natural temperature even though the plants received the same, or less, light energy compared with those under long day conditions. Only when the light intensity was as low as 200 to 400 F.C. did plants in long day produce more tillers. By contrast, Mitchell (22) reported that ryegrass under 18 hours photoperiod tillered faster than ryegrass under eight hours photoperiod. He illustrated that a reduction in quantity of light available to the plant may induce lateral bud inhibition irrespective of whether intensity is reduced and period of illumination held constant, or intensity is held constant and period of illumination reduced. Cooper (11) found that by increasing natural daylength with a supplementary period of low intensity illumination the rate of tillering of ryegrass did not increase. Nittler et al. (25), in three varieties of orchardgrass, found that there was little difference among varieties in tiller production when they were grown with 2200 F.C. for 12.5 hours or with 1300 F.C. for 16 hours. Less light, 650 F.C. for 16 hours or 1300 F.C. for eight hours, produced greater varietal differences. They concluded that differences between varieties were caused by low quantity of light received and not by the length of photoperiod.

Temperature. It has been reported that temperature plays an important role in tillering and growth of perennial grasses. Mitchell (19), working with young plants growing at a light intensity of 2700 F.C. noted that tillering was most active at 13 and 18°C. in perennial ryegrass, and 24 and 29°C. in orchardgrass. He also found that lowering the temperature from 18 to 10°C. increased mean tiller number of S23 ryegrass (21). Perennial ryegrass grown at 25°C. by day decreased in tiller numbers with an increase in night temperature from 10 to 15 and 25°C., Alberda (1). This response appeared to be correlated with the total soluble carbohydrate content of the plant. When grown at 15°C. by day the plants responded less markedly to variations in night temperature.

Mitchell and Lucanus (24) showed that tillering in orchardgrass and perennial ryegrass grown at a 16°C. day temperature was increased by lowering the night temperature from 7 to 1.7°C. Bommer (5) found that plants of false oatgrass (*Arrhenatherum elatius*) tillered more at 5-15°C. than at 15-25°C. in short days irrespective of the conditions imposed during a pretreatment period. It was found by Templeton *et al.* (32) that tillering of young tall fescue plants was favored by a period of daily exposure to a temperature of 7°C. as compared to growth at 22°C. continuously. Tillering was highest when exposure to low temperature occurred during the light period only.

Defoliation. Evidence on the effect of defoliation on tillering has been presented by Mitchell (22). He reported that removal of approximately 80% of the leaf tissue of perennial ryegrass at a temperature of 22°C. checked the rate of increase in tiller numbers. Another defoliation seven days later further delayed initiation of new tillers. Alberda (1) has shown that immediately after cutting, tiller formation of perennial ryegrass was stopped whereas uncut plants showed a linear increase with time. Repeated cutting of short-rotation ryegrass checked tiller formation only temporarily but greatly reduced tiller size, Mitchell and Cole (23). Stapledon *et al.* (30) reported that orchardgrass cut to ground level every three weeks produced 152 tillers throughout the season as compared with 230 when plants were cut to six inches every three weeks.

Nitrogen and Irrigation. The influence of nitrogen and soil moisture on tillering of forage plants has been studied very little. Langer (17) reported that a combination of three levels of NPK had a significant effect on tillering of timothy. Nitrogen at a concentration of 150 P.P.M. in the culture solution produced considerably more tillers over the whole range of treatments than either of the other two elements at their highest level. A considerable increase in tillering of orchardgrass due to the application of nitrogen was reported by Stapledon *et al*. (30). Peterson and Loomis (27) found that nitrogen fertilization in early fall stimulated tillering and increased the number of flowers in Kentucky bluegrass. Gardner (12) showed that Marquis wheat produced more tillers when the soil was at 50% than at 25% of water holding capacity.

The Effect of Environmental Factors on Carbohydrate Contents

Alberda (1) concluded that factors which tend to lower carbohydrate content of perennial ryegrass tend to reduce tillering and root growth. He reported a decided decline in soluble carbohydrates of perennial ryegrass stubbles when light intensity was reduced from 41,000 ergs/cm^2/sec. to 22,000 ergs/cm^2/sec. The relationship between reserve carbohydrate content of orchardgrass and tillering has been shown by Ward and Blaser (35). They reported that the rate of tillering was much higher for plants containing high carbohydrate reserves as compared with plants low in reserves.

The effect of defoliation on carbohydrate content was reported by Baker and Garwood (2). They found that total soluble carbohydrate of orchardgrass was higher in swards cut infrequently. Huokuna (15) reported that plants cut to 10 cm. contained more than twice the carbohydrate content of those cut to 3 cm. Little differences appeared between those cut at 6 and 10 cm. Alberda (1) reported that soluble carbohydrates in the stubble of ryegrass increased exponentially in uncut plants. After four weeks the amount was ten times higher than at the beginning of the experiment. In the cut plants, the amount dropped from about 350 to 32 mg. per pot during the first week after cutting. There was then a gradual increase and after three weeks the original level was resumed.

Sullivan and Sprague (31) clipped perennial ryegrass plants at a height of 1.5 inches above the surface of the soil and allowed them to recover under controlled environmental conditions with four temperature variables, namely at 50-60, 60-70, 70-80, and 80-90°F., with daytime temperatures 10°F. above those of the night. They found that roots and stubbles underwent rapid losses in sucrose and fructosan during the early part of the experiment but the losses were partly replaced later under the low temperature conditions. Under the highest temperature these losses were not replaced but continued, especially in the roots, almost to the point of exhaustion and in some cases to the death of the roots.

Alberda (1) reported a considerable drop in the soluble carbohydrates of ryegrass stubbles when night temperature increased from 3 to 28°C. Hurd-Karrer and

Dickson (16) also reported that wheat plants accumulated less carbohydrates as the temperature became higher. Sprague and Sullivan (29) reported that the total water soluble carbohydrates were higher in orchardgrass stubble than in the tops and roots and this could be largely attributed to the predominance of fructosan in the stubble. After each cutting of the tops, fructosan and sucrose of the stubble and roots decreased in percentage in accordance with their probable role of reserve substances. The decrease in each case seemed proportional to their concentration, greater decreases occurring, particularly in the roots, when their percentages were high. Reducing sugars decreased after cutting only when, under condition of high nitrogen, their percentages were high. After initial drops the percentages of all soluble carbohydrates were restored before the time of the next cutting.

Under high nitrogen nutrition the percentages of fructosan and sucrose were less than under low nitrogen. The addition of nitrogen at the higher level, while not affecting the reducing sugar content immediately, caused striking increases in reducing sugars a few weeks later and then these sugars apparently acted as reserve substances.

In a study on the effect of different levels of fertilizer treatment on the water-soluble carbohydrates of ryegrass, meadow fescue, timothy, and orchardgrass by Waite (33), it was found that as the amount of fertilizer applied was increased, the number of cuts in the season increased, the crude protein content of the grass increased, and the soluble carbohydrate content, particularly the fructosan fraction, decreased.

The general effect of increasing amounts of fertilizer in lowering the percentage of the total soluble carbohydrates in all the grasses was brought about mainly by a large reduction in the fructosan content. Those grasses, such as orchardgrass and timothy in which the protein content increased most as the result of the fertilizer treatment, contained very little soluble carbohydrate.

From the average weight of soluble carbohydrates produced at each cut by the three fertilizer treatments it appeared that ryegrass differed from the other three species in being able to maintain a high yield of soluble carbohydrate at the medium rate of fertilizer, whereas in fescue, timothy, and particularly orchardgrass application of even this amount of fertilizer lowered the yield of soluble carbohydrates.

Waite and Boyd (34) studied the changes in the amounts of the water soluble carbohydrates in four perennial grasses during their normal growth cycle from May to October and subjected them to several cuttings during the growing season. The soluble carbohydrates of the earlier cuts of all species ranged from 16 to 26% to about mid-June. The values in July, August, and September fell to about one-half or one-quarter of the amount present in May and early June. It was noted that, of the fractions contributing to the total soluble carbohydrates (free hexoses, sucrose, and fructosan), the low values of the fructosan caused the drop in total sugars. It was also noted that in the last cut of the grasses the total soluble carbohydrate content had risen to a higher value. This may have been the result of the slower growth in autumn than that for the summer.

Weinmann (37), in four warm season species, found carbohydrate reserves mostly active in the autumn. He reported that organic reserves were translocated in the autumn and early winter from the shoots to the roots where they were stored to be drawn upon the following spring for regrowth.

EXPERIMENT I. THE EFFECT OF LIGHT, DEFOLIATION, AND NITROGEN ON TILLERING AND SOLUBLE CARBOHYDRATES OF ORCHARDGRASS

This experiment with orchardgrass was conducted in the greenhouse to study the following:
1) tillering and growth, as influenced by nitrogen, light intensity, and defoliation; 2) to relate the growth and tillering with carbohydrate content of the stubbles; and 3) to evaluate the interrelationships of defoliation, nitrogen, and light intensity on root growth.

Material and Methods

Three orchardgrass tillers were planted in one-gallon metal pots containing a mixture of sand and soil, on August 20, 1962. All tillers were taken from a single clone to control genetic variability. The tillers were allowed to grow in full sunlight outside the greenhouse until September 18, 1962. The pots were then divided into three replications and assigned to factorial treatment combinations (3 nitrogen rates, 3 defoliations, and 3 light intensities). The three levels of nitrogen, N-0, N-200, and N-400 pounds per acre, were established by using a solution of ammonium nitrate. Defoliation treatments were: D-1.5, cut to 1.5 inches when 3-4 inches high; D-3, cut to 3 inches when 6-8 inches high; and D-6, cut to 6 inches when 8-10 inches high. The light intensities were: (L-1) normal sunlight, (L-.5) 50% sunlight, and (L-.25) 25% sunlight. Light intensity levels were obtained by shading with plastic screening with variable mesh to give the desired intensity in this greenhouse experiment. Soil moisture was maintained near field capacity.

Tillers were counted at the beginning and thereafter at weekly intervals. Only two of the three plants in each pot were used for tiller counts; the other plants were sacrificed for carbohydrate analysis and yield when treatments were imposed and also at later intervals.

At the end of the experiment, on November 17, 1962, the plants were removed from the soil, washed, and divided into morphological parts: roots, stubbles, and leaves. Roots and leaves were dried and data on the dry weight were recorded. The stubble materials were oven-dried and ground; 125 mg. samples were then placed in an open test tube. Cold water (30 ml.) was added to the samples and extracted in a boiling water bath. Polyethylene bottles filled with cold water were inserted over the test tubes to prevent evaporation. The samples were boiled for 45 minutes, frequently agitated to insure thorough extraction, and filtered through Whatman's No. 42 filter paper. The samples were filtered into 100 ml. volumetric flasks; 2.5 ml. of 25% HCl and distilled water were added to bring the filtrate to 50 ml. The filtrate was then placed in a boiling water bath for 30 minutes for hydrolysis; after this it was cooled and neutralized with 25% NaOH solution (using methyl red as indicator) and made up to 100 ml. volume. Aliquots of 0.2 ml. were used for carbohydrate analysis, using Nelson's chromogen reagent with Somogyi oxidizing agent for color development. Readings on color intensity were made on a colorimeter.

Results

__Tillering__. Light intensity, nitrogen fertilization, and defoliation all had significant effects on tillering of orchardgrass, Table 1. At the end of 50 days there were 10, 2.7, and 0.7 new tillers per treatment for L-1, L-.5, and L-.25, respectively. Heavy defoliation retarded tillering of orchardgrass; there were 1.9, 3.7, and 7.7 tillers for D-1.5, D-3, and D-6, respectively. Nitrogen fertilization increased tillering, but tillering was no better for N-400 than for N-200. Without adding nitrogen to the soil, there was an average of 1.7 tillers as compared with 9.4 tillers for N-200.

Nitrogen responses varied with light and defoliation treatments, and light responses also varied with defoliation treatments; these interactions are given in Figures 1, 2, and 3. Under L-1, there was a decided increase in tillering as defoliation intensity was relaxed, Figure 1. Tillering increased little with reduction in defoliation for L-.25, and effects were intermediate with L-.5.

The interrelationship of light intensity and nitrogen fertilization is shown in Figure 2. With

Table 1. The effect of light intensity, defoliation, and nitrogen on orchardgrass tillering (mean values per pot).

Nitrogen	L-1				L-.5				L-.25				Grand Mean
	Defoliation				Defoliation				Defoliation				
lb/A	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	
0	2.0	2.3	3.0	2.4	0.4	3.3	2.0	1.9	0	0.7	1.4	0.7	1.7
200	6.0	10.7	25.0	13.9	2.0	2.3	6.3	3.5	0	1.4	0.7	0.7	9.4
400	6.3	10.7	24.3	13.7	0.7	2.0	5.0	2.6	0	0.7	1.7	0.8	5.7
Mean	4.8	7.9	17.4	10.0	1.0	2.5	4.4	2.7	0	0.9	1.3	0.7	4.5

The following were significant at the 1% level: light (L), nitrogen (N), defoliation (D), NXD, LXN, and LXD.

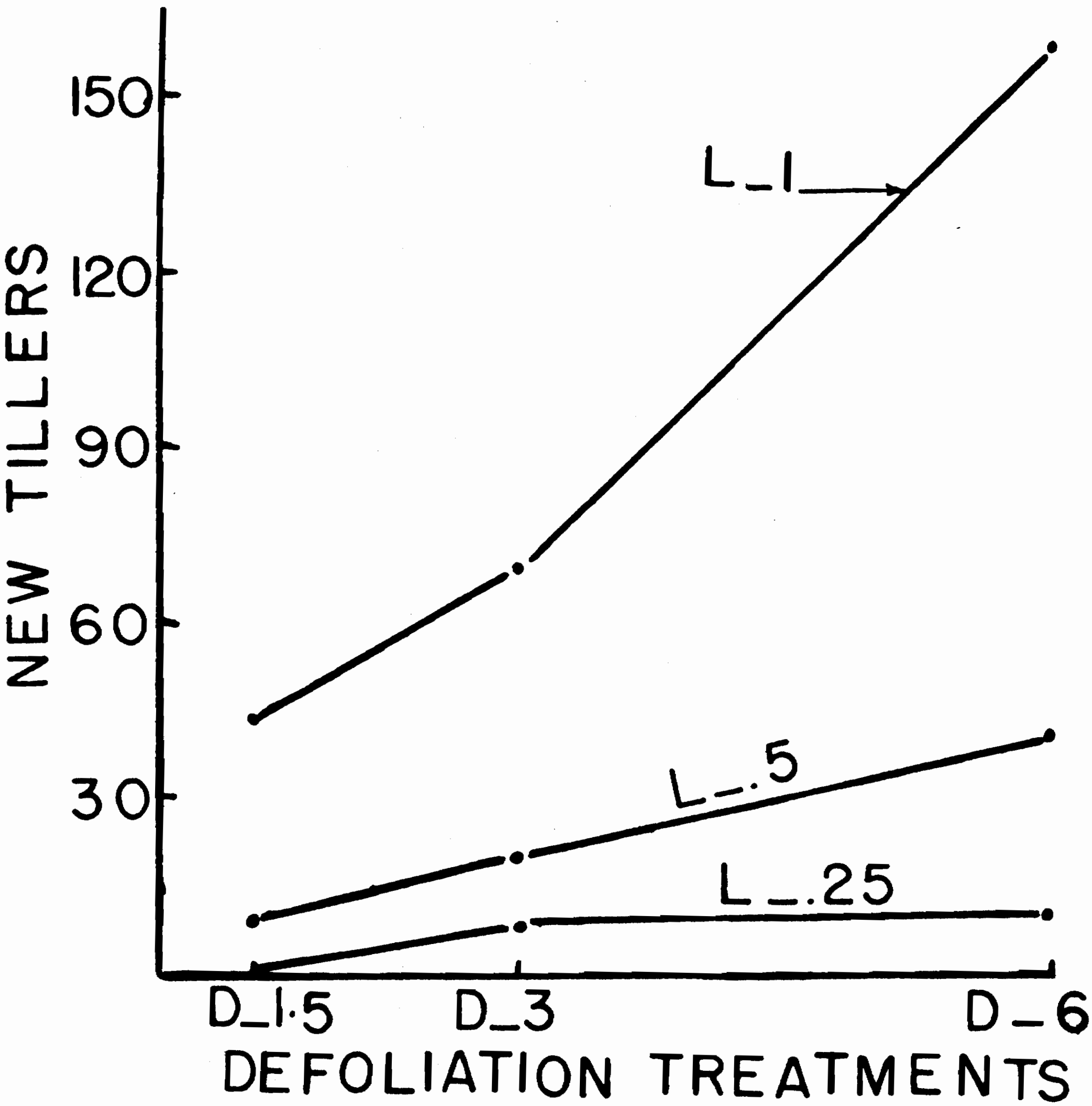

Figure 1. The effect of defoliation and light intensities on tillering of orchardgrass during a 7-week period.

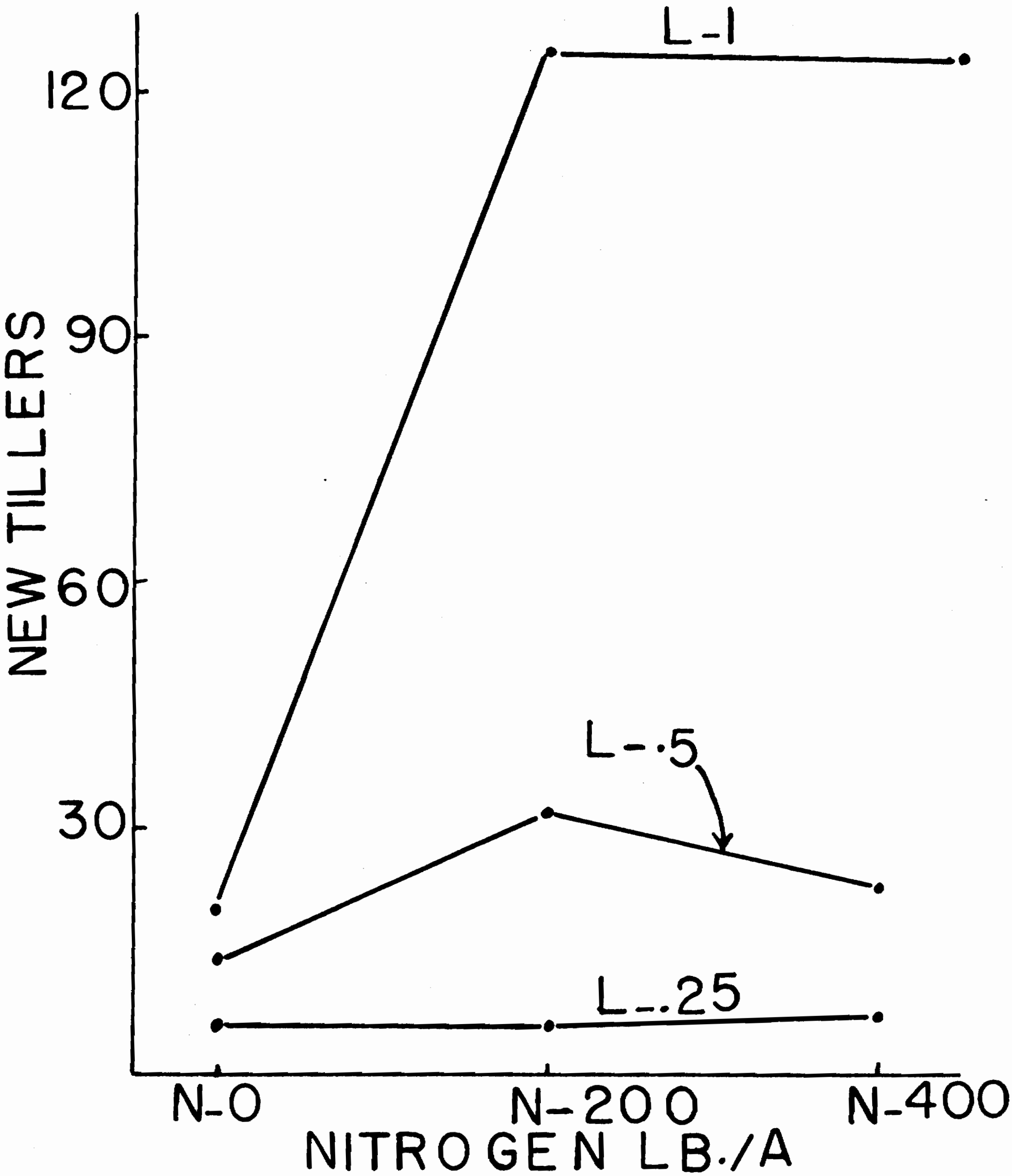

Figure 2. The effects of light intensities and nitrogen rates on tillering of orchardgrass during a 7-week period.

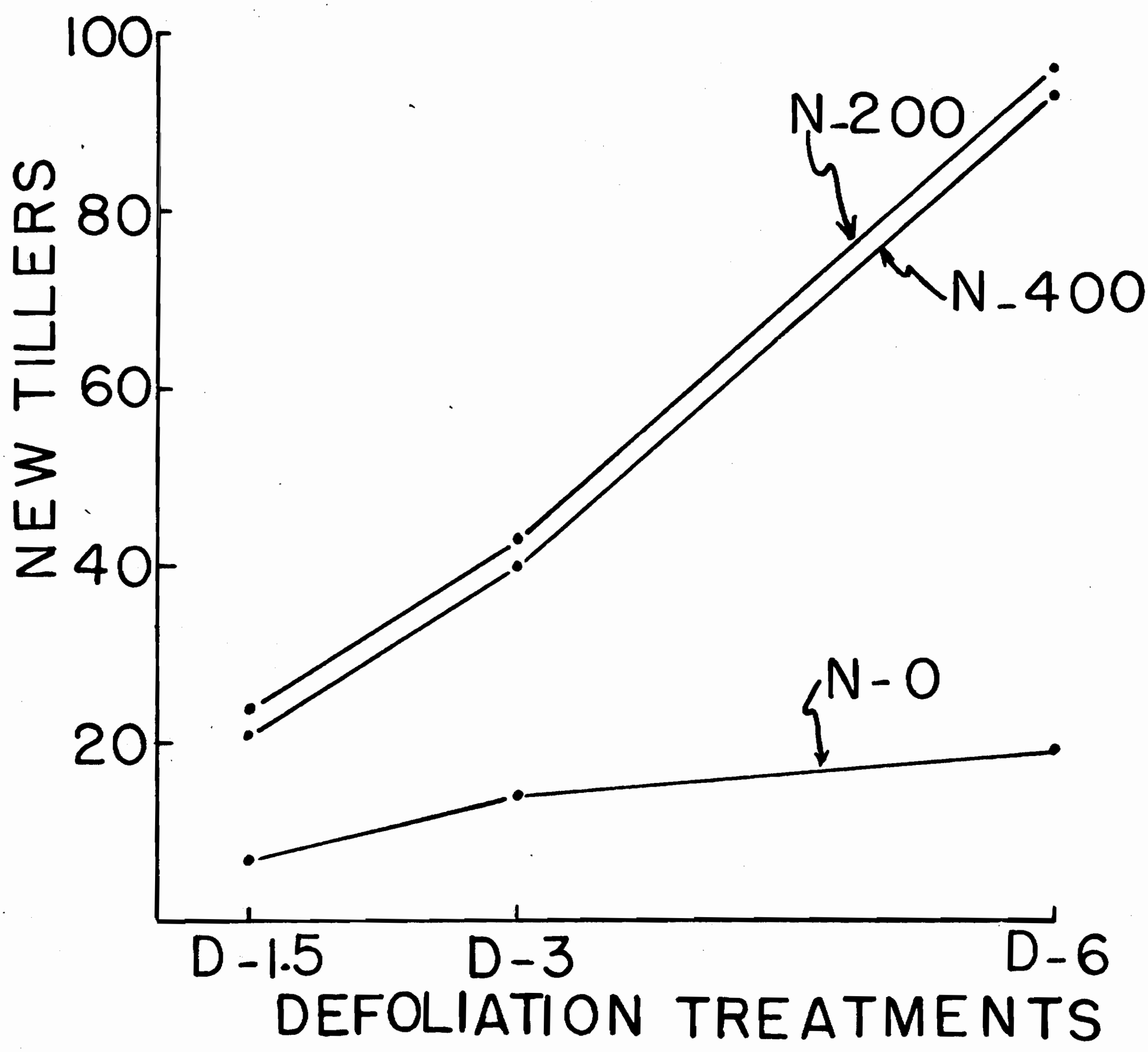

Figure 3. Tillering of orchardgrass as affected by nitrogen and defoliation during a 7-week period.

L-1 there was a decided increase in tillering with N-200, but no further increase with N-400. Conversely, tillering was not augmented with N increases with L-.25; and the increases in tillering with added N were small with L-.5 as compared with L-1.

Nitrogen fertilization caused a sharp increase in tillering under light defoliation pressure, but response was slight at the N-0 level, Figure 3.

Dry Weight. The dry weights of plants as influenced by light, defoliation, and nitrogen variables are shown in Table 2. These responses are closely associated with the tillering effects. Light intensity had a near linear effect on yield, the weights being 1.39, 2.89, and 6.90 gm., respectively, for L-.25, L-.50, and L-1. Yields were increased as nitrogen fertilizer was added to the 200 lb. rate after which there were no further increases. The mean yields for the various defoliations (average of all light and nitrogen variables) were 0.89, 2.64, and 7.64 gm. per treatment for defoliation to 1.5, 3, and 6 inches, respectively.

The dry matter responses differed with treatments as shown by the significant interactions given in

Table 2. The effect of light, nitrogen, and defoliation on the dry weight of orchardgrass clippings (stubbles excluded).

Nitrogen	L-1				L-.5				L-.25				Grand Mean
	Defoliation				Defoliation				Defoliation				
lb/A	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	
0	1.30	2.65	5.31	3.08	0.67	1.97	3.75	2.13	0.15	0.62	2.57	1.11	2.13
200	2.15	5.05	20.80	9.33	0.38	1.65	6.33	2.79	0.34	0.83	3.96	1.71	4.61
400	2.17	7.72	14.99	8.29	0.79	2.41	8.09	3.76	0.12	0.89	3.00	1.34	4.46
Mean	1.87	5.14	13.70	6.90	0.61	2.01	6.06	2.89	0.20	0.78	3.18	1.39	3.73

The following were significant at the 1% level: light (L), nitrogen (N), defoliation (D), NXD, LXN, and LXD.

Figures 4, 5, and 6. Dry weights increased as defoliation intensities decreased for all three light intensities; however, the response was much larger with normal light than for the reduced light intensities. The increase in dry matter with relaxed defoliation was higher for L-.5 than for L-.25.

The clipping weights increased as 200 lb. N was added for all the light intensities; however, the response was much larger with L-1 as compared to the other two light intensities, Figure 5. Increasing N to 400 lb. caused slight reductions in dry matter yields with L-1 and L-.25 as compared with a slight increase with L-.5. The clipping weights as interrelated with defoliation and N are given in Figure 6. There was a sharp increase in yields with N-200 and then a decrease at N-400 for L-1. Conversely, there were small increases in yields as more nitrogen was added with heavy and medium defoliation.

Carbohydrates. The water soluble carbohydrates in the basal inch of orchardgrass stubble increased as light intensity increased, Table 3. The soluble carbohydrates averaged for D-3 and D-6 and all

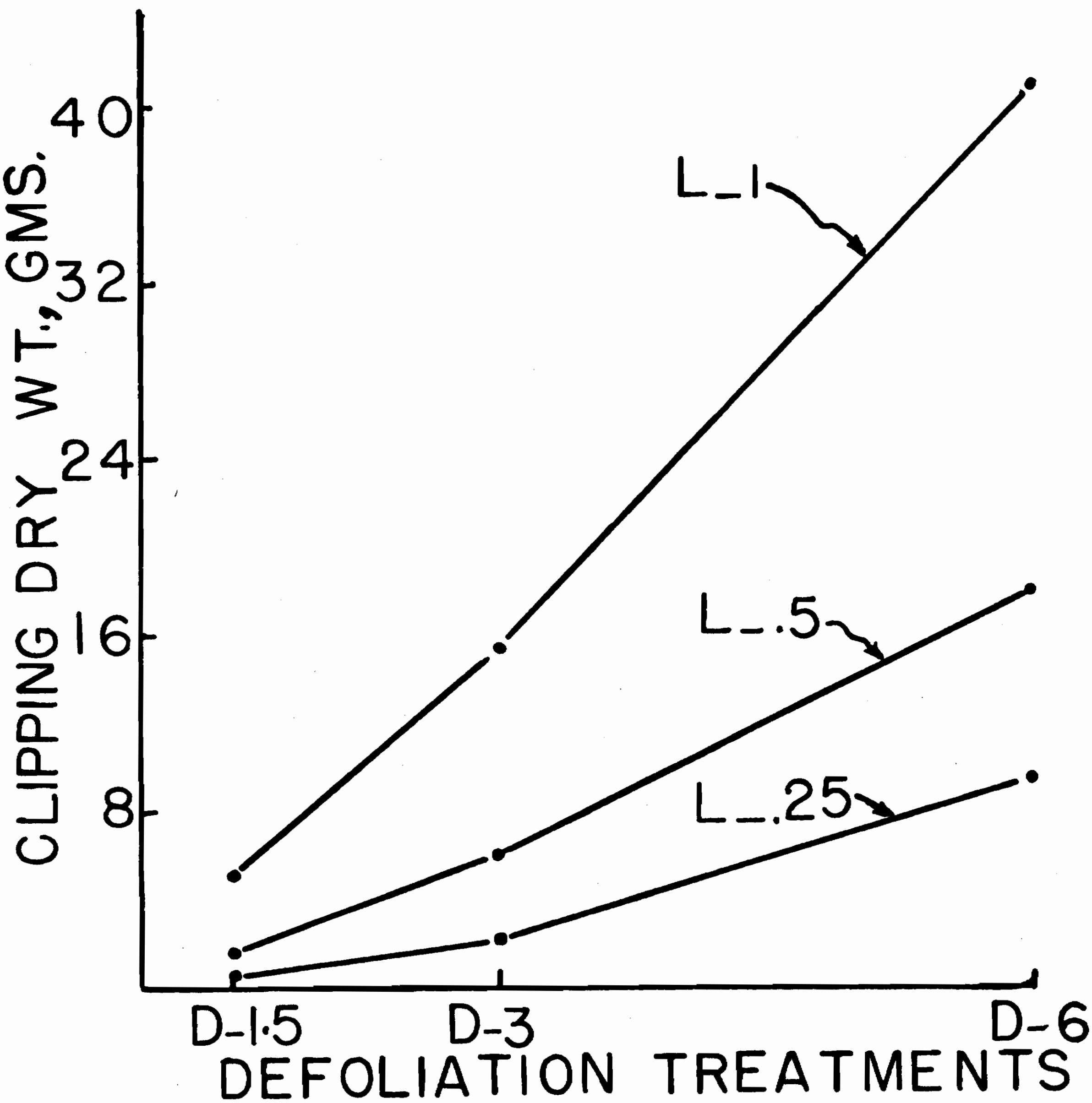

Figure 4. The effect of defoliation and light intensity on the dry yields of orchardgrass clippings during a 7-week period.

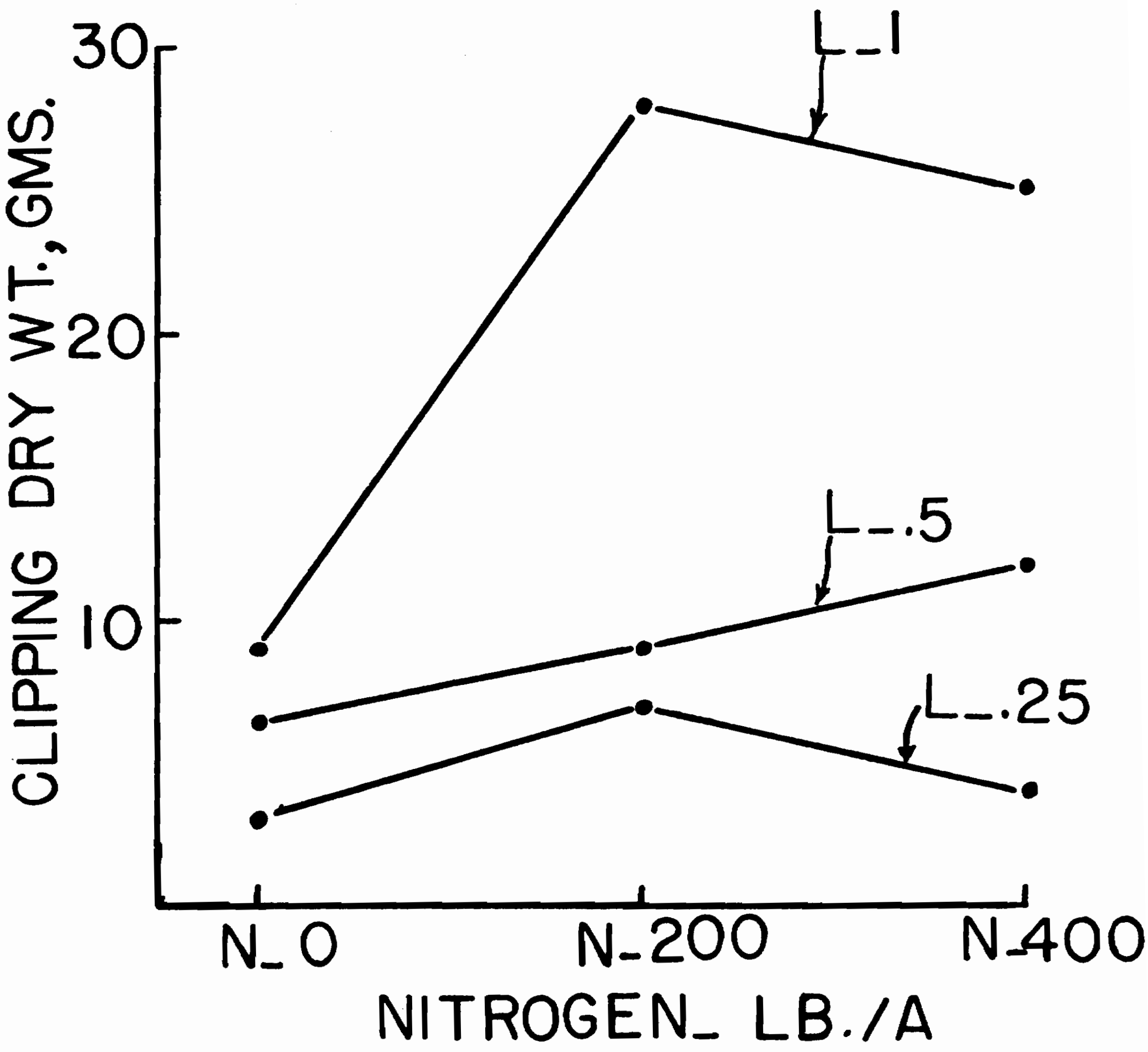

Figure 5. Dry weight of clippings as affected by light and nitrogen during a 7-week period.

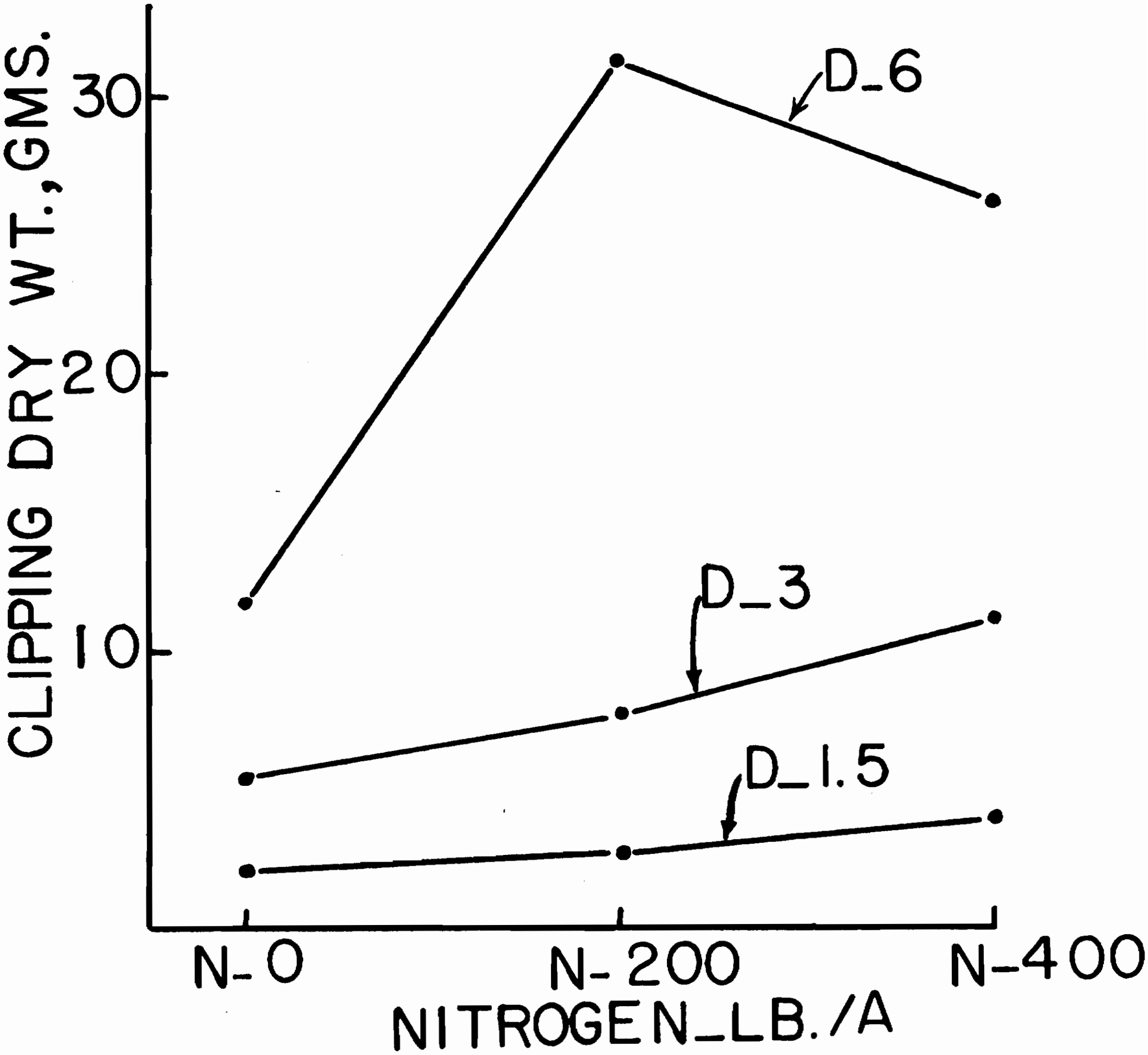

Figure 6. The influence of nitrogen and defoliation on dry weight of orchardgrass clippings during a 7-week period.

Table 3. Water soluble carbohydrates of orchardgrass stubble as influenced by light, defoliation, and nitrogen at the end of a 7-week period.

Nitrogen	L-1				L-.5				L-.25			
	Defoliation				Defoliation				Defoliation			
	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean*
lb/A	%	%	%	%	%	%	%	%	%	%	%	%
0	11.1	26.0	37.9	25.0	5.7	12.8	21.1	13.2	3.21	6.3	14.3	10.3
200	6.8	10.0	12.1	9.6	4.5	8.8	16.8	10.0	--	5.2	10.9	8.1
400	6.1	10.1	7.9	8.0	3.9	9.1	12.4	8.5	--	7.0	8.9	8.0
Mean	8.0	15.4	19.3	14.2	4.7	10.2	16.8	10.6	--	6.2	11.4	8.8

* Means of D-3 and D-6 as plants in some or all replicates provided insufficient material for analyses.

Statistical analyses were made in two ways: 1) Excluding D-1.5 because many plants died at L-.25; statistically significant differences at the 1% level were: light (L), nitrogen (N), defoliation (D), NXD, LXN, and LXD. 2) Excluding L-.25; statistically significant differences at the 1% level were: light (L), nitrogen (N), defoliation (D), NXD, LXD, and LXN.

nitrogen treatments made up 8.8, 13.5, and 17.4% of the dry matter for L-.25, L-.5, and L-1, respectively. Nitrogen fertilization decreased soluble carbohydrates; the average values for all light treatments and D-3 and D-6 were 20.1, 10.7, and 9.1%, respectively, for N-0, N-200, and N-400. Carbohydrates decreased with more severe defoliation. The carbohydrates averaged 6.4, 12.8, and 18.1, respectively, for D-1.5, D-3, and D-6. These latter values are averages for the two higher light intensities. The carbohydrate content as influenced by light differed with defoliation and nitrogen treatments, Table 3. Reducing the leaf area by defoliation decreased the soluble carbohydrates with all light treatments, but the decline in carbohydrates was faster with the lower light intensity. For example, there was a 20% decrease in soluble carbohydrates as defoliation increased from D-6 to D-3 under L-1 as compared with 46% with L-.25 for similar defoliation. When N-200 was applied, there was a much sharper decrease in soluble carbohydrates with L-1 than for L-.5. Carbohydrates did not drop significantly with nitrogen for L-.25. The carbohydrate contents were similar for N-200 and

N-400 for all light treatments. Carbohydrate content for N treatments differed with defoliation, Table 3.

Intense defoliation caused a rapid drop in soluble carbohydrates with N-0 as compared with N-200 or N-400. With N-400, the carbohydrates did not differ between D-3 and D-6; the values were only slightly higher for D-3 than for D-1.5.

Root Weight. Defoliation and light intensity affected root weights more than nitrogen, Table 4. Root weight averaged for all factorial treatments for L-1, L-.5, and L-.25 were 4.79, 1.93, and 1.02 gm., respectively. Heavy defoliation significantly decreased root dry weight. The weight of roots for the various defoliations averaged for all factorial treatments were 0.83, 2.25, and 4.32 gm. for D-1.5, D-3, and D-6, respectively. There was a slight decrease in root weights as nitrogen rates increased; the average values for all light and defoliation treatments were 2.94, 2.71, and 2.08 gm. for N-0, N-200, and N-400, respectively.

The influence of light on root weight varied with defoliation. Severe defoliation caused a significant drop in root weight with all light treatments.

Table 4. The effect of light intensity, defoliation, and nitrogen on the root weights in grams dry matter per treatment.

Nitrogen	L-1				L-.5				L-.25				Grand Mean
	Defoliation				Defoliation				Defoliation				
lb/A	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	
0	1.68	5.27	10.66	5.87	0.70	1.66	3.74	2.03	0.27	0.69	1.79	0.92	2.94
200	1.84	4.12	9.52	5.16	0.59	1.64	3.05	1.76	0.30	0.89	2.46	1.22	2.71
400	1.35	3.65	4.98	3.33	0.64	1.61	3.77	2.00	0.12	0.73	1.89	0.91	2.08
Mean	1.62	4.35	8.39	4.79	0.64	1.64	3.52	1.93	0.23	0.77	2.05	1.02	2.58

The following were significant at the 1% level: light (L), defoliation (D), and LXD; at the 5% level: nitrogen (N).

EXPERIMENT II. THE EFFECT OF TEMPERATURE, NITROGEN, AND DEFOLIATION ON TILLERING AND SOLUBLE CARBOHYDRATES OF ORCHARDGRASS

The following experiment was conducted in controlled environment chambers. The influence of different temperatures, defoliation treatments, and nitrogen rates on tillering, dry weight, and carbohydrate reserve in orchardgrass was studied.

Material and Methods

Individual tillers from one orchardgrass genotype were transplanted into pots containing a mixture of sand and soil as for Experiment I. All pots were placed in the greenhouse and nutrient solution without nitrogen was applied equally to all pots. On February 14, 1963, the pots were assigned at random to two groups and placed in each of two controlled environment chambers with 50-60°F. (T-1) and 70-80°F. (T-2) night-day temperatures. A 10-hr. photoperiod was maintained and the pots in each chamber were divided into three replications with six factorial treatments (3 defoliations with 2 nitrogen levels).

The defoliation treatments were: D-1.5, cut to 1.5 inches when 3.5 inches high; D-3, cut to 3 inches when 7 inches high, and D-6, cut to 6 inches when 9 inches high. Nitrogen was applied at 0 and 200 lb. per acre.

Tillers were counted every week. At the end of the experiment the tillers were removed from the soil, washed, and clipped free of roots and leaves. The basal 1-1/2 inch section of tillers were oven-dried, ground, then analyzed for water soluble carbohydrates as for Experiment I.

Results

Tillering. Temperature, defoliation, and nitrogen fertilization had significant effects on tiller initiation of orchardgrass, Table 5. The average number of tillers were 14 and 44 for T-1 and T-2, respectively. Severe defoliation reduced tillering; there were 15, 24, and 48 tillers, respectively, for D-1.5, D-3, and D-6. Nitrogen fertilization increased tillering; the means for N-0 and N-200 for all temperature and defoliation factorial treatment combinations were 8.3 and 49.7 tillers, respectively.

Table 5. The effect of temperature, nitrogen, and defoliation on tillering and dry weights of orchardgrass.

Nitrogen	T-1 50-60°F. Defoliation				T-2 70-80°F. Defoliation				Grand
lb/A	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	Mean
Number of Tillers									
0	6	5	8	6.3	10	8	13	10.3	8.3
200	9	15	41	21.7	35	67	131	77.7	49.7
Mean	7.5	10.0	24.5	14.0	22.5	37.5	72.0	44.0	29.0
Clipping Dry Weights									
0	4.65	7.32	9.69	7.22	5.58	7.49	10.72	7.93	7.58
200	4.59	10.48	18.34	11.14	12.79	17.96	27.22	19.32	15.23
Mean	4.53	8.90	14.01	9.12	9.14	12.73	18.97	13.63	11.41

The following were significant at the 1% level: for tillering temperature (T): defoliation (D), nitrogen (N), DXN and TXN; and for clipping weights: nitrogen (N), defoliation (D); at the 5% level: DXN.

Nitrogen responses interacted significantly with defoliation and temperatures. Relaxed defoliation gave greater responses in tillering as nitrogen was increased than did heavy defoliation. Nitrogen fertilization increased tillers more at the higher than at the lower temperature.

Dry Weight. The effects of temperature, nitrogen, and defoliation on dry weight are closely associated with tillering responses, Table 5. Nitrogen increased the dry weights from 7.58 to 15.23 gm. for N-0 and N-200, respectively. Yields were increased as defoliation intensities were decreased; the mean yields for defoliation treatments (average of all temperatures and nitrogen factorial treatments) were 6.83, 10.86, and 16.49 gm. for D-1.5, D-3, and D-6, respectively.

Figure 7 shows the significant interactions for cutting heights and nitrogen. Dry matter and tillering responses were closely associated. There were sharp increases in yields and tillering as defoliation intensity decreased with N-200; but these responses were small or insignificant with N-0.

Carbohydrates. The differences in soluble carbohydrates of the basal inch of orchardgrass

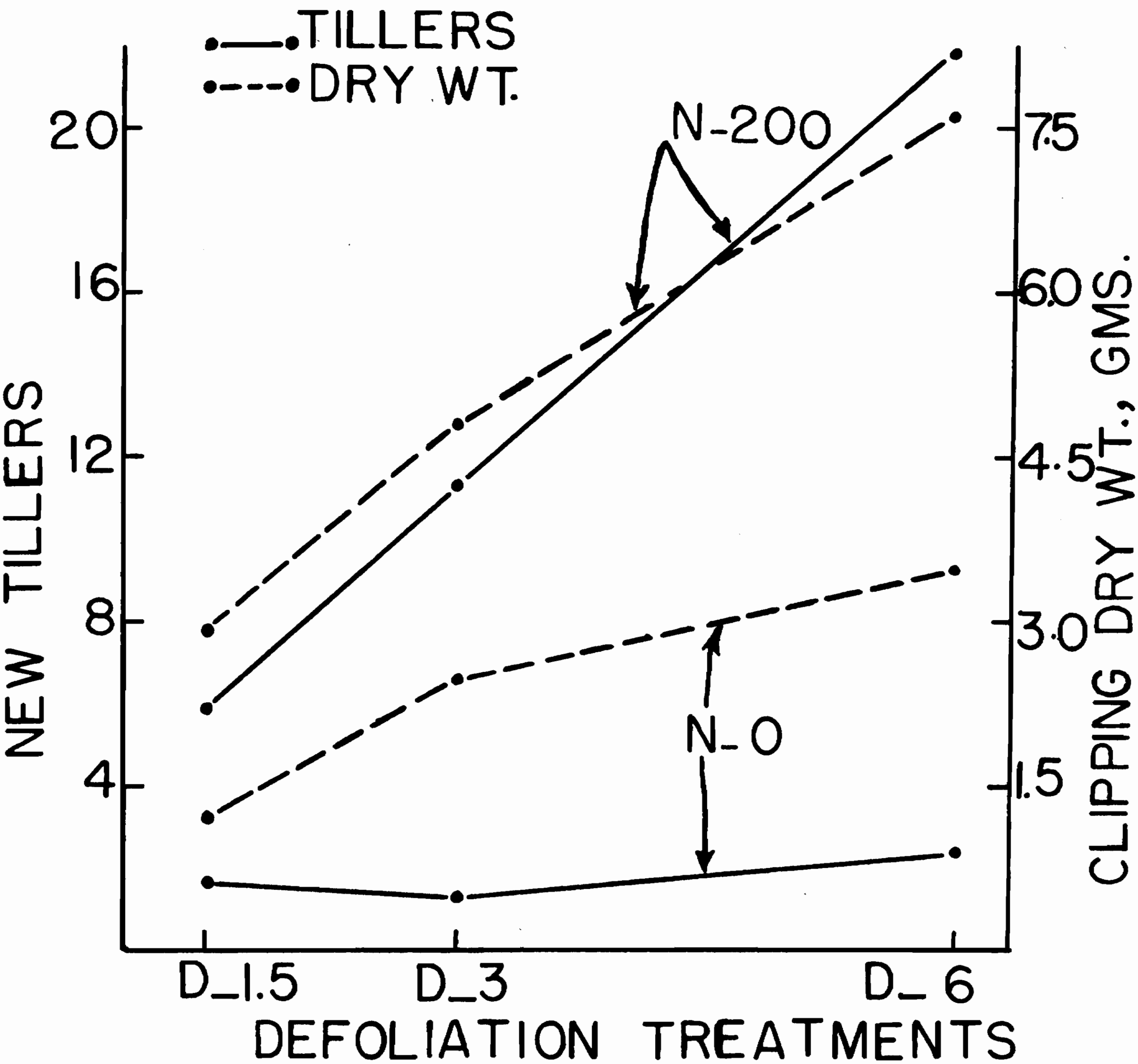

Figure 7. The effect of defoliation and nitrogen on tillering and yield of orchardgrass clippings during a 5-week period.

stubble at various temperatures, defoliations, and nitrogen rates were highly significant, Table 6. Soluble carbohydrates decreased as temperature increased; the average content for T-1 was 39.8% as compared to 25.5% for T-2. Soluble carbohydrates were reduced by heavy defoliation; the contents for D-1, D-3, and D-6 (averaged for temperature and nitrogen treatments) were 27.7, 31.6, and 38.6%, respectively. Nitrogen rate decreased soluble carbohydrates; the mean values for all temperatures and defoliation were 40.3 and 25% for N-0 and N-200.

The influence of temperature on carbohydrates of orchardgrass significantly varied with defoliation and nitrogen treatments, Table 6. Increasing defoliation intensity caused a rapid drop in carbohydrate content with both temperature treatments, but the reduction was faster with the higher than the lower temperature. Nitrogen application caused a sharper decline in soluble carbohydrates of orchardgrass with T-2 as compared with T-1. There was a 67.7% decrease in soluble carbohydrates when N-200 was applied under T-2 as compared with 21.0% with T-1.

Table 6. The effect of temperature, nitrogen, and defoliation on soluble carbohydrates of orchardgrass stubbles.

Nitrogen	T-1 50-60°F.				T-2 70-80°F.				Grand Mean
	Defoliation				Defoliation				
	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean	
lb/A	%	%	%	%	%	%	%	%	%
0	38.9	44.4	50.2	44.5	27.7	34.4	46.1	36.0	40.3
200	33.1	32.3	39.8	35.1	11.3	15.4	18.4	15.0	25.0
Mean	36.0	38.3	45.0	39.8	19.5	24.9	32.3	25.5	32.7

The following were significant at the 1% level: temperature (T), defoliation (D), nitrogen (N), DXN, TXD, and TXN.

Soluble carbohydrates of orchardgrass for defoliation treatments differed with nitrogen rates. Severe defoliation reduced carbohydrates with N-0 more than with N-200. There was a 15% difference in soluble carbohydrates as defoliation increased from D-6 to D-1.5 under N-0 as compared with a 7% drop with N-200.

EXPERIMENT III. THE EFFECT OF PHOTOPERIOD, LIGHT INTENSITY, NITROGEN, AND DEFOLIATION ON SOLUBLE CARBOHYDRATES AND TILLERING OF ORCHARDGRASS

This experiment with orchardgrass was conducted in controlled environment chambers to study the following: 1) the effect of daylength, nitrogen, and defoliation on tillering; 2) to evaluate the interrelationship of changes in soluble carbohydrates with tillering and yield.

Material and Methods

Three orchardgrass tillers of a given genotype were planted in one-gallon metal pots. The plants were then grown in the greenhouse under normal light until well established. Four weeks later the pots were assigned random treatments and placed in controlled environment chambers.

The factorial treatment combinations were: 1) photoperiod treatments: P-1, 18 hours high light intensity and 6 hours dark; P-2, 9 hours high light intensity and 15 hours dark; and P-3, 9 hours high light intensity followed by 9 hours low light intensity and then 6 hours dark. The high light intensity was 3100 F.C. in each controlled environment chamber and the low light intensity was about 300 F.C. 2) The defoliation treatments were: D-1.5, plants 3-4 inches high cut to 1.5 inches; D'-15, plants 6-8 inches high cut to 1.5 inches; D-3, plants 6-8 inches high cut to 3 inches, and D-6, plants cut to 6-8 inches daily. 3) Three levels of nitrogen were applied, 0, 75, and 225 lb. N per acre.

At the end of the experiment the plants were washed and divided into two parts, stubbles and clippings. The basal inch sections of the stubble for all treatments and replicates were oven-dried, ground, and analyzed for water soluble carbohydrates, as for Experiment I. The clippings were dried and dry weight data were recorded.

Two plants in each pot were used for making tiller counts when the experiment began and at weekly intervals. The temperature was maintained at 75°F. in all environment chambers.

Results

Tillering. Table 7 gives the average increases in tillering during six weeks as influenced by photoperiod, nitrogen, and defoliation. There was a significant increase in tillering for P-1 and a slight increase for P-2 and P-3. There were 7.2, 4.7, and 2.1 tillers per plant for P-1, P-2, and P-3, respectively. Severe defoliation retarded tillering; the average increases for D-1.5, D'-1.5, D-3, and D-6 were 3.6, 3.0, 5.0, and 7.9 tillers, respectively. Nitrogen had a significant positive effect on tillering; there was an average of 2.0 tillers for N-0 as compared with 5.1 and 6.3 tillers, respectively, for N-75 and N-225.

The interaction of nitrogen with photoperiod is shown in Figure 8. With an 18-hour photoperiod (P-1), there were large increases in tillering as N increased. There were no tillering responses as N was increased from N-75 to N-225 with P-2 and P-3. When nitrogen was increased from N-0 to N-75 there was more tillering for P-2 than for P-3. The significant interaction of defoliation with photoperiods on tillering of orchardgrass is shown in Figure 9. There was a sharp increase in tillering as defoliation was decreased

Table 7. Average number of new tillers per plant of orchardgrass produced during six weeks by photoperiod, nitrogen, and defoliation.

Nitrogen lb/A	P-1 Defoliation D-1.5	D'-1.5	D-3	D-6	Mean	P-2 Defoliation D-1.5	D'-1.5	D-3	D-6	Mean	P-3 Defoliation D-1.5	D'-1.5	D-3	D-6	Mean	Grand Mean
0	2.8	1.5	2.3	3.3	2.5	3.2	1.7	1.7	2.3	2.2	1.5	0.7	1.3	2.3	1.5	2.0
75	7.0	6.0	7.3	8.2	7.1	3.5	2.0	8.2	12.2	5.6	0.7	0.7	1.8	7.2	2.5	5.1
225	10.2	12.2	10.7	17.6	12.1	3.0	1.5	9.3	12.2	6.5	0.7	0.8	2.3	5.7	2.4	6.3
Mean	6.7	6.6	6.8	9.7	7.2	3.2	1.7	6.4	8.9	4.7	1.0	0.7	1.8	5.1	2.1	4.5

The following were significant at the 1% level: photoperiod (P), nitrogen (N), defoliation (D), NXD, DXP, and NXP.

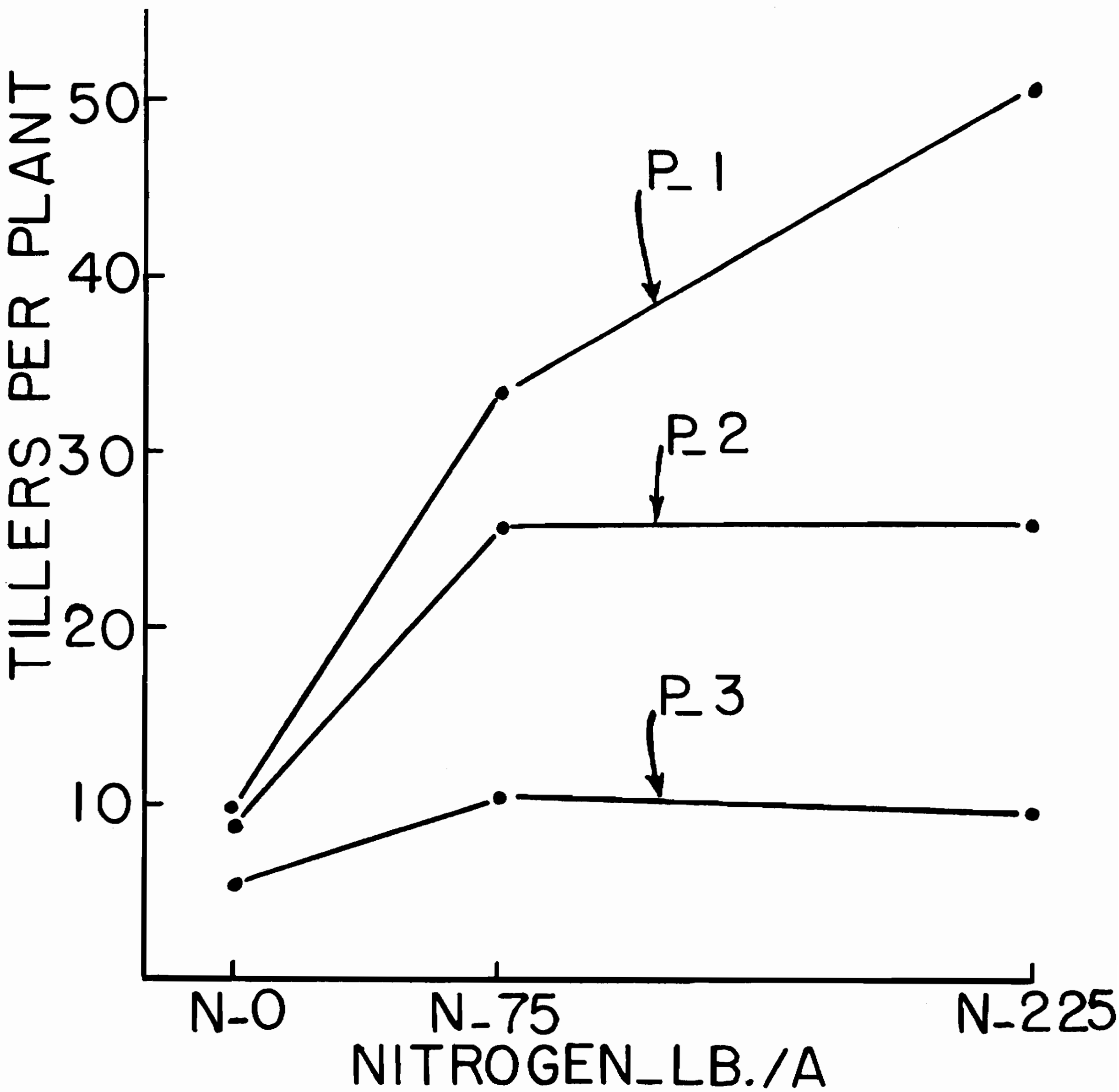

Figure 8. The effect of photoperiod and nitrogen application on tillering of orchardgrass during a 6-week period.

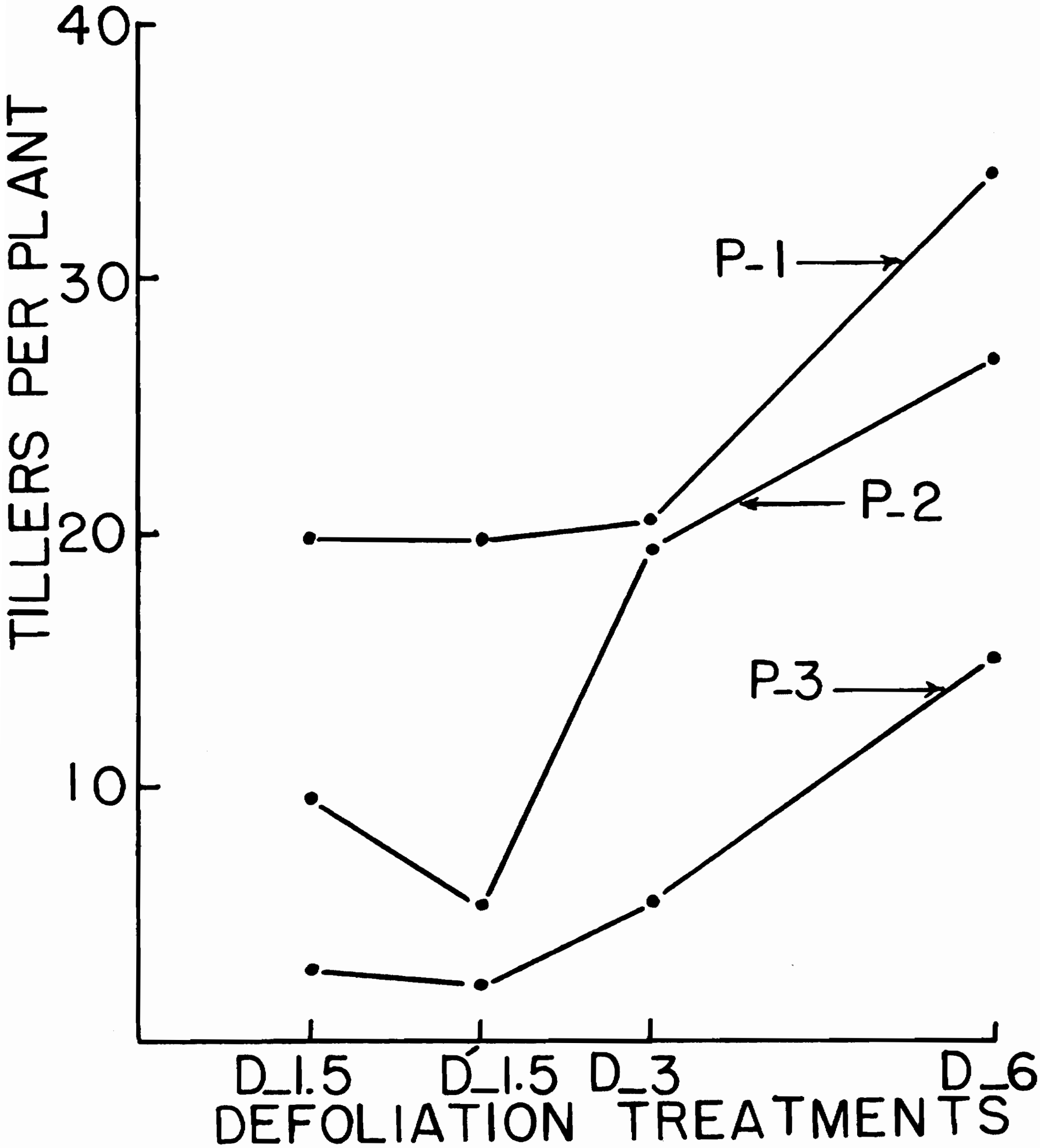

Figure 9. The effect of defoliation and day length on tillering of orchardgrass during a 6-week period.

from D-3 to D-6 with all photoperiods. A slight decrease in tillering occurred when plants were defoliated to D'-1.5; this drop was sharper with P-2 than for P-3.

Tillering responses from nitrogen varied with defoliation, Figure 10. Plants with defoliation treatments D-3 and D-6 produced many tillers as nitrogen rate increased, but there were small differences in tillering without N for the defoliation practices. Cutting to 1.5 inches (D-1.5 and D'-1.5) gave the poorest tillering. Tillering tended to be better for D-1.5 than for D'-1.5 with N-0 and N-75, but the reverse occurred with N-225.

Dry Weight. The clipping yields were influenced by photoperiod, nitrogen, and defoliation, Table 8. The average yield was 2.79 gm. for P-1 as compared to 1.47 gm. for P-3. Yields were significantly increased with added nitrogen. Defoliation also influenced yields; the clipping weights were 0.53, 0.88, 1.98, and 4.29 gm., respectively, for D-1.5, D'-1.5, D-3, and D-6.

The effect of photoperiod on clipping weights of orchardgrass differed with nitrogen as shown by the significant interactions, Table 8 and Figure 11.

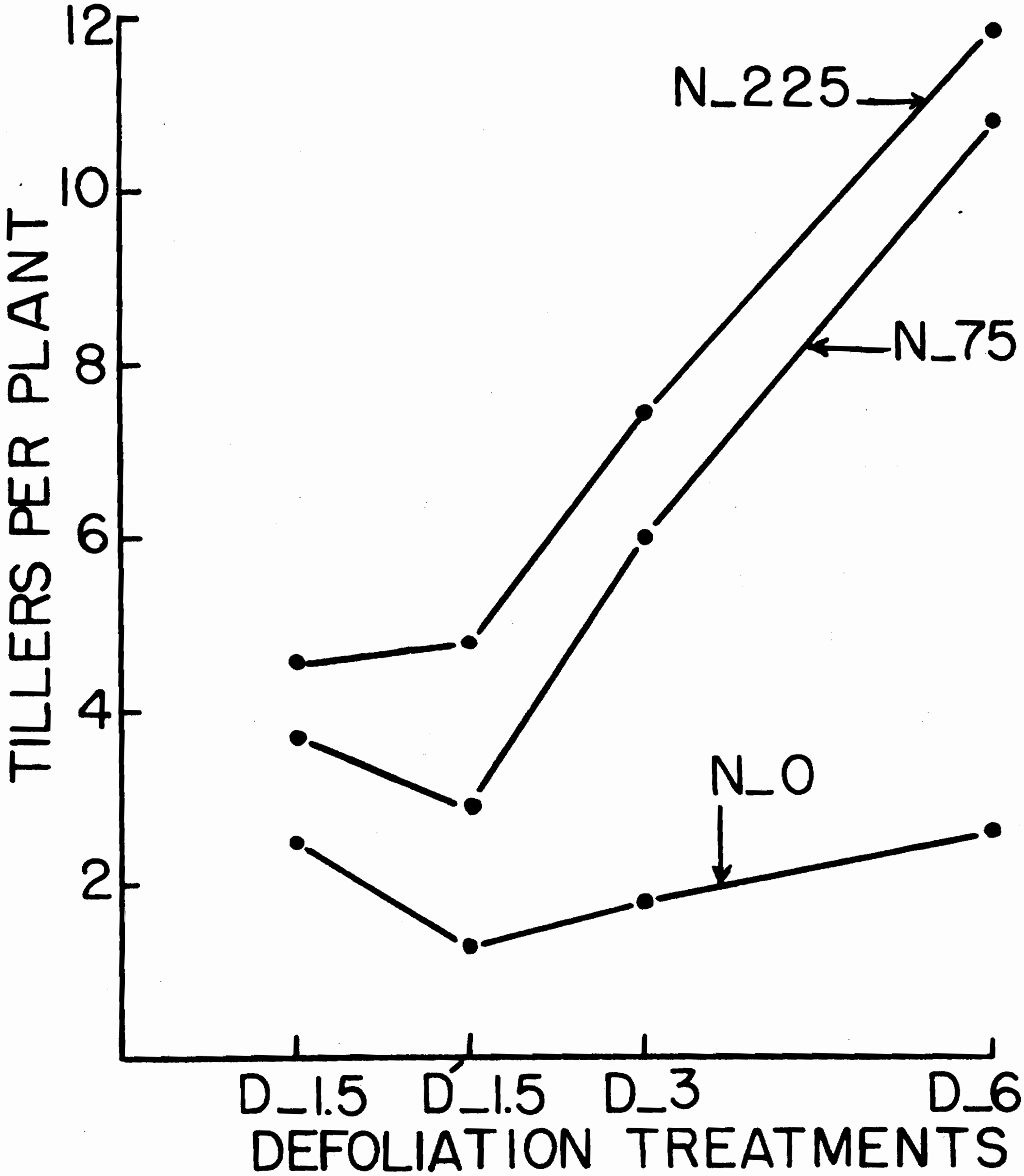

Figure 10. Tillering of orchardgrass as affected by nitrogen and defoliation during a 6-week period.

Table 8. The effect of photoperiod, nitrogen, and defoliation on yield of clippings (grams per pot) of orchardgrass.

Nitrogen lb/A	P-1					P-2					P-3					Grand Mean
	Defoliation					Defoliation					Defoliation					
	D-1.5	'D-1.5	D-3	D-6	Mean	D-1.5	'D-1.5	D-3	D-6	Mean	D-1.5	'D-1.5	D-3	D-6	Mean	
0	0.52	0.53	1.01	2.33	1.10	0.40	0.35	0.72	1.38	0.71	0.27	0.50	1.15	1.75	0.92	0.91
75	0.85	1.63	3.43	6.67	3.19	0.43	0.71	2.12	4.07	1.83	0.32	0.57	2.01	4.53	1.86	2.29
225	1.20	2.42	4.15	8.52	4.07	0.43	0.62	1.78	4.96	1.95	0.35	0.55	1.47	4.40	1.69	2.57
Mean	0.86	1.53	2.86	5.84	2.79	0.42	0.56	1.54	3.47	1.47	0.31	0.54	1.54	3.56	1.47	1.91

The following were significant at the 1% level: nitrogen (N), defoliation (D), photoperiod (P), NXD, NXP, and DXP.

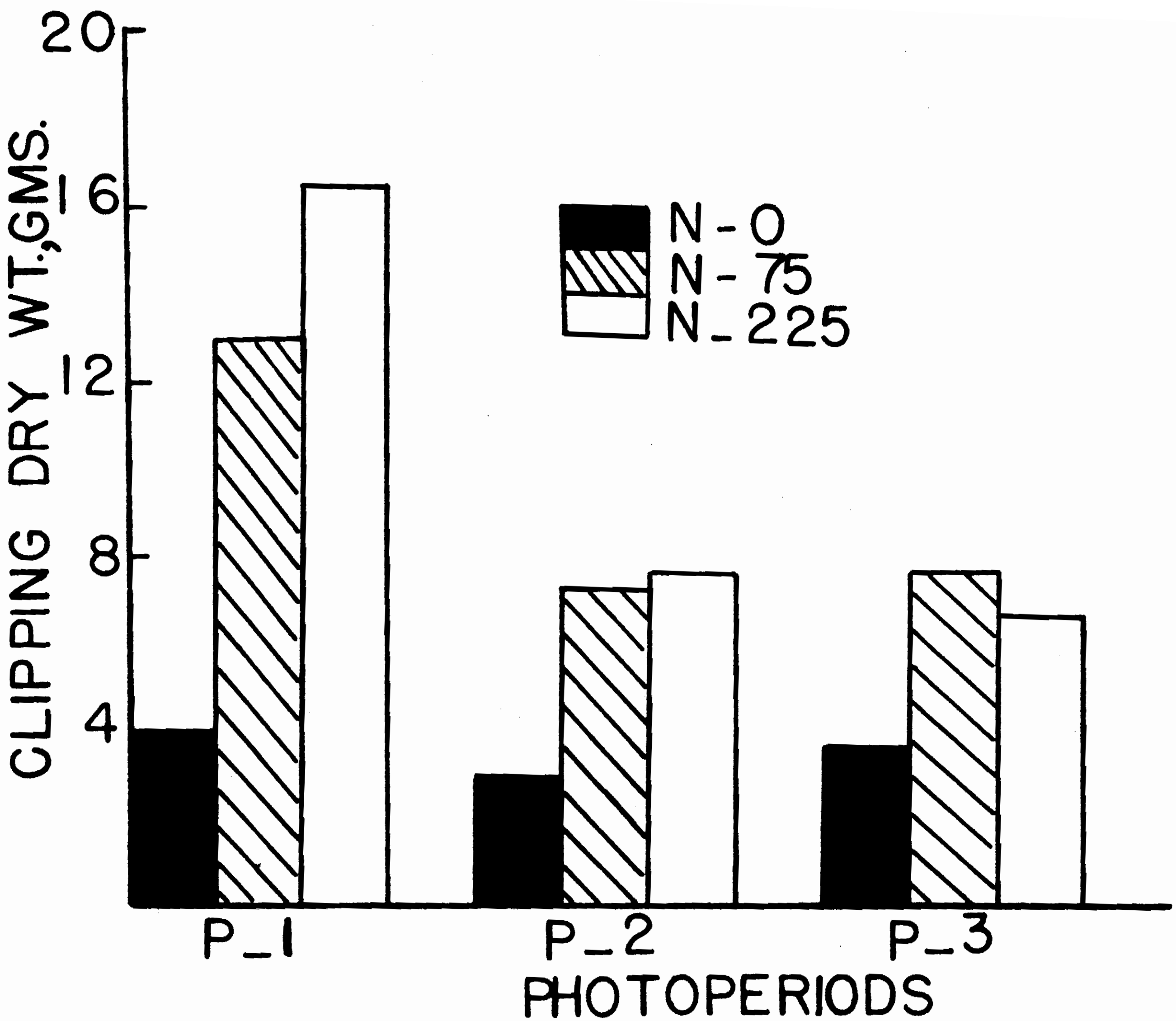

Figure 11. The effect of day length and nitrogen on clipping dry weights of orchardgrass during a 6-week period.

Clipping weights were low with all light treatments in the absence of nitrogen. However, there were large increases in yield with N-75 and additional smaller increases with N-225 under P-1. With P-2 and P-3, the yield increases were small with N-75, and N-225 did not give additional increases in yield. The nitrogen by defoliation interaction is shown in Figure 12. There were large increases in clipping weights as defoliation was relaxed with N-225 as compared with the lower rates of nitrogen. The significant photoperiod-defoliation interaction shows that intense defoliation reduced clipping weights for all photoperiods, but there were sharper yield declines with P-2 and P-3 than for P-1.

Carbohydrates. The differences in soluble carbohydrate contents of orchardgrass at various photoperiods, nitrogen and defoliation were highly significant, Table 9. The carbohydrates averaged for all factorial treatment combinations for P-1, P-2, and P-3 were 27.8, 12.5, and 14.5%, respectively. Intense defoliation caused a sharp drop in soluble carbohydrates. The average values for D-1.5, D'-1.5, D-3, and D-6, respectively, were 11.0, 14.6, 21.2, and 26.3%.

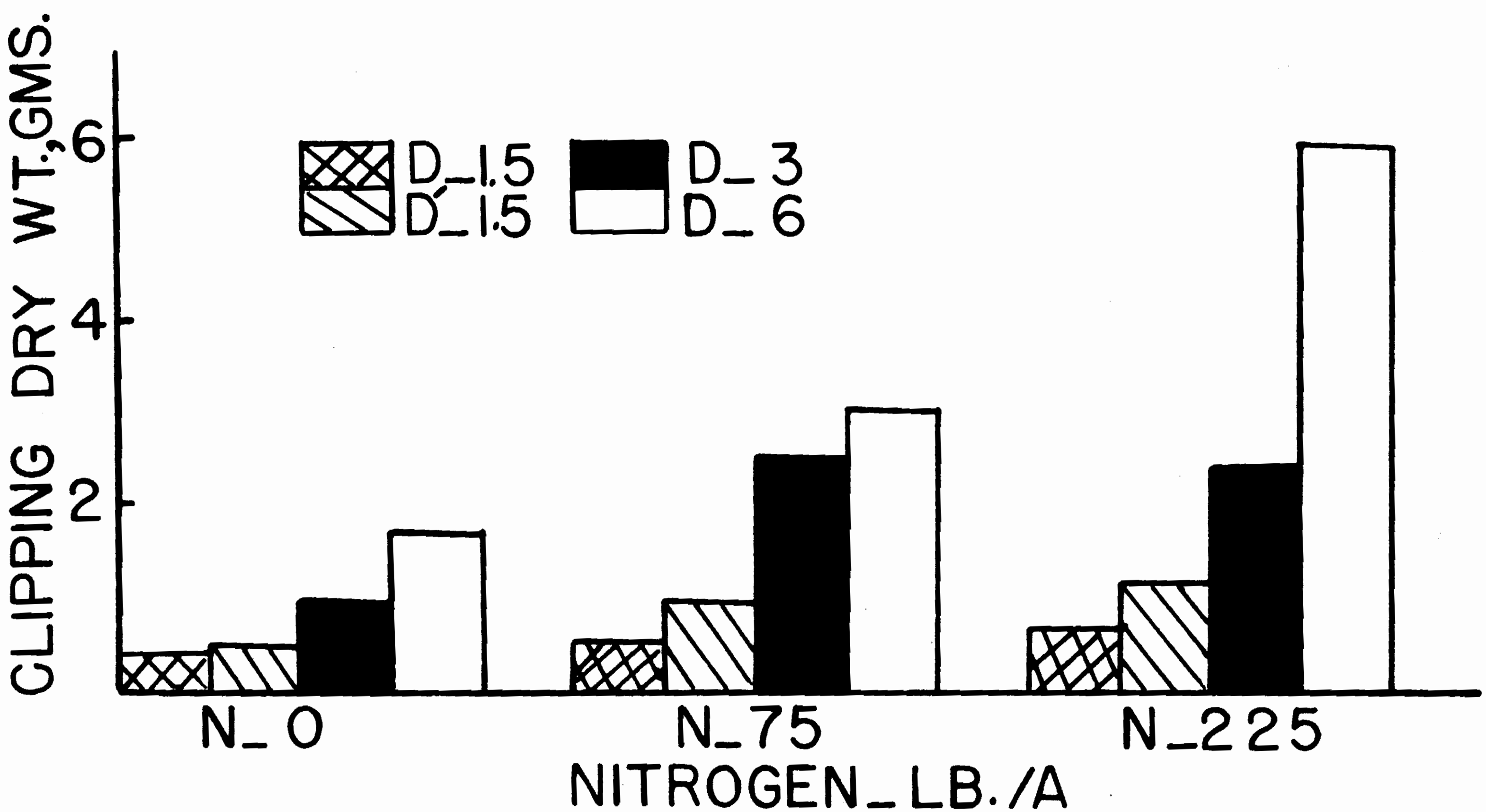

Figure 12. The effect of defoliation and nitrogen on clipping dry weights of orchardgrass during a 6-week period.

Table 9. The effect of photoperiod, nitrogen, and defoliation on water soluble carbohydrates of orchardgrass stubbles.

Nitrogen	P-1					P-2					P-3					Grand Mean
	Defoliation					Defoliation					Defoliation					
lb/A	D-1.5 %	'D-1.5 %	D-3 %	D-6 %	Mean %	D-1.5 %	'D-1.5 %	D-3 %	D-6 %	Mean %	D-1.5 %	'D-1.5 %	D-3 %	D-6 %	Mean %	%
0	24.9	26.8	29.8	36.2	29.4	7.6	12.6	21.7	28.3	17.6	4.7	11.7	24.2	28.2	17.2	21.4
75	22.2	28.7	33.2	32.2	29.1	4.6	6.7	14.7	19.4	11.4	7.2	8.0	15.5	21.4	13.0	17.8
225	13.9	20.2	31.3	34.7	25.1	3.6	5.4	9.0	16.5	8.6	10.0	11.8	11.7	19.4	13.2	15.6
Mean	20.3	25.2	31.4	34.4	27.8	5.3	8.2	15.1	21.4	12.5	7.3	10.5	17.1	23.0	14.5	18.2

The following were significant at the 1% level: nitrogen (N), defoliation (D), photoperiod (P), NXD, PXD, and NXP.

Soluble carbohydrates decreased as nitrogen rate was increased; the average content for N-0 was 21.4% as compared with 17.8 and 15.6%, respectively for N-75 and N-225.

The combined photoperiod-defoliation and nitrogen-photoperiod effects on carbohydrate content of orchardgrass were highly significant. There was a linear relationship between defoliation and soluble carbohydrates with all photoperiod treatments. With P-2 and P-3 the differences in carbohydrates were not highly significant under all levels of defoliation, but this difference in carbohydrates was much higher between P-1 and the two other photoperiods.

The significant interaction between photoperiod and nitrogen is shown in Figure 13. When nitrogen was increased from N-0 to N-225 there was a drop in soluble carbohydrates with all photoperiod treatments, but this decline was sharpest with P-2. The carbohydrate contents of orchardgrass were similar for N-0 and N-75 with P-1, but there were sharp declines with P-2 and P-3. The carbohydrate reductions between N-75 and N-225 were steeper for P-1 and P-2 than for P-3.

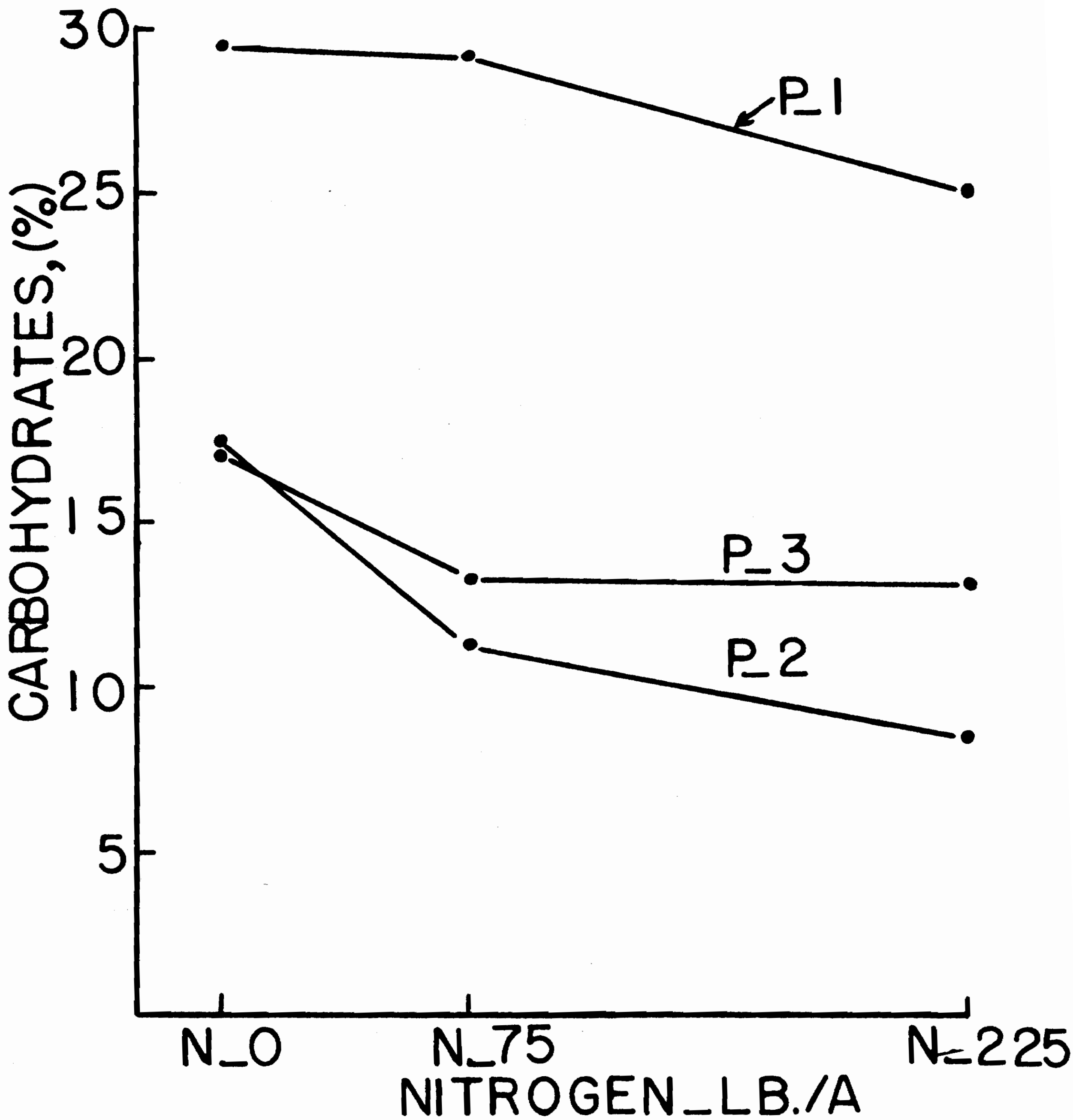

Figure 13. The effect of nitrogen and day length on water soluble carbohydrates (percent of dry matter) of orchardgrass stubble during a 6-week period.

With heavy defoliations, the differences in soluble carbohydrates in the stubble with nitrogen rates were small; however, there were more differences in carbohydrates between the nitrogen rates with relaxed defoliation, Figure 14.

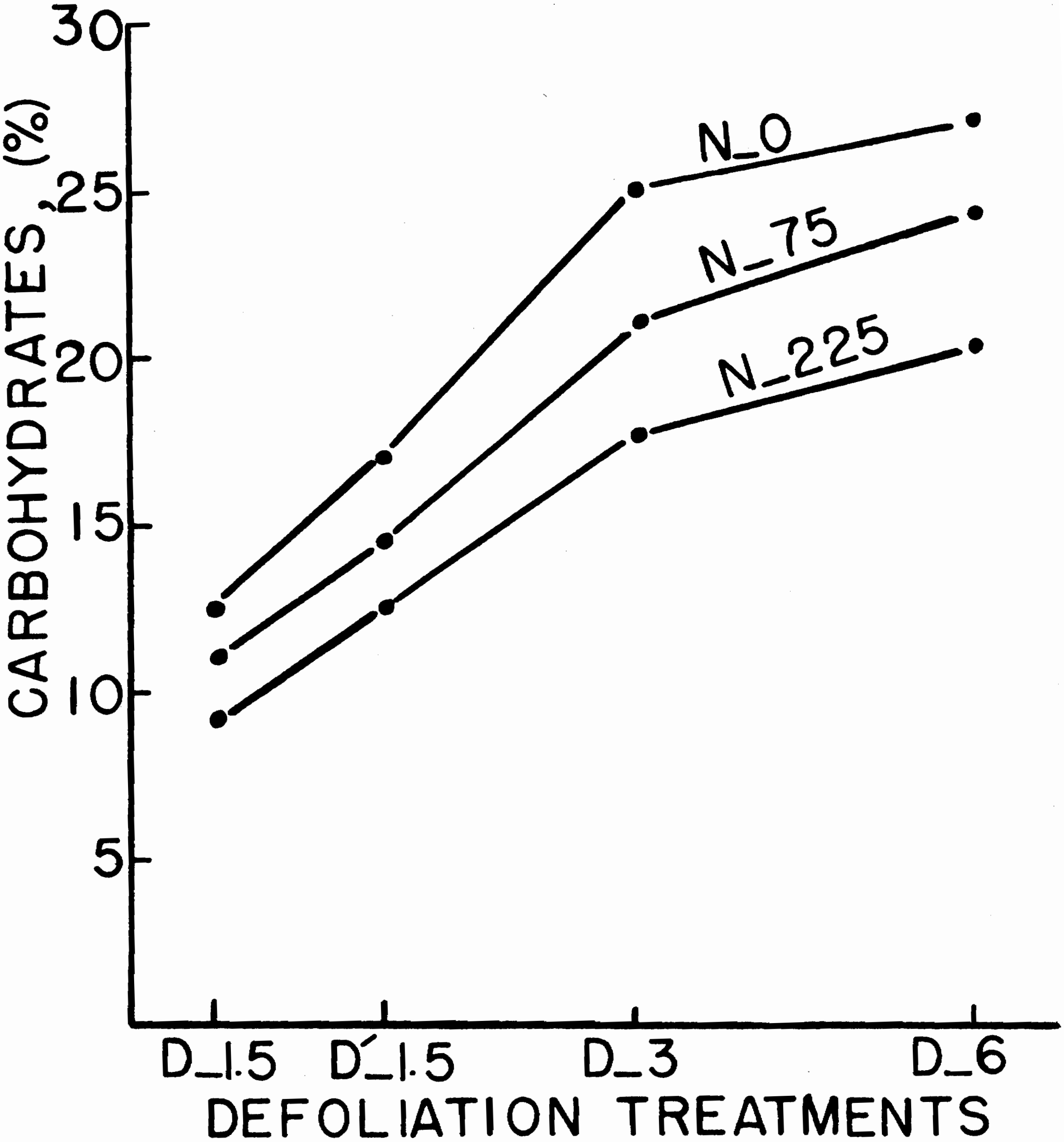

Figure 14. Soluble carbohydrates (percent of dry matter) of orchardgrass stubble as influenced by nitrogen and defoliation during a 6-week period.

EXPERIMENT IV. THE EFFECT OF LIGHT INTENSITY, IRRIGATION, NITROGEN, AND DEFOLIATION ON TILLERING AND CARBOHYDRATE CONTENT OF ORCHARDGRASS

This experiment was undetaken to study seasonal tillering of orchardgrass as influenced by nitrogen fertilization, defoliation intensity, light intensity, and irrigation. Data were also obtained on soluble carbohydrate content of stubble portions of plants for making associations with tillering.

Material and Methods

Orchardgrass tillers from one genotype were transplanted to the field in September, 1962. The young tillers were equally spaced one foot apart in square plots 9 feet by 9 feet. Ten-foot alleys were left between plots to adequately control light and water among the individual plots. Eighteen plots were established, but only 12 of them were suitable for experimental work because of severe winter killing. The 12 plots were divided into three randomized blocks. Each of these blocks with four plots were assigned factorial combinations of 2 light intensities with and without irrigation. Normal light intensity (L-1) and approximately 50% of normal light (L-.5) was obtained by using a plastic screen. The screen cages were 2.5 feet high and 10 feet square. Water was added as often as needed for the irrigated plots. Each of the four plots in each replicate was further divided by two and given random assignments of nitrogen at the rate of 25 lb. (N-25) and 375 lb. (N-375) per acre. Each of the nitrogen subplots was then further divided into three subplots for three defoliation intensities. The defoliation treatments were D-1.5, D-3, and D-6; the orchardgrass plants were cut back to a height of 1.5, 3, and 6 inches, respectively, every two weeks.

The experiment was initiated on April 20, 1963. Tillers were counted when the treatments were imposed and every two weeks thereafter for one plant in each treatment. Other plants within each of the replicate plots were sacrificed in May and September for carbohydrate analysis. The basal inch of stubble was used.

Results

__Tillering__. The rate of tillering of orchardgrass for different light, soil moisture, defoliation, and nitrogen treatments at various dates during the 1963 season is shown in Table 10. The rate of tillering was greatly increased by improving soil moisture with irrigation. There were 89.2 tillers per plant when irrigated as compared to a seasonal average of 63.9 without irrigation. Nitrogen fertilization significantly increased tillering, but there was a much greater tillering response due to nitrogen in the presence of irrigation as compared to unirrigated plots. The average number of tillers per plant for N-25 and N-375 with irrigation was 67.1 and 113.3, respectively, as compared with 60.3 and 67.4 tillers for the two nitrogen treatments for the nonirrigated plots. The season was exceedingly dry; the total average rainfall per month during May, June, July, August, and September was 2.7, 1.7, 3.0, 2.2, and 3.8 inches, respectively. Nitrogen fertilizer in the absence of irrigation remained on the soil surface for many days because of the acutely dry summer season.

Table 10. The effect of irrigation, seasonal changes, nitrogen, light intensities, and defoliation on tillering of orchardgrass.

Season	L-1								L-.5							
	N25 Defoliation				N375 Defoliation				N25 Defoliation				N375 Defoliation			
	C-1.5	C-3	C-6	Mean	C-1.5	C-3	C-6	Mean	C-1.5	C-3	C-6	Mean	C-1.5	C-3	C-6	Mean
								Irrigated								
May	18	13	21	17.3	40	52	53	48.3	6	14	11	10.3	9	40	35	28.0
June	44	70	80	64.6	89	141	126	118.6	52	66	97	71.7	51	80	132	87.7
July	71	109	132	104.0	181	236	274	231.3	66	87	154	102.3	59	114	189	120.7
August	54	107	124	95.0	145	196	259	200.0	35	72	133	80.0	29	103	184	105.3
September	30	78	93	67.0	85	157	181	141.0	4	62	108	58.0	4	70	164	79.3
Mean	43.4	75.4	90.0	69.6	80.0	156.4	178.6	138.3	32.6	60.2	100.6	64.5	30.4	81.4	140.8	84.2
								Nonirrigated								
May	10	13	21	14.6	8	13	23	14.7	13	3	4	6.7	3	3	3	3.0
June	68	59	101	76.0	50	66	124	80.0	23	70	83	58.7	32	86	101	73.0
July	83	103	124	103.3	79	101	173	117.6	39	99	116	84.7	39	107	137	94.3
August	31	96	103	76.7	48	91	136	91.7	16	71	104	63.7	21	72	121	71.3
September	15	77	115	69.0	36	85	108	76.3	3	44	102	49.7	10	53	91	51.3
Mean	41.4	69.6	92.8	67.9	44.2	71.2	112.8	76.1	18.8	57.4	81.8	52.7	21.0	64.2	91.0	58.7

The following were significant at the 1% level: irrigation (I), nitrogen (N), defoliation (D), season (S), NXI, SXN, and SXD; and at the 5% level: light (L), NXL, and DXN.

Tillering of orchardgrass was associated with defoliation. The highest tiller number occurred with D-6 and the lowest with D-1.5. There was an average of 39.0, 79.4, and 110.9 tillers per plant, respectively, for D-1.5, D-3, and D-6.

Light caused a significant increase in tillering; there were 87.9 tillers per plant when averaging all L-1 treatments as compared with 65.0 tillers for L-.5. These large increases were somewhat surprising because temperatures were expected to be lower on the shaded plots. Temperature and moisture data are based on observations, but this contention is supported by data. Brown and Blaser (10), in unpublished work, reported that shading to 50% sunlight reduced noon and 4 P.M. temperatures at the soil surface by 10 to 15°F. on days of high solar radiation. The corresponding reduction on days of low radiation was only 2 or 3°F. Temperature at the other positions in the sod profile were affected by shade in the same way, but to a lesser extent.

Tillering varied during the season. The number of tillers per plant increased through July after which there was a decline. Unfortunately, the tillering rate during the season cannot be ascertained since a record of tiller mortality was not kept. Although the data do not support the observations, new tillers occurred all season and the rate of new tiller development was faster during the April-July period than for the July-September period.

Tillering of orchardgrass for N treatments varied with light and also with defoliation as shown by the significant interactions, Table 10. Relaxed defoliation caused a larger increase in tillering with N-375 than with N-25; tillering was similar for the two nitrogen treatments at D-1.5. When nitrogen was increased from N-25 to N-375 there was a large increase in tillering for L-1 as compared with L-.5. The effect of N also differed with irrigation. Tillering was similar for N-25 and N-375 for nonirrigated plots, but there was a much higher increase in tillering with high N and irrigation as compared with low irrigation treatments.

The effect of seasonal changes varied with nitrogen and defoliations. When plants were severely defoliated (D-1.5) and left with low leaf area throughout the season, they produced fewer tillers than plants with high leaf area, D-6. The increase in tillering with the increase in leaf area up to D-3 was not significant in the May-July period, but it was higher in the following months. After July there was a faster drop in tillering with D-1.5 than with D-3 and D-6. An increase in nitrogen rate caused a sharp increase in tillering in June and July, but after July a sharper reduction occurred with N-375 than with N-25.

Carbohydrates. Soluble carbohydrates were decreased slightly as light intensity was reduced during May, but there was a sharp reduction in September; there was a 15% drop in soluble carbohydrates as light intensity was decreased to 50% of normal for May as compared with a 57.5% drop by September. Under normal light (L-1), the soluble carbohydrate contents for May and September were similar. With normal light, the initial soluble carbohydrates in April were 27.2% as compared with 12.9% and 9.0% for May and September, respectively.

Soluble carbohydrates showed erratic behavior with light intensity especially during May and for severe defoliation during September.

Nitrogen fertilization decreased soluble carbohydrates of orchardgrass; soluble carbohydrates for N-25 were 12.8% versus 9.1% for N-375. Soluble carbohydrates dropped with reduction in leaf area. The carbohydrate averages for D-1.5, D-3, and D-6 were 6.0, 11.0, and 15.5%, respectively.

Carbohydrate contents of orchardgrass with defoliation varied with nitrogen, Table 11. Severe defoliation (D-1.5) caused a drastic drop in soluble carbohydrates with both nitrogen treatments; however, there was a larger increase in soluble carbohydrates with N-25 than for N-375 with relaxed defoliation (D-3). As defoliation was further relaxed (D-6) the increases in soluble carbohydrates for N-25 and N-375 were similar. The data indicate that there would have been further increases in soluble carbohydrates with increased leaf area.

Table 11. The effect of light, defoliation, and nitrogen on water soluble carbohydrates of orchardgrass stubbles.

Nitrogen	L-1				L-.5			
	Defoliation				Defoliation			
	D-1.5	D-3	D-6	Mean	D-1.5	D-3	D-6	Mean
lb/A	%	%	%	%	%	%	%	%
May								
25	8.8	19.3	23.5	17.2	5.4	10.1	17.9	11.3
375	6.3	10.7	14.5	10.5	6.9	13.6	16.1	12.2
Mean	7.6	15.0	19.0	13.9	6.2	11.9	17.0	11.8
September								
25	7.9	18.1	22.3	16.1	3.8	5.4	10.1	6.4
375	2.6	6.0	19.0	9.2	4.6	4.3	4.3	4.4
Mean	5.3	12.1	20.7	12.7	4.2	4.9	7.2	5.4

The following were significant at the 1% level: nitrogen (N), defoliation (D); and at the 5% level: NXD.

Initial soluble CHO content of stubble was 27.2% on April 19, 1963.

DISCUSSION

Orchardgrass is generally used in mixed associations with legumes such as alfalfa and ladino clover; but it is also used alone to a limited extent where it is fertilized liberally with nitrogen. Information on tillering and lateral spread, herbage growth, and persistence as interrelated to environmental factors is important in diagnosing and predicting growth responses and plant succession. In the experiments reported here, orchardgrass was grown alone; individual tillers were used to have a simple plant system to study imposed factors and their interrelationship on growth.

Light. Tillering and yield of clippings of orchardgrass were reduced as normal daylight intensity was reduced by shading. Reduced light intensity in a greenhouse (Experiment I) and field experiment (IV) reduced tillering by 73 and 26%, respectively. The magnitude of tillering was directly associated with water soluble carbohydrates in the basal portion of stubble. There was a marked increase in carbohydrate content as light intensity increased to normal daylight. It is apparent that light energy increased the rate of photosynthesis, which augmented stubble carbohydrates. The association of high stubble carbohydrates and high tillering rates of orchardgrass in these experiments agrees with research reported by Ward and Blaser (35).

Photoperiod and light intensity were studied in growth chambers. Tillering occurred at a faster rate with an 18-hour than for a 9-hour day (3100 F.C. in both chambers). The magnitude of stubble carbohydrates was associated with tillering. On the other hand, a 9-hour day at 3100 F.C. (P-2) produced more tillering of orchardgrass than the same treatment plus 9-hour incandescent light (P-3). This is in agreement with Cooper (11) who reported that supplementary low intensity illumination did not increase tillering. The difference between the latter treatments may have been caused by the production of an inhibitor, since carbohydrates were slightly higher for P-3 than for P-2.

Tillering and carbohydrate accumulation increased in a field experiment as daylength increased during the spring season. Dry weights of clippings, with light variables, paralleled tillering responses and carbohydrates.

Temperature. Although the results demonstrate that temperatures play an important role in tillering of orchardgrass, the optimum temperature for tillering was not established and remains unknown. Tillering and foliage growth was very slow at 50-60°F. as compared with 70-80°F. night-day temperatures. There was a sharp increase in stubble carbohydrates with low temperatures. On the other hand carbohydrate accumulation, *per se*, is not of ultimate importance if temperatures are sub-optimum for growth.

It is generally believed that photosynthesis and growth processes have different optimum temperatures. When temperatures are high, metabolic respiration apparently exceeds photosynthesis; but with low temperatures, respiration is probably lower than photosynthesis. Hence, the fluctuation in carbohydrate content of orchardgrass stubble may be caused by shifts in the photosynthesis/metabolic respiration ratios. Sullivan and Sprague (31) found that high temperatures caused a reduction in photosynthesis and an increase in respiration so that carbohydrates were depleted at high temperatures. It may also be postulated that high temperatures may cause inactivation of enzymes that are essential for carbohydrate metabolism.

Under field conditions (Experiment IV) there was a decided increase in tillering between April and June. The causes of increases in tillering in this experiment cannot be diagnosed since daylength and temperatures increased concurrently. The reductions in total number of tillers per plant after June may have been associated with high temperatures, a reduction of solar energy, and/or the increased plant size. As plants increased in size there was probably self-shading and less light energy for tillers in the central portion of the plants.

Irrigation. Irrigation (Experiment IV) increased tillering by 30% over no irrigation when all factorial treatment combinations were averaged. Such pronounced increases in tillering from irrigation would not normally be expected as rainfall in 1963 was unusually low. It is possible that irrigation had an indirect beneficial effect on tillering by reducing temperatures due to increased transpo-evaporation.

Defoliation. Some research conducted in New Zealand shows a near linear relationship between dry matter production and leaf area, Brougham (7).

Maximum rates of dry matter production occurred when the leaf area was of a magnitude for near maximum light interception. Experiments reported here show increased tillering and dry matter production when leaf areas were increased by relaxed defoliation. The improved tillering with leaf area is indirectly attributable to accumulations of stubble carbohydrates; the magnitude of carbohydrate accumulation was associated with the magnitude of leaf area and light energy absorption. The increased yields of herbage as leaf areas were increased (lax defoliation) may be attributed to high light interception, Brougham (7). This oversimplified relationship is not acceptable as leaf area accumulations are invariably associated with water soluble carbohydrates. This study shows that stubble carbohydrate accumulates as leaf area increases. Although foliage was not analyzed, soluble carbohydrates no doubt increased as leaf area increased.

Root development when experiments were terminated was much poorer for low leaf areas (intensive defoliation) as compared with higher leaf areas (lax defoliation). The poor root development with intensive defoliation may be attributed to deficiencies of energy carbohydrates and slow translocation to basal parts of orchardgrass. It is reported that root growth takes place only when carbohydrates tend to accumulate (13).

Nitrogen. It has been pointed out that nitrogen stimulates tillering and growth, and retards soluble carbohydrate accumulated in the stubble of orchardgrass. Nitrogen stimulates synthesis of organic nitrogen compounds and the production of new tissue in rapid growth. The high energy requirements for such fast growth are apparently obtained from photosynthesis and soluble carbohydrates in plant tissue. When growth of orchardgrass was retarded because of a low nitrogen supply, the energy requirements for growth metabolism were apparently lower than photosynthesis. Thus, a net accumulation of soluble carbohydrates seems to depend on the ratio of energy fixed/energy used for growth; low and high carbohydrate accumulation for high and low nitrogen, respectively.

High accumulation of carbohydrates did not stimulate tillering when nitrogen levels were too low for rapid growth. When growth rates are seriously retarded by low nitrogen and when leaf area and light intensity are high, carbohydrate accumulation may be expected. Sprague and Sullivan (29) reported that soluble carbohydrates in the stubble of orchardgrass dropped to lower levels with liberal than with low nitrogen fertilization. They also found that high nitrogen fertilization decreased the fructosan and sucrose content of ryegrass, while insoluble and soluble nitrogen contents were high. The reverse occurred under low nitrogen.

Root growth was better with low nitrogen than with high nitrogen fertilization. The low root weights with liberal nitrogen were apparently caused by deficiencies of energy substrates in rooting zones. Any factor which tends to reduce soluble carbohydrates may reduce root weights (1).

Interrelationship of Light, Defoliation, and Nitrogen. An attempt is made in this section to interpret the biological implications of significant interactions given in the tables and figures.

A. Light-defoliation. It was pointed out that tillers or yields of orchardgrass increased more with high light intensity and lax defoliation than for similar defoliation treatments with low light intensity. When comparing combinations of defoliation and light intensity (Experiments I, III, and IV), the combined effect of high light intensity and high leaf area, no doubt, maximized carbon fixation by photosynthesis. A comparison of Figures 1 and 4 indicates that growth had first access to photosynthetic products, as the dry matter yields were increased more than tillering as leaf area increased (relaxed defoliation). Tillering rates appear to be associated with carbohydrate levels in all of the experiments where some other factors such as nitrogen and temperature are not limiting growth. The high tillering rate for the combined effects of high leaf areas and high light intensity may be attributed to accumulations of soluble carbohydrates in the basal part of orchardgrass. The higher yield increases with the lax defoliation-high light intensity combination as compared to other light-defoliation treatments may be attributed to: 1) high growth rate of old shoots due to a high rate of photosynthesis, and 2) the increase in the number of lateral tillers per plant.

B. Light-nitrogen. There were sharper increases in tillering and/or yield when N was increased from low to medium or high levels in combination with high light as compared with lower light intensities. The sharp yield increases from the medium to high nitrogen-high light combination may be attributed to the higher carbon synthesis and its rapid elaboration into various growth products. At high nitrogen-low light combinations, the low photosynthesis per se and also the low soluble carbohydrate for metabolic functions may retard rate of growth. Nocturnal growth may be especially retarded by low carbohydrates.

Nitrogen fertilization reduced soluble carbohydrates in the stubble with all light treatments; however, there was usually a sharper decline in carbohydrates with low light as compared with higher light intensities when nitrogen was added to both light treatments. New tiller formation occurs at stubble bases in orchardgrass, where chlorophyll may be limited in new tillers and there is shading by older tillers; thus the carbohydrate level at the base may be highly correlated with new tiller development. Also high light intensity will improve light at the level where new tillers develop;

thus the higher light intensity would be more influential than low intensity when the nitrogen supply is adequate. When nitrogen levels are high, there are high demands for energy for tillering and growth of old tillers; thus it appears that the complimentary effect from high light-high nitrogen combination may stimulate tillering and growth.

C. Defoliation-nitrogen. The interactions of tillering and/or yield as influenced by defoliation-nitrogen combinations (Experiments I, II, III, and IV) were highly significant. Orchardgrass clipped to maintain high leaf areas produced comparatively more tillers and/or higher yields with added nitrogen than for plants with low leaf areas. There were reductions in soluble carbohydrates in the stubble because of nitrogen fertilization, Figure 14, but soluble carbohydrates with high nitrogen fertilization were lower with intensive than with lax defoliation. Thus it appears that tillering and growth were influenced directly by photosynthetic products as well as indirectly by energy reserves (soluble carbohydrates).

The results of this study strongly imply that tillering of orchardgrass increases under environmental and morphological conditions that favor potentially high stubble carbohydrates. In addition, the environment must be favorable for reasonably rapid growth as tillering cannot occur when factors such as nitrogen or water supply limit growth. High leaf areas, high light intensity, long days, and their interrelationship favor carbohydrate accumulation and tillering.

The productivity and survival of orchardgrass, as is common with other perennial grasses with an aggregate of tillers, depends on the length of life and physiological responses of individual tillers to various environmental factors. It appears that the growth responses of the aggregate of tillers is dependent upon individual tillers. Thus the understanding of growth responses of tillers as interrelated to natural and imposed environmental factors should serve as a valuable guide for defoliation management practices. Grazing or mechanical methods of defoliation may put the plant under severe stress that will reduce production or longevity. The best quality of forage for ruminants is young, leafy, nonstemmy herbage because of its high digestibility and high ingestion. It is common experience that yields decline with heavy defoliation; the results of this research support this contention. Frequent defoliation apparently cause reduced yields because of the combined effects of low leaf area and low carbohydrate reserves and their effect on formation of new tillers and growth of old tillers.

With systems where animals graze one pasture continuously, there is variable defoliation ranging from near complete defoliation to no defoliation. Such a grazing practice seems harmful because of removal of leaves and even stubble portions of the plant; under severe grazing stress carbohydrates would be depleted. The slow formation of new tillers and growth of old tissue would account for a succession of forage species. The common farm experience of encroachment of undesirable grasses and weeds is no doubt attributable to the slow regrowth and tillering rate of orchardgrass as compared to other species under such practices.

The data reported here support the principle of rotational grazing or similar management practices for best yields and tillering. The results suggest that leaving 6-inch sod residues after grazing or clipping would produce much higher yields than leaving 3 or 1-1/2 inch sod residues. Such a conclusion may not apply to sod conditions. The space planted technique used in these experiments allowed for reasonably good light penetration at the base of plants where new tillers developed. It is expected that the low light intensity at the basal part of plants with a 6-inch sod residue might seriously retard tillers in spite of high carbohydrates which stimulate tillering. It also appears that leaving a 6-inch sod would tend to reduce yields because of mortality of older shoots that would not be harvested. It is likely that further work may prove that it is best to alter the height of the ungrazed sod residue during the season pending new shoot development. The practice of leaving a high sod to accumulation carbohydrates for new shoot development and subsequent close cutting or grazing to remove the old sod to encourage new tiller development might be a desirable practice. Information on the season of most vigorous tillering as interrelated to natural and imposed factors should be considered in manipulating the defoliation practices in grazing or mechanical harvesting.

SUMMARY AND CONCLUSION

Experiments were conducted in the field, greenhouse, and controlled environment chambers to study single environmental factors and their interrelationship to tillering, growth, and carbohydrate content of orchardgrass. Several factorial treatment combinations were imposed on individual tillers from one orchardgrass genotype in four experiments.

1) Tillering and yield of orchardgrass were best under normal or full light intensity. Reduced light intensity in Experiments I and IV lowered tillering by 73 and 26%, respectively. There was a marked increase in water soluble carbohydrates as light energy increased up to normal sunlight.

2) Tillering and growth were very low at 50-60°F. as compared with 70-80°F. night-day temperature. There was a sharp increase in water soluble carbohydrates of the stubble with the low as compared with the higher temperature. Carbohydrate accumulation was low at the high temperature due to the rapid growth and tillering.

3) Irrigation increased tillering by 30%. In addition to supplying a near optimum water supply, it is likely that irrigation favored growth by lowering temperatures due to increased transpo-evaporation.

4) There were increases in tillering and dry matter production when defoliation intensities were relaxed. This improved tillering and yield with larger leaf areas is attributed to a higher amount of soluble carbohydrates at stubble bases where new tillers formed. Root development was much poorer for low leaf areas (intensive defoliation) as compared with high leaf areas (lax defoliation).

5) Nitrogen stimulated tillering and herbage growth, thus there was low carbohydrate accumulation in the stubble of orchardgrass. The stimulation of the growth metabolism processes by nitrogen, no doubt, produces high energy requirements which accounts for low carbohydrate accumulation. On the other hand, high accumulation of carbohydrates did not stimulate tillering and/or growth when low soil nitrogen limited growth.

Root weights were higher with low nitrogen than with high nitrogen fertilization; the lower root weights for high nitrogen treatments were apparently caused by low energy substrates.

6) Certain interactions were significant and the biological implications were discussed.

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Hamid Auda

ABSTRACT

Tillering and Carbohydrate Content of Orchardgrass
as Influenced by Environmental Factors

by

Hamid Auda

Experiments were conducted in the field, greenhouse, and controlled environment chambers to study the effect of environmental factors on tillering, growth, and carbohydrate content of orchardgrass. Tillers of one genotype were studied with several variable factors (light, temperature, moisture, nitrogen, and/or defoliation) in each of four experiments. Factorial treatment combinations were used in each of the four experiments to study single factors and interactions.

Tillering declined to 73 and 26% of normal light when light intensity was reduced in the greenhouse and field, respectively. In the controlled environment chambers, tillering rates were higher with an 18-hour than for a 9-hour day with 3100 F.C. in both chambers. Soluble carbohydrates in the stubble were associated with tillering. There was a marked increase in water soluble carbohydrates as light energy increased up to

normal sunlight. Dry matter production was associated with tillering and carbohydrate contents of orchardgrass, factors which increased tillering augmented clipping dry weights.

Tillering and foliage growth were much higher when day temperature was 80°F. as compared with 60°F. There was a sharp increase in soluble carbohydrates with low temperature, but at the high temperature carbohydrates did not accumulate as they were apparently utilized for fast growth and tillering. Carbohydrate accumulation *per se* was not associated with tillering nor yields when temperatures were sub-optimum for fast growth.

Tillering was increased 30% by irrigation. Tillering of orchardgrass plants, defoliated to 1.5, 3, and 6 inches in combination with other treatments, showed increased tillering and dry matter production as defoliation intensities were relaxed. High tillering rates were associated with the magnitude of carbohydrates in orchardgrass stubble. Root development at the end of the experiment was much poorer for intensive defoliation as compared with lax defoliation.

Nitrogen stimulated tillering and retarded soluble carbohydrate accumulation in orchardgrass stubbles. Nitrogen stimulated the production of new tissue and nitrogen compounds at the expense of stored carbohydrates in the stubbles. With slow orchardgrass growth under low nitrogen, soluble carbohydrates in the stubble accumulated. There was good evidence that soluble carbohydrates are directly associated with tillering and growth of orchardgrass when factors such as light, nitrogen, and water do not limit growth. Carbohydrate accumulation *per se* is not associated with tillering, if any environment growth factor is sub-optimum for tillering and growth.