Restitution of Growth In Nitrogen Deficient Sugar Beet Plants[1]

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In agricultural, as well as natural environments, wide fluctuations in the levels of individual environmental factors are common. Plant growth may be restricted by an unsuitable level of a particular factor, e.g., deficiencies of water or nutrients, while all other factors are optimal for growth. Under these circumstances, it is useful to know how the plants react as the deficiency develops and when the restriction is alleviated.

A renewal of normal leaf development commonly is observed after nitrogen deficient sugar beet plants are supplied with nitrogen. Associated with this is a decline in sucrose concentration in the roots. Root growth is also renewed, but there is conflicting evidence on the manner in which it occurs. Loomis and Nevins (3)[3] found considerable lag between the time nitrogen was resupplied to deficient plants growing in nutrient culture and the time root growth was renewed. In contrast, Ulrich (7) found that supplying nitrogen to plants grown in pots with soil shortly after they became deficient resulted in a rapid renewal of root growth.

Both from an ecological and from an economic standpoint, it is of interest whether growth occurs at an above normal rate during restitution. Such phenomena have been studied intensively with higher animals and have been termed "compensatory growth" (9). It appears appropriate to employ this same terminology in discussing plant growth. Compensatory growth has been observed in several plant species during recovery from moisture stress (literature reviewed by Stocker, 5). Owen (4) reported that this phenomenon occurred with sugar beet but his data appear inconclusive. Ulrich (8) observed compensation to the effects of temperature in that sucrose yields from plants which had experienced a period of growth in a hot climate and were then transferred to a cold climate, exceeded yields from plants which remained continuously in either hot or cold climates.

Less information is available on recovery from nutrient deficiencies. Compensatory growth did not occur in the nitrogen experiments cited above (3,7) although it might be expected

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[3] Numbers in parentheses refer to literature cited.

if a substrate, normally limiting, were to accumulate during the period of stress. With sugar beet, the accumulation of sucrose in the storage roots is promoted by nitrogen deficiency. This sucrose is available for growth and might contribute to an above-normal growth rate when nitrogen again becomes available. This was not observed in the pot experiments but it may be that compensatory growth relationships are different for plants grown in competitive stands than for plants grown in pots. In the present experiment, the influence of a period of nitrogen deficiency on subsequent growth in a high-nitrogen environment was studied under field conditions.

Methods

The crop was grown on Holtville clay loam soil at the University of California Imperial Valley Field Station. This soil releases large amounts of nitrogen but at a rate too low for maximum growth of sugar beet and a luxury level of nitrogen nutrition is maintained only by applying 200 to 400 pounds nitrogen per acre. The seed (Holly HH-3) was planted October 9 on double row beds (14-26 inch spacing). Thirty-five pounds phosphorus as treble superphosphate, and 100 pounds nitrogen as ammonium sulfate were applied per acre in the shoulders of the beds at planting. An additional 50 pounds of nitrogen per acre were applied to all plots in November. Nitrogen was the only limiting nutrient during the growth of the crop. Furrow irrigations kept the plants well supplied with water.

The experiment consisted of four nitrogen treatments arranged in a randomized block design with six replications. The treatments were designed so that the growth of high-nitrogen plants could be compared to that of low-nitrogen plants with or without fertilization. The treatments were established beginning February 23, when the plants approached a nitrogen-deficient condition, by sidedressing ammonium nitrate to appropriate plots as shown in the following table:

Treatment		Pounds of nitrogen applied per acre on:			
		Feb. 23	Mar. 13	Apr. 4	Apr. 23
A	High nitrogen	200	0	0	200
B	Low nitrogen Fertilized after 3 weeks deficiency	0	200	0	0
C	Low nitrogen Fertilized after 6 weeks deficiency	0	0	200	0
D	Low nitrogen	0	0	0	0

The plots were irrigated on the same day that nitrogen was applied.

The differences among the treatments may be seen from the tissue analysis (1) data presented in Figure 1. The plants which were not fertilized on February 23 became deficient about March 1 (NO_3-N in petioles of recently matured leaves dropped below 1000 ppm dry weight). With this soil there may be a 1-week delay following application of ammonium nitrate before nitrate appears in the plants (2). Thus, the refertilized low-nitrogen plants (B and C) were deficient for about 3 and 6 weeks, respectively. The high-nitrogen plots (A) approached a deficient level on April 23 at which time they were fertilized with an additional 200 pounds nitrogen per acre. During May, treatment B, the first to be refertilized, and then treatment C, became nitrogen deficient again; no more nitrogen was applied to these plots.

Harvests were made at 3-week intervals beginning February 20 and extending to June 26. On each date the beets from 60 feet of row in each plot were harvested. Fresh and dry weights of roots and tops (including crowns) were measured; sucrose concentration was determined on samples of roots[4].

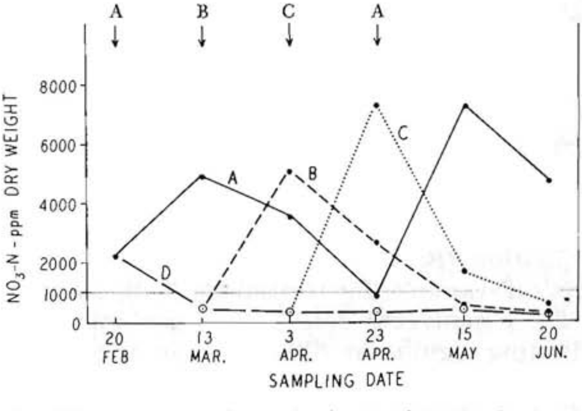

Figure 1.—The concentration of nitrate-nitrogen in recently mature petioles from plants receiving various experimental treatments. Letters refer to treatments and vertical arrows indicate dates when 200 lb. nitrogen/acre was applied to various treatments.

Results

As shown in Figure 2, the yield of fresh tops from the high nitrogen plants (A) increased rapidly between February 20 and

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[4] The Holly Sugar Corporation generously conducted these determinations as well as having supplied the seed.

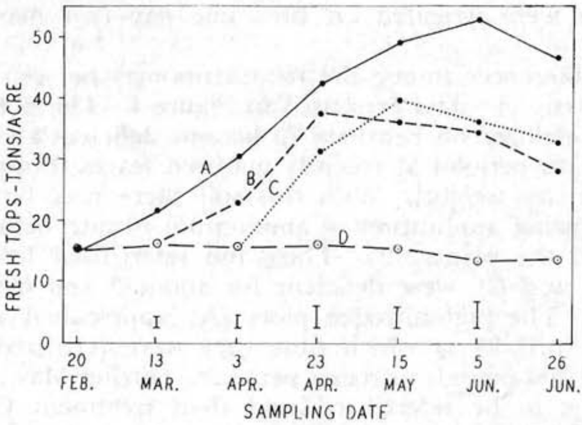

Figure 2.—Yields of fresh tops from sugar beet plants as affected by various nitrogen regimes. The vertical lines correspond to the LSD_{05}.

Table 1.—Absolute and relative rates of top growth between April 3 and April 23. (Means within a column followed by the same letter are not significantly different from each other, P = .95.)

Treatment	Absolute growth rate Lb/acre day		Growth relative to mean of April 3 and April 24 yields Lb/acre day	
	Fresh wt	Dry wt	Fresh wt	Dry wt
A	1140a	192a	0.016a	0.026a
B	1420b	160a	0.024b	0.025a
C	1480b	159a	0.032c	0.028a
D	76c	60b	0.002d	0.013b

June 5 and then declined. Yields of tops from low-nitrogen plants (D) remained approximately constant near 15 tons per acre; with refertilization (B and C), top growth was greatly stimulated. In an analysis of variance for treatments A, B, and C for April 3 and April 23, a significant date × nitrogen interaction was obtained indicating significant differences in the growth rates of these treatments. This is considered in detail in Table 1.

On a fresh basis, but not on a dry basis, the growth of the refertilized plants exceeded that of the high nitrogen plants. Considering that there was some delay after April 3 before the plants in treatment C obtained appreciable nitrogen from the soil, their peak growth rate was undoubtedly greater than the mean value shown. In the present case, there is no evidence of exponential growth and relative growth has been calculated as the ratio of daily growth to mean weight. The relative growth rates shown in Table 1 are lower than commonly reported for plants due to the large size of the plants on April 3. On a fresh basis, the refertilized plants showed the highest relative growth rates and on a dry basis they equalled that of the high-nitrogen plants.

Root yields are summarized in Figure 3. The degree of nitrogen deficiency obtained may be ascertained by comparing growth rates of high- (A) and low-nitrogen (D) plants. Between March 13 and April 23 the yield of roots from low-nitrogen plants increased 460 lb/acre day or only 70% as rapidly as the high-nitrogen rate of 650 lb/acre day. Refertilized plants quickly recovered the same absolute rate of growth as the high-nitrogen

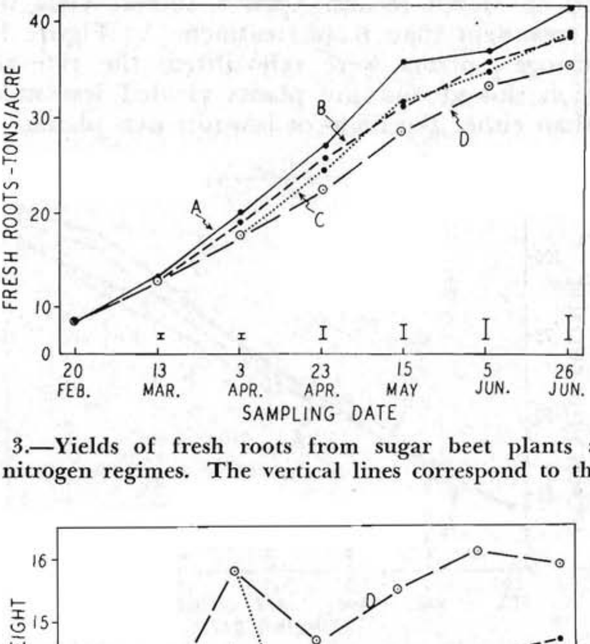

Figure 3.—Yields of fresh roots from sugar beet plants as affected by various nitrogen regimes. The vertical lines correspond to the LSD_{05}.

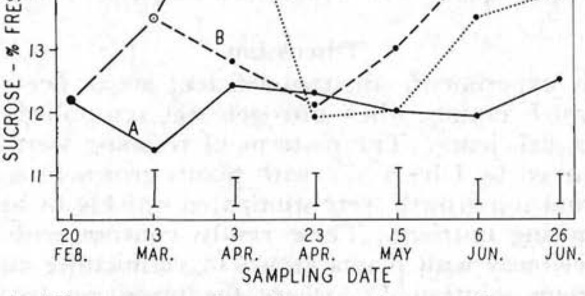

Figure 4.—The concentration of sucrose in sugar beet storage roots as affected by various nitrogen regimes. The vertical lines correspond to the LSD_{05}.

plants, i.e., between April 3 and April 23, treatments A, B, and C all increased 660 lb/acre day and compensatory growth did not occur. Treatments B and C ultimately produced the same root yield and were intermediate between treatments A and D.

After February 20, sucrose concentration in the low-nitrogen (D) plants increased rapidly to near 16% while that in the high-nitrogen (A) plants remained near 12% (Figure 4). The low-nitrogen plants returned to the lower value within 3 weeks after refertilization. With treatment D, the increase in sucrose concentration offset, for a period of time, the lower rate of root growth and on March 13 and April 3, sucrose yield was higher from this treatment than from treatment A (Figure 5). When the low-nitrogen plants were refertilized, the rate of sucrose accumulation slowed and the plants yielded less sucrose after April 23 than either the high- or low-nitrogen plants.

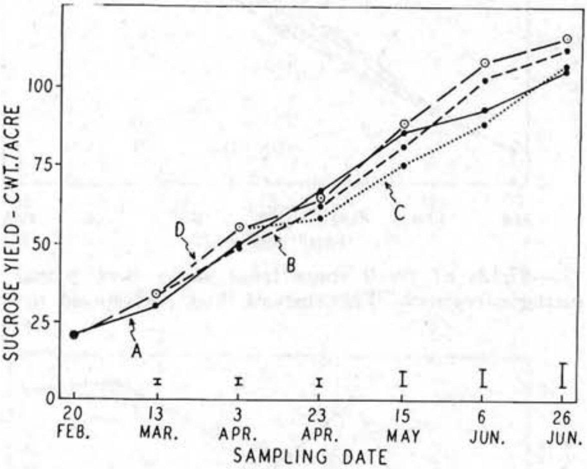

Figure 5.—Sucrose yields in sugar beet storage roots as affected by various nitrogen regimes. The vertical lines correspond to the LSD_{05}.

Discussion

In this experiment, nitrogen-deficient sugar beet plants renewed growth rapidly when nitrogen was resupplied after 3 or 6 weeks of deficiency. The patterns of response were similar to those obtained by Ulrich (7) with plants grown in soil in pots, i.e., root and top growth were stimulated quickly by applications of the limiting nutrient. These results contrast with those obtained previously with plants grown in vermiculite and watered with nutrient solution (3) where the transition from high to low nitrogen occurs rapidly and the degree of deficiency is more severe than with plants grown in soil. It appears that the growth of refertilized plants may be more dependent upon the degree than upon the length of the deficiency. This could be studied by conducting the experiment on several soils having a wide range of nitrogen supplying power.

Compensatory growth may be defined as greater than normal absolute or relative growth over the same interval of time or at the same stage of development. In this study the plants were all in a vegetative phase of development and the only usable measure of stage of growth is plant size. Since similar plant sizes occurred at different times and under different environments, specific comparisons in plant growth, as shown in Table 1, were made only for the April 3-April 24 interval of time. Under the conditions of the experiment, this was the only period during which all treatments could be compared on a proper basis and the only period during which either of the refertilized treatments showed what might be termed compensatory growth for either roots or tops. Compensatory growth (on absolute and relative bases) occurred with fresh tops but not with dry tops or other characters.

The relative growth rates presented in Table 1 were calculated on mean weight of tops which correlates well with leaf area, rather than on total plant weight. Leaf areas were not measured but can be estimated for treatments A and D from the performance of similar plants in an adjacent experiment; on April 3, leaf areas for these treatments equalled approximately 8 and 4 acres leaves per acre land, respectively. From this it appears that the relative regrowth of fresh tops was inversely related to the initial leaf area. This is the reverse of what is observed with seedling stands or after defoliating a pasture but is expected with high leaf area where there is considerable mutual shading of leaves. However, the inverse relationship between top weight and regrowth is not apparent in the relative growth of dry tops. Thus the compensatory growth of fresh tops in the refertilized plants was in the enlargement of the young leaves and was evident as an increase in succulence. Evidently the nitrogen-deficient crop had a greater potential for leaf growth than did the high-nitrogen crop.

The use of relative growth rates implies a dependence of growth upon size of plant, i.e., upon the "capital" for growth. The present results indicate that the relative growth of a plant community with closed canopy may have little meaning since the community has passed the logarithmic phase of growth and light or some other environmental factor rather than the size of plants is limiting. The individual plants in the community have a potential for much higher growth rates than is possible under competitive conditions and this apparently was expressed during restitution after the intensity of competition had been reduced by the period of nitrogen deficiency. It is not possible from the present data to determine whether the higher rate of leaf growth was "normal" or "above normal" for that environment and initial leaf area.

Total crop growth rates (dry matter increase per unit land area per day) were measured. Unfortunately, the dry matter determinations on roots were variable and the data have not been presented here. However, it was possible to conclude that the refertilized plants had lower growth rates than the high-nitrogen plants and there was no evidence, from this index, of compensatory growth.

Most of the carbohydrates used during regrowth presumably were supplied from current production while a lesser portion may have come from sucrose which had accumulated previously in the roots. Since sucrose continued to accumulate in the roots of the refertilized plants, current production of carbohydrates apparently exceeded use during this period. And, since the accumulation was at a low rate, it seems probable that under other conditions, more favorable for growth or less favorable for photosynthesis, a net loss of sucrose from the roots would have been observed.

From a practical point of view, these results are helpful in interpretating situations where nitrogen-deficient sugar beet plants experience an increase in the supply of available nitrogen. This may result from the growth of roots into unexplored volumes of soil, from an increase in nitrification, from leaching of surface accumulations of nitrate into the root zone (6), or from fertilization. An important conclusion from this experiment is that an increase in nitrogen supply did not cause a compensatory increase in sucrose yield but, instead, reduced the ultimate yield of sucrose below that of plants which remained at either high or at low nitrogen. Evidently, sugar beet should not be allowed to become nitrogen-deficient in midseason before applying supplemental nitrogen and care should be taken to avoid increases in nitrogen supply during the preharvest period.

Summary

The effects of a period of moderate nitrogen deficiency on the subsequent growth of plants in a high-nitrogen environment was investigated with sugar beet grown under field conditions. Growth of storage roots and of tops increased very soon after nitrogen was applied. During the restitution phase, fresh weight

of tops of the refertilized plants increased at an above normal, "compensatory", rate. However, the absolute increase of total dry matter and of dry matter in tops was less than with the high-nitrogen plants.

Sucrose accumulated more slowly in the storage roots of refertilized plants than in the roots of plants that were maintained at either continuous high or continuous low nitrogen. A net loss of sucrose did not occur indicating that the renewed growth of tops was supported by current photosynthesis and by carbohydrates which had accumulated in the leaves.

Allowing sugar beet to become nitrogen deficient before applying supplemental nitrogen appears to be a poor practice in the commercial production of sucrose.

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