EFFECTS OF RELATIVE HUMIDITY, OXYGEN, AND CARBON DIOXIDE ON INITIATION AND EARLY DEVELOPMENT OF STOLONS AND TUBERS

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Abstract

Russet Burbank potatoes were grown in the greenhouse to explore the effects of soil O_2, CO_2, and relative humidity on tuberization. The composition of the gas phase surrounding the below ground stem and stolons was controlled at various levels. Prolonged levels of CO_2 greater than 5% produced large lenticels and, in combination with high relative humidity suppressed the number of stolons. Oxygen levels of 5% or less in prolonged contact with the stolons and underground portion of the stem were favorable to stem decay by pathogens but did not affect lenticel size. Isolating the stolons in a low relative humidity environment delayed tuber set, but increased the number of tubers per plant. This effect of low humidity suggests that the onset of tuberization involves at least two inductive factors, one of which is not translocated among stolons.

Introduction

It is well known that short days and cool temperatures, <25 C, favor tuber set. Soil conditions may be important also. Growers and field advisors have, for example, occasionally noted increased numbers of undersized potatoes on plants grown in soils that are kept unusually wet—suggesting the soil gas composition may be a factor. This has not been studied in any rigorously controlled manner though there is some evidence that intermittent low oxygen can decrease tuber quality (1, 2, 8). The study reported here obtained information on how the soil gas composition in the zone around the stolons can affect the stolons and tubers.

Materials and Methods

Russet Burbank potatoes were grown from single eyes scooped from seed pieces. They were started in one liter plastic containers. The roots grew through holes (2.5 mm diameter) in the bottom of containers into at least 3 liters of a sand, vermiculite, peat mix containing adequate plant nutrients. The seed piece, a portion of the stem, and the stolons remained in the plastic containers throughout the study (Figure 1). The plant tops, sealed with a

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FIG. 1. The effect of 15% CO_2 on the lenticels of small tubers developing in a plastic container. An airtight lid fits on the front of the container enclosing the tubers for the controlled gas treatments. The edge of the pot holding the roots is visible at the bottom of the picture and some of the lower leaves on the plant are visible at the top.

nontoxic silicone rubber[2] where they grew out of the containers, were subject to the ambient greenhouse environment.

As soon as the plants were well rooted into the soil mix below the container, the vermiculite and sand in the container were washed away leaving only the seed piece, the developing shoot, and a few fine roots that soon dried up. When the shoot was 10 to 15 cm above the container, the gas treatment was started and continued until the end of the study. Using cylinders of commercial grade N_2, CO_2, O_2, and an air compressor to force these gases through mixing manifolds containing needle valves and flow meters allowed the atmosphere in the containers to be controlled as desired. All the gas mixtures were humidified by bubbling through distilled water and fed into each stolon container at a rate of 50 or 100 ml per minute.[3] The containers were painted black on the inside and silver (aluminum) on the outside to stop light penetration and reflect heat.

Supplemental lights were used as needed to maintain at least a 14 h day length. The study period included four winter seasons with one or two experiments per season, starting sometime in December through February and completed no later than early June.

Statistical analysis of the results included standard deviations and student's "t-test" treating individual plants as non-paired samples.

Results and Discussion

Carbon Dioxide and Oxygen

Table 1 presents the number of tubers formed on plants subjected to different gas compositions. Also included are the tubers from two control plants that grew normally in pots without their stolons in the soil-free, atmosphere controlled containers. All of the plants that did not have soil around their stolons eventually set more tubers than the controls. This was true in all similar trials during the four-year study period. The start of tuber set was always delayed by several weeks when there was no soil around the stolons. Consequently, more stolons formed and eventually resulted in many more, but much smaller tubers than those in the control. For example, tubers from a trial using eight plants are shown in Figure 2. Plants 1, 2, and 3 set more tubers in 32% O_2 than plants 4, 5, and 6 with their stolons in 16% O_2 and 16% CO_2. The difference is statistically significant at the 1% confidence level. Plants 4, 5, and 6 had more tubers than the two controls whose stolons grew normally (significant at the 5% level). The small size of the tubers that

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[2] Dow Corning 738 RTV (noncorrosive electronics grade). Trade names and company names are included for the benefit of the reader and do not imply any endorsement or preferential treament of the product listed by the U.S. Department of Agriculture.

[3] This method of controlling the environment around the stolons and developing tubers was suggested by Dr. C.B. Holder, formerly of the University of Idaho.

TABLE 1. — *The tuber set and lenticel development on individual plants as affected by various gas mixtures around dry stolons compared to two normally potted control plants. The balance of the gas mixtures was nitrogen.*

Environment surrounding stolons	Number of tubers per plant	Lenticels
1. Ambient air	16	Inconspicuous
2. 10% O_2, 10% CO_2	18	Moderately prominent
3. 32% O_2, trace CO_2	26	Inconspicuous
4. 16% O_2, 16% CO_2	10	Very prominent
5. 18% O_2, 11% CO_2	8	Prominent
6. 19% O_2, 5% CO_2	11	Noticeable
7. Soil control	3	Inconspicuous
8. Soil control	4	Inconspicuous

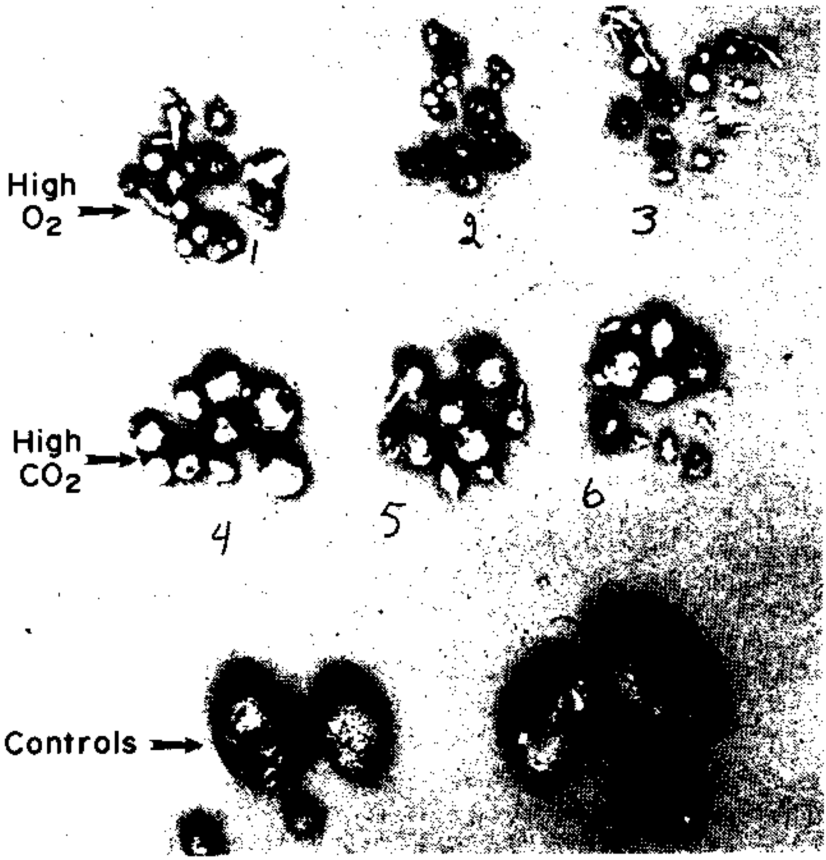

FIG. 2. Tubers set under two different gas treatments (32% O_2, trace CO_2 and 16% O_2) on dry stolons compared to the large tubers that developed in a normal pot culture.

developed in the soil free containers, as compared to the controls, was at least in part due to the delayed tuber set. They may have also been influenced by a lack of calcium, a large part of which is normally obtained from the soil surrounding the tubers.[4] The abnormally large tuber set may be useful to those interested in producing many small tubers per plant to increase germplasm developed by cell culture.

It is well known by growers that wet soil conditions favor large prominent lenticels. It has been supposed that this may be an indicator of O_2 stress since most of the O_2 entry into the tuber occurs via the lenticels (3). However, the lenticel ratings in Table 1 show that lenticel prominence was linked to high CO_2 levels rather than to low O_2 per se. In other tests, oxygen levels as low as 5% did not cause prominent lenticels when the CO_2 was held below 1%. An example of "very prominent" lenticels on small tubers is shown in Figure 1. Also present are callus-like lesions on the stem and roots, similar to those on the lenticels. These lesions are associated with the high CO_2. It was noted that prolonged O_2 levels of 5% or less in the containers favored rotting of the stem, often causing death of the plant.

Table 2 summarizes the results of a trial in which the seed piece and stolon containers were filled from the start with a moist sand, vermiculite, peat moss mixture. There were four plants in each of four treatments. Tuber set in this study was delayed by unseasonably warm greenhouse temperatures in April and May that intermittently rose into the range of 30-35 C. The study was ended when the plants were near bloom and the first tubers in normally potted plants were beginning to form. There were a few small tubers in containers treated with ambient air, or with the 35% O_2, but none in the two 10% O_2 treatments. There were significantly (1% confidence level) fewer stolons in the high CO_2 container and their shapes were strikingly different—short and thickened, Figure 3. The means for the ambient air control and the two treatments with traces of CO_2 were not statistically different. High levels of CO_2 in the soil obviously affected the growth patterns of the potato plants.

TABLE 2. — *The effect of various gas mixtures on the number of stolons that developed before tuber set.*

Gas treatment in the stolon container		Number of stolons per plant	
% O_2	% CO_2	mean	SD
10	15	5.3*	1.0
10	trace	15.0	2.2
35	trace	11.8	3.0
ambient air		13.5	2.5

*Significantly different from the control at the 95% confidence level.

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[4] Dr. R.B. Dwelle, personal communication.

FIG. 3. Short thick stolons and lesions on the stem associated with prolonged high CO_2 levels in the soil.

Relative Humidity Around the Stolon

In some preliminary trials, the containers enclosing the stolons were filled with coarse, dry sand. Tuber set results were similar to those shown in Table 1 and Figure 2 except when the sand was inadvertently moistened. When the relative humidity was high enough to promote the development of fine roots on the stolons, tuber set was not as severely delayed compared to the controls. Consequently, an experiment was carried out to investigate this specific situation. In each of eight containers, when the plants had developed to the point where the gas treatment would normally be imposed, a single stolon was routed down through one of the root holes in the bottom of each container so that it could grow into the soil with the roots. The gas around the stolons in the containers was ambient air. When the plants were about to bloom, aluminum foil cups were shaped around the stems just above four of the containers, filled with peat moss, and kept moist. Eighteen days later all eight plants were removed and inspected. There were no tubers on any of the stolons in the eight containers, and there were no fine roots on these stolons. Each of the stolons in the soil below the containers had a large tuber except one stolon that had not grown well into the soil. All four of the peat moss cups above the containers had roots, stolons, and small tubers.

This suggests that there are at least two inductive factors required for early tuber set. First, the plant must reach some minimum size or stage of growth for tuber set to begin. This stage may be delayed by high temperature. Secondly, the relative humidity must be high enough around individual stolons to develop fine roots, though root initiation may be only casually related to tuber set. Because no tubers developed on the dry stolons between the tubers in the soil and those higher up on the stem in the moist peat moss, the factor linked to high humidity is evidently not translocated among stolons.

Tubers do not set on rooted cuttings from plants that have not themselves set tubers until the cuttings grow into plants of normal tuber setting size. However, when cuttings are rooted from a plant that has tubers, some of the cuttings may set tubers while still very small, Figure 4. This is evidently a carry-over of the "first inductive factor" tuber set requirement. When the relative humidity around the plant stem is raised high enough to produce root initiation, the second inductive factor is satisfied and tubers form. When tuber set is prevented on large plants by dry stolons and high temperatures, "aerial" tubers may develop as swellings of the stems. As this extreme condition approaches, tubers may also form on the stolons in spite of low humidity. This, like normal tuber set, is probably temperature dependent.

Hormone levels, conducive to tuber initiation, are an ongoing topic in the current literature. Studies previous to 1978 were reviewed by Moorby (8) who concluded, "This mass of apparently contradictory evidence illustrates the futility at the present time of trying to give any definitive explanation of the mechanism of tuber initiation." A number of papers have since been published (3, 5, 6, 7, 9, 10) exploring the effect of levels and ratios of starch, cytokinins, ethylene, gibberellic acid, auxins, and abscisic acid to tuber initiation, but Moorby's conclusion still stands.

FIG. 4. Cuttings from a tuber producing plant that developed, in addition to roots, small tubers at stem nodes below the surface of the rooting media.

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