

† THE EFFECT OF TEMPERATURE ON THE GROWTH AND
COMPOSITION OF THE STUBBLE AND ROOTS OF
PERENNIAL RYEGRASS¹ ✓

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(WITH SIX FIGURES)

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In a previous paper (12) it was reported that, when perennial ryegrass (*Lolium perenne* [L.]) was partly defoliated, the remaining plant parts underwent a progressive loss in soluble carbohydrates, namely sugars and fructosan, for a period of several weeks. This loss from the stubble and roots accompanied a rapid formation of new tissue above ground. When new top growth had produced sufficient photosynthetic area to manufacture its own organic matter, storage of soluble carbohydrates took place. When the percentages of the constituents were plotted against time as the abscissa, the soluble carbohydrates displayed a typical U-shaped curve. Many factors undoubtedly influence the slope and extent of this curve and some of these are being investigated. The present report concerns the relationship of temperature to the composition of ryegrass after cutting.

The earlier paper included a review of the literature pertinent to the subject of reserves. Since then, other reports concerned with the analyses of forage grasses have verified the fact that soluble carbohydrates and starch function as reserves. More complex carbohydrates and those more resistant to hydrolysis, are not so regarded. Some of these recent papers are by BENEDICT and BROWN (2), PHILLIPS and SMITH (9), McILVANE (8), WEINMANN and REINHOLD (18), and WEINMANN (13, 14, 15, 16). A review by Weinmann covers the general subject of reserves in grasses (17).

Reserves in grasses are closely connected with the resistance of the plants to high temperatures. JULANDER (6) showed that grasses withstood limited exposures to a temperature of 48° C (118.4° F) when they had been previously hardened to dry conditions and had not been severely clipped. Both of these last conditions were conducive to the accumulation of reserve carbohydrates. He also noted differences between species, Kentucky bluegrass dying sooner at this temperature than Bermuda grass and a number of range grasses. At lower temperatures, grasses will survive for longer periods. According to HARRISON (5), Kentucky bluegrass grew very little at a constant temperature of 100° F after having been defoliated, and died

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in about six weeks. At 80° F top growth was rapid but no new roots were produced and shoots from the rhizomes appeared above ground only under conditions of low nitrogen nutrition. Although no analyses were made of these plants it is assumed that the rapid top growth, combined with frequent clipping, soon depleted the carbohydrate reserves and led to their exhaustion. At 60° F growth was more normal for the species. According to LOVVORN (7), when four species of grasses were cut frequently, the yields were lower at 80° than at 65° F. BROWN (3) grew four grasses at a number of constant temperature levels between 40° and 100° F. In some species the optimum temperature for top growth was not the same as the optimum for root and rhizome production. For three grasses having lower optimum temperatures (70–90° for herbage, 50–70° for roots and rhizomes), namely Kentucky bluegrass, Canada bluegrass and orchard grass, an increase in temperature was associated with increased fiber and decreased nitrogen-free extract contents in above-ground and below-ground parts. Protein was at a minimum at 60° or 70° and was greater at both lower and higher temperatures. In Bermuda grass, which had an optimum growth temperature of 100°, fiber and nitrogen-free extract increased with rising temperature, the former to reach a limit of increase at 70°, the latter at 100°. The protein minimum was at 80–90°, somewhat higher than with the other grass species. In other studies of grasses, composition was not reported (4, 10, 11).

No information seems to be available concerning the composition of ryegrass at various temperatures. As it has been successfully grown only in cool temperate regions, its optimum temperature for growth is probably low. The temperature range in the studies reported here covers the optimum for growth of this species.

Materials and methods

The objective of the experiment here reported was to determine the effects of air and soil temperatures on the reserves of the stubble and roots of perennial ryegrass following clipping. Four temperature conditions were provided by growing plants in chambers with artificial light of 525 foot-candlepower intensity at the ground level. Air and soil temperatures were maintained by a time-cycle control so that maximum temperatures prevailed from 10 A.M. to 2 P.M. and minimum temperatures from 10 P.M. to 2 A.M. each day with gradual changes between them. Four such alternating air and soil temperature ranges were used: (1) 50°–60°, (2) 60°–70°, (3) 70°–80°, and (4) 80°–90° F. A 14-hour day was provided throughout the experiment and adequate soil moisture was maintained at all times.

The ryegrass clone used in a previous trial (12) was increased vegetatively to provide uniform material. Individual tillers, trimmed to remove all roots and old leaf growth, were placed in tap water for several days until new roots formed, then five tillers were planted in each of a number of one-gallon glazed crocks. The soil consisted of equal parts of a fertile Hagers-

town silty clay loam and river bottom sand, the latter to improve the texture of the soil and to facilitate washing of the roots when the plants were taken up. After about three months' growth in the greenhouse at 70° F under a 16-hour day (provided by supplementary Mazda light), the plants were clipped to a height of 1.5 inches above ground and placed in the chambers. At the time of clipping six pots were selected at random and the plants were removed, washed, and were used for dry weight determination and for chemical analysis. The data obtained from these are referred to as the "original" dry weights and the "original" composition. From the remainder of the plants placed in the chambers, four pots, selected at random, were removed for weight measurements and for chemical analysis at stated times, namely, after 4, 9, 14, 21, 28 and 40 days of exposure to the various temperature conditions. The leaf growth above the 1.5 inch level is referred to as "tops" and the remainder, except for the roots, as "stubble." The stubble was composed almost entirely of leaf tissue, largely leaf sheaths since the blades were removed with the tops and the stems in vegetative tillers of this grass species are very small. The roots were trimmed off with shears after having been washed in cold tap water.

Two separate trials were conducted to provide replication of results. The plants used in the first trial were started in the greenhouse December 9, 1942, and allowed to grow until March 13 when they were all clipped and placed in the chambers at the same time. Plants used in the second trial, also grown in the greenhouse, were not all started on the same date, but rather at succeeding intervals so that each group would have the same growth period as the comparable group in the first trial. Thus these plants were ready to place in the chambers when space became available following the removal of plants of the first trial. With this arrangement in the second trial, the plants were not all moved into the chambers at the same time but they came out on nearly the same date. For this reason there were six "original" samples in the second trial (or replication) but only one in the first.

The tops, stubble, and roots were analyzed separately by methods described earlier (12).

Results

PRELIMINARY ANALYSES FOR SOLUBLE CARBOHYDRATES

A preliminary sampling of plants was made on March 2, 11 days before the plants of the first trial were clipped and moved to the chambers. Analyses were carried out immediately to determine whether the plants contained reserve carbohydrates in sufficient amount for the studies planned. The results of the analyses are presented (table I) as the average of two samples, each consisting of material from five pots. As previously noted, the leaves and roots furnish a large part of the dry matter of the plant but their soluble carbohydrate content is relatively low. While the stubble contains less than 30 per cent. of the total dry matter it is higher in sugars and

much higher in fructosan than are either leaves or roots. Thus the lower parts of the above-ground portion of the plant contain more carbohydrates than the upper parts, and clipping (or grazing) removes an increasing proportion of them as the defoliation approaches ground level. In these plants the storage of reserve carbohydrates was found to be sufficient for the purposes of the experiment as planned.

TABLE I

YIELD AND CARBOHYDRATE CONTENT OF PARTS OF RYEGRASS PLANTS ON MARCH 2.

PART OF PLANT	WEIGHT OF PART IN PERCENTAGE OF WHOLE PLANT	CARBOHYDRATES, IN PERCENTAGE OF DRY WEIGHT		
		REDUCING SUGARS	SUCROSE	FRUCTOSAN
Upper 2/3 of leaves	15.4	2.3	7.6	1.0
Lower 1/3 of leaves	12.6	3.0	7.0	4.6
Upper 1/2 of stubble	10.6	6.8	9.1	21.7
Lower 1/2 of stubble	18.4	3.1	7.8	26.3
Roots	43.0	1.0	4.4	2.7

GROWTH OF CLIPPED PLANTS IN CONTROL CHAMBERS

The amount of growth made by the plants in the chambers was measured by determining at each sampling date the fresh weights of the new

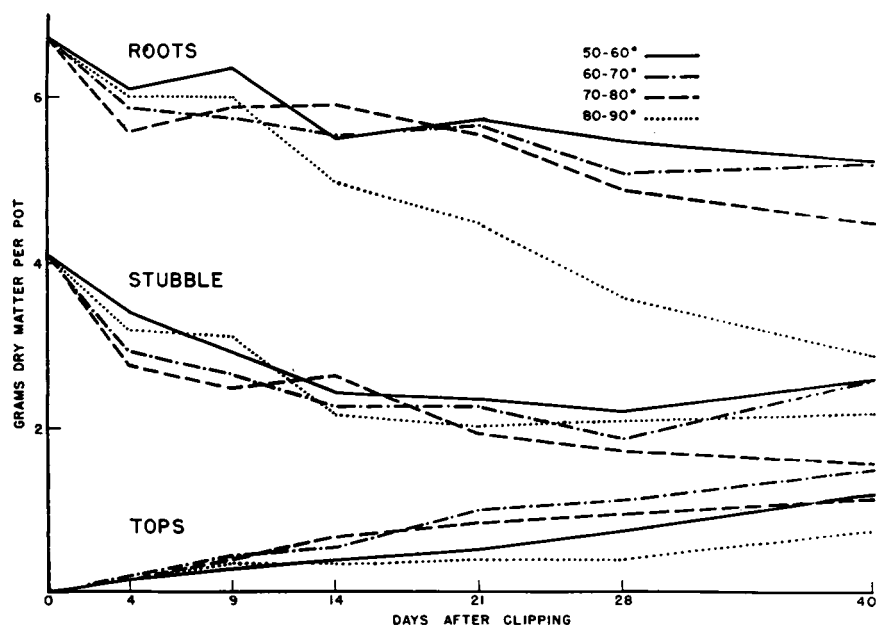


FIG. 1. Changes in the dry weights of the roots, stubble and tops of perennial ryegrass at four different temperature conditions.

top growth and the dry weights of top growth, stubble, and roots. The

variation in size of the plants on the days of clipping and the discrepancies between the two trials (or replications) made the dry weight changes brought about by temperature differences appear somewhat irregular. Using a mean of the "original dry weights" and the means of the two trials at the different sampling dates, the lines of figure 1 were drawn. It may be seen that there were some fluctuations, particularly at the early dates, but the general trends of dry matter yields are unmistakable.

New top growth appeared quickly following clipping and continued at all temperatures for the duration of the experiment. Differential rates of growth due to temperature were variable for the first two weeks but were more consistent for the later periods. The most top growth was produced by the series at 60–70°. While this series was somewhat higher in top growth yield than the average of the others at the three early sampling dates, it was highest of all series at the last three successive dates. On the other hand the 80–90° series was consistently lowest for the last four successive dates. The optimum temperature for this clone of ryegrass to produce foliage under the stated environmental conditions is therefore near 60–70°, with less and slower growth occurring at higher and lower ranges. The moisture content of the new foliage was also affected by temperature, and roughly correlated with yield. At the 40-day sampling the fresh top growth of the 60–70° series contained 18.6 per cent. dry matter, and that of the 80–90° series contained 23.5 per cent. dry matter.

While new tops were growing, stubble and roots were losing weight, rapidly for the first few days and less rapidly thereafter. In the stubble, which included new foliage below the 1.5 inch level as well as older leaf sheaths, a loss in weight was evident at all temperatures for the first two weeks after clipping. The plants at the two lowest temperatures soon ceased to lose weight but those at 70–80° continued to lose for the duration of the experiment. In the roots, a more or less steady loss in dry matter continued during the entire period. The two lower temperature series behaved alike but at higher temperatures the loss in weight was accentuated with the rise in temperature.

During the recovery period certain differences in the new leaf growth were apparent. At the time of the 21-day sampling, it was noted that the plants at 50–60° were second best in appearance and had leaves 2–5 inches long; those at 60–70° were healthy, vigorous, and of good color and had leaves 5–8 inches long; at 70–80° the plants had more spindly leaves and did not appear vigorous; at 80–90° growth was poorest, leaves were 1–5 inches long and very dark green, and roots were brown and discolored. At the end of 40 days the leaves at the lowest temperature were broadest and most vigorous in appearance; at 60–70° the leaves were slightly narrower and slightly darker green; at 70–80° the plants were still less vigorous; at 80–90° growth was stunted, the leaves were very dark green and had the lowest moisture content, and the roots were very dark brown—many may

have been dead. It was evident that the high air and soil temperatures were unfavorable for the growth of perennial ryegrass. New leaf growth was produced somewhat faster at 60–70°, but after forty days a more vigorous growth was apparent at 50–60° F.

It should be noted here that recovery in these plants grown under artificial conditions was not as rapid as in those previously reported under greenhouse conditions (12). In the greenhouse the roots and stubble, after initial weight fluctuations lasting for a few weeks, began to increase steadily in weight. During the 40-day recovery period under controlled environments as reported here, the roots and stubble did not attain weights comparable to those of plants sampled at the time of clipping and removal from the greenhouse. Lower light intensities and lower carbon dioxide concentrations in the chambers may have been factors limiting growth.

COMPOSITION CHANGES OF CLIPPED PLANTS IN CONTROL CHAMBERS

On March 13 when all the plants included in the first trial were clipped, some of them were prepared for analysis. Two complete samples representing the tops from six plants and the stubble and roots from seven others were analyzed. In the second replication there were six "original" compo-

TABLE II

MEAN DRY WEIGHTS AND COMPOSITION OF PARTS OF PLANTS WHEN PLANTS WERE MOVED INTO CONTROL CHAMBERS.

	FIRST REPLICATION			SECOND REPLICATION		
	LEAVES	STUBBLE	ROOTS	LEAVES	STUBBLE	ROOTS
Dry weight per pot, grams	1.78	4.82	6.94	2.21	3.37	6.49
Sol. matter, %	35.0	18.8	14.7	31.4	14.3	15.0
Reducing Sugars, %	3.8	3.4	1.2	1.4	2.5	0.8
Sucrose, %	6.2	6.2	5.5	5.5	4.5	6.0
Fructosan, %	27.5	4.9	29.3*	5.8
Cellulose, %	21.2	26.4
Pentosan, %	14.0	18.6
Lignin, %	3.6	10.3
Sol. nitrogen, %	0.30	0.09	0.05	0.20	0.08	0.05
Insol. nitrogen, %	2.06	0.60	0.59	1.73	0.49**	0.59**
Total nitrogen, %	2.36	0.69	0.64	1.93	0.57	0.64
Sol. nitrogen, in % of total nitrogen	12.8	13.1	8.3	10.5	13.3	7.5
Crude ash, %	7.7	9.1	14.4	8.8	8.3	9.6
Calcium, %	0.47	0.19	0.30
Phosphorus, %	0.13	0.10	0.08

* Only four "original samples", two lost.

** Only five "original samples", one lost.

sitions at as many different dates with six pots contributing to each and their composition and weight were necessarily variable. For brevity only the mean values are presented here (table II).

The changes in composition of the plants at the various temperatures

in the control chambers are next considered. Changes in the sucrose content are illustrated in figure 2. In the stubble these changes followed a U-shaped curve, sucrose reaching a low point about two weeks after clipping and rising thereafter. The lowest temperature series, 50–60°, showed con-

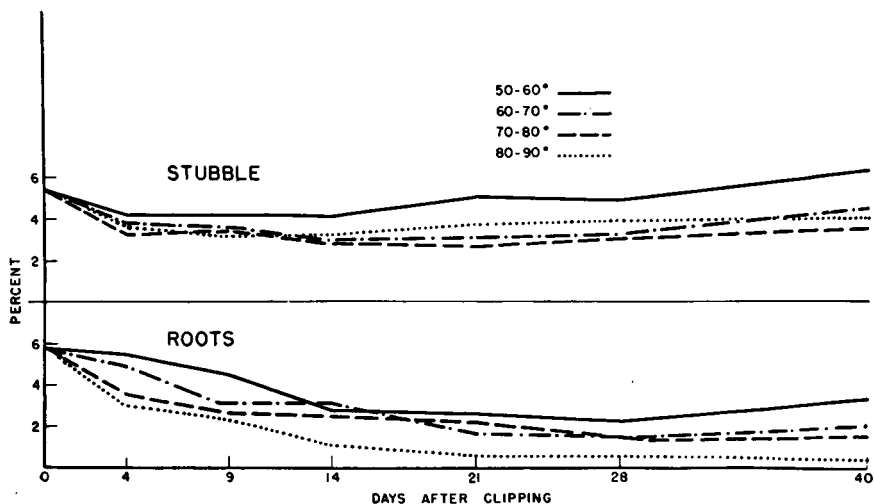


FIG. 2. Changes in the sucrose content of the stubble and roots of perennial ryegrass at four different temperature conditions.

siderable increases at the later periods, with sucrose exceeding its original concentration. In the roots the original concentration of sucrose was of the same order as that in the stubble but the initial fall was of longer duration, lasting about four weeks. Appreciable restorage occurred only in the 50–60° series, and to a lesser extent than in the stubble. The final sucrose concentration was definitely a function of temperature, the higher temperatures causing greater sucrose losses.

Reducing sugars were determined separately. Beginning in the stubble at 3 per cent. they showed a more gradual fall than did sucrose and showed little response to temperature, all four series ending in a range of 1.7 to 2.1 per cent. In the roots, reducing sugars were of minor importance, having an initial value of only 1 per cent. and fell uniformly to about 0.2 per cent. with no noticeable temperature effects. Because of the minor importance of reducing sugars in the roots and their failure to respond to temperature in either plant part, a graph for total sugars (reducing sugars plus sucrose) resembles that of sucrose but shows relatively smaller fluctuations.

The previously noted importance of fructosan as a reserve carbohydrate is confirmed by these experiments. In the stubble it amounted to more than one fourth of the dry matter at the time of clipping and a good part of this rapidly disappeared. The changes are illustrated in figure 3. As with sucrose, utilization was more rapid at higher temperatures and restorage took place only at the lower temperatures. In the roots, fructosan amounted

only to about 7 per cent. of the total dry matter. Its rate of utilization was similar to that in the stubble and, considering that the roots exceeded the stubble in total weight, its loss from the roots was considerable. The regularity of the loss of fructosan with rise in temperature was almost without exception, both in the stubble and in the roots.

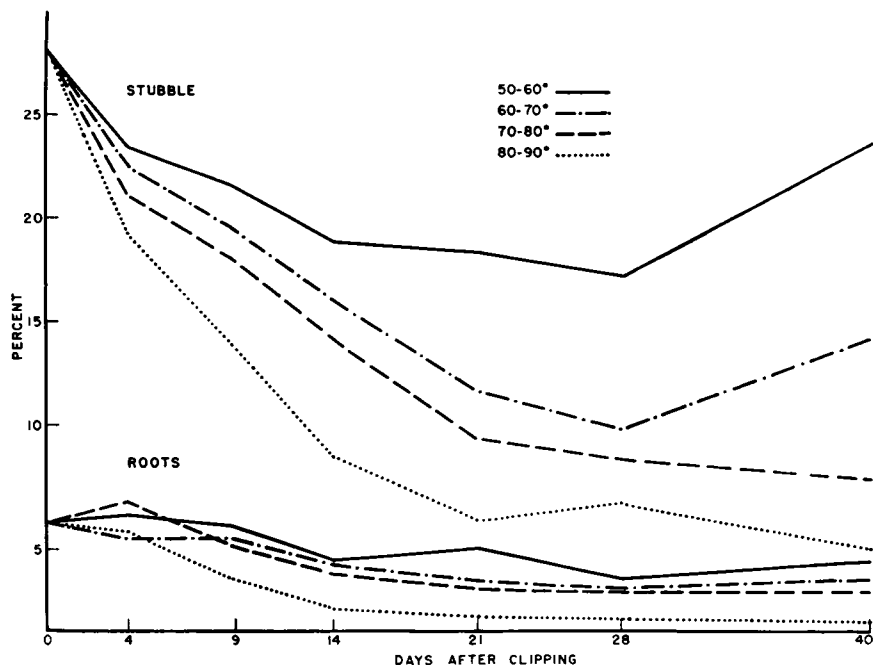


FIG. 3. Changes in the fructosan content of the stubble and roots of perennial ryegrass at four different temperature conditions.

On the other hand, the structural constituents, cellulose, lignin, and pentosan, did not undergo loss after clipping. Because of the loss of soluble carbohydrates these structural constituents at first rose rapidly in percentage but after several weeks leveled off. Where carbohydrate restorage took place later in the stubble of two series, namely the 50-60° and the 60-70°, cellulose dropped slightly and displayed an inverted U-curve. The roots made continual increases in both cellulose and pentosan and both plant parts made a steady increase in lignin, a normal aging process. The effect of temperature on these structural constituents was opposite to that noted on the soluble carbohydrates in that they were highest in the high temperature series. For brevity the effects of only two extreme conditions, the 50-60° and the 80-90°, on these substances in the stubble are illustrated in figure 4.

Total nitrogen of tops and stubble is illustrated in figure 5. A general downward trend in the total nitrogen of the new leaf growth as it ages is normal. In this experiment the series at the highest temperature showed the least decline. In the stubble the inclusion of new leaf area among the

older tissue might delay this downward trend but only in the highest temperature series was an increase noted. The total nitrogen of the roots is of

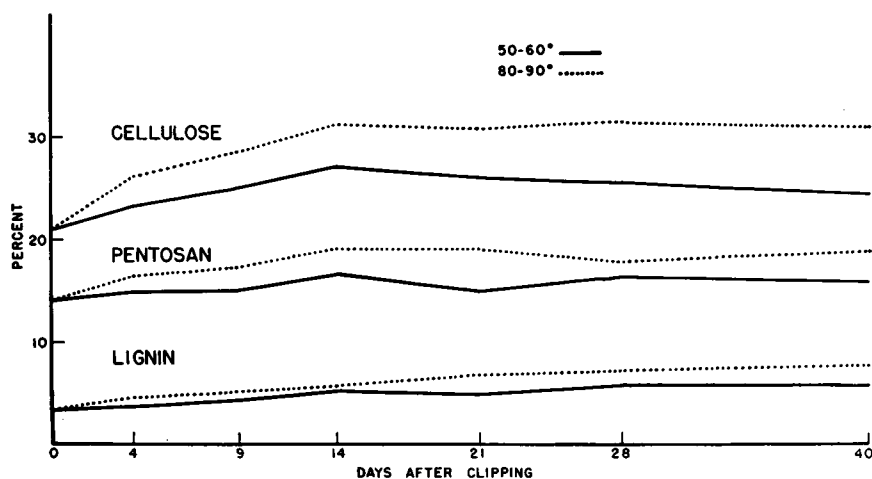


FIG. 4. Changes in the cellulose, pentosan, and lignin contents of the stubble of perennial ryegrass at two different temperature conditions (one replication only.)

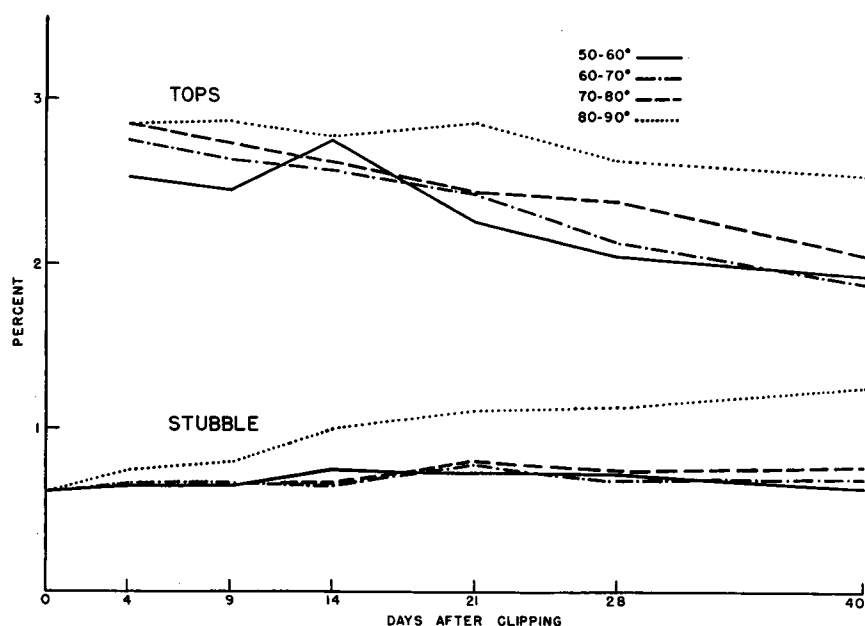


FIG. 5. Changes in the total nitrogen content of the tops and stubble of perennial ryegrass at four different temperature conditions.

the same order as that of the stubble and gives much the same picture. The highest temperature series, 80-90°, was slightly superior to the other series in total nitrogen at the last three sampling dates. Since this series showed

the greatest loss in carbohydrates, its higher protein content may be apparent only.

That high temperature has some influence on the nitrogen metabolism is obvious when the soluble as well as total nitrogen is considered. Some data are illustrated in figure 6 in which the soluble nitrogen is expressed in

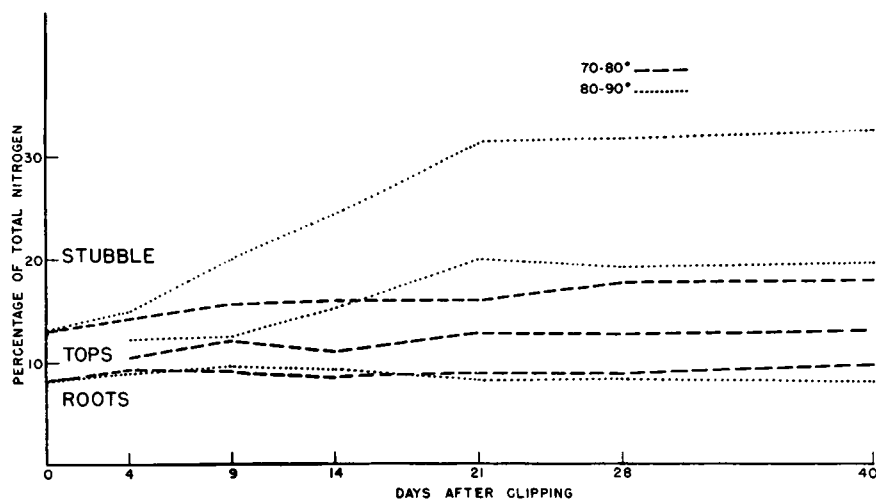


FIG. 6. Changes in soluble nitrogen, expressed as percentage of total nitrogen, in stubble, tops, and roots of perennial ryegrass at two different temperature conditions.

percentage of total nitrogen. The proportions of soluble nitrogen were distinctly higher in the stubble and tops in the 80-90° series than in the 70-80° and the latter was not greatly different from the other two low temperature series not shown in figure 6. The temperature effect on total nitrogen was not limited to an increase in soluble nitrogen; insoluble nitrogen was also higher in both the stubble and roots of the 80-90° series.

Total ash, phosphorus and calcium were also determined on the stubble and roots of the first replication. With the exception of a slightly higher calcium content of the stubble and roots of the highest temperature series at the later sampling dates no differences in these constituents were noted.

Discussion

These experiments demonstrate that high temperatures play a role in the productivity and survival of grasses. The range of temperatures at which the controlled chambers operated included the optimum temperature for the growth of new leaf tissue since its maximum yield occurred in one of the intermediate series, the 60-70°, and the maximum formation of carbohydrates also occurred within the range. At a temperature lower than the optimum for growth, synthesized carbohydrates were stored, but at temperatures higher than the optimum, they were rapidly dissipated without

having served as reserves in the sense that they contributed to the formation of new tissue. Whatever may be the effect of temperature on the rate of production of carbohydrates by photosynthesis, a rise in temperature will increase their loss by respiration. An excessive rate of respiration brought about by continued high temperature should lead to the exhaustion of carbohydrate reserves, and to the death of the plant, especially of one that has been defoliated.

Defoliation caused a rapid digestion of protein in the stubble and roots. In the highest temperature series, namely the 80–90°, the proportion of total nitrogen soluble in alcohol continued to increase at a more rapid rate and for a longer period than in plants at lower temperatures. While no analyses were made of this fraction, it contained, undoubtedly, amino acids and perhaps nitrogenous salts. Respiration is not confined to carbohydrates alone, but also affects amino acids and proteins, leaving residues relatively rich in nitrogen, such as amides and ammonium salts. The accumulation of one or more of these substances is characteristic of plants at high temperatures. The death of a plant at high temperature has been ascribed to the accumulation of ammonia (1). In these experiments the roots were more seriously injured by high temperatures than was the stubble. In a period of 28 days they changed color from white to brown and their sucrose and fructosan contents fell to near zero. It appears therefore that when plants are placed under adverse temperature conditions the roots are the first to die, an observation reported by others (4, 11). If the death of the roots is brought about by the exhaustion of carbohydrates, by the increase in ammonium salts or similar nitrogenous compounds and by an adverse effect of these compounds on protoplasm, the tops cannot survive long. The lower moisture content of the tops of the high temperature series may be a symptom of the failing capacity of the roots to take up water.

These experiments also suggest that temperature is one factor in the failure of perennial ryegrass to be adapted to the climate of much of the United States. The reduction of reserve carbohydrates with rising temperature agrees with the observation of BROWN (3) who found that nitrogen-free extract decreased with rising temperature in those species which normally grow in cool climates. In Bermuda grass he observed that nitrogen-free extract increased with rising temperature up to 100° F, the highest temperature he worked with. There is undoubtedly some relationship between carbohydrate accumulation and stability, and the ability of a plant to withstand high temperatures.

Plants at high temperatures behaved in some respects like plants that had been placed in darkness in a previous study (12), since both environmental conditions led to a rapid dissipation of carbohydrate reserves and to the digestion of protein. However, in one respect the nitrogenous metabolism was different. The plants in darkness accumulated a high concentration of nitrates which disappeared later, when the plants were

dying. No nitrates were found at any time in plants in these temperature studies though it must be noted that these plants grew in soil while those placed in darkness were in gravel cultures, constantly supplied with nutrients.

The effect of high temperature upon uncut and undisturbed plants cannot be determined from these studies but it appears from other work (6) that plants with high reserves, and incidentally plants not recently defoliated, are better able to withstand high temperatures than those recently cut. Defoliation alone (mowing or grazing) stimulates metabolic activities such as growth, nutrient absorption, translocation and respiration. The additional stimulus of high temperature at the same time may lead to unfavorable results by speeding up those processes, particularly respiration, and this may lead to an exhaustion of reserves.

Summary

Perennial ryegrass plants were clipped at a height of 1.5 inches above the surface of the soil and allowed 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° above those of the night. Dry weight yields were taken and chemical analyses were made of the stubble, roots, and new top growth of plants under each of the four temperature conditions at 3, 9, 14, 21, 28 and 40 days after the beginning of the treatment. New top growth was most rapid at 60–70°, and least at 80–90°. In all four temperature series both roots and stubble decreased in total dry weight throughout the 40-day period following clipping. The losses were most rapid and extensive at the higher temperatures. The roots and stubble underwent rapid losses in sucrose and fructosan during the early part of the experiment but these 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. Protein metabolism was characterized by an increase in the proportion of soluble nitrogen immediately after the leaves were clipped, and at the highest temperature this proportion continued to increase for a long period in the tops and stubble. Other constituents, lignin, cellulose, hemicellulose and ash, were not particularly affected by leaf removal or temperature except that their percentages were increased where soluble carbohydrates had been withdrawn.

In this experiment a high temperature adversely affected ryegrass by rapid dissipation of reserve carbohydrates, slowing down the production of new leaf growth, and in general inhibiting recovery from the effects of defoliation. At the end of a 40-day exposure to a temperature range of 80–90° F, the plants were stunted, the leaves were spindly and dark green, and the roots were discolored and near death. All parts were relatively

high in total nitrogen, and especially in soluble nitrogen, and were approaching exhaustion of soluble carbohydrates.

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