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Potato Tubers and Soil Aeration[1]

J. W. Cary[2]

ABSTRACT

Potato plants are more sensitive to soil oxygen stress than many other common crops. Some recent literature suggests this may be due to a relatively high oxygen requirement for tuber growth, rather than a greater requirement for the roots per se. Consequently, the oxygen consumption of growing potato tubers (*Solanum tuberosum* cv. Russet Burbank) was measured in the field on a Portneuf silt loam (coarse-silty, mixed, mesic Durixerallic Calciorthid). Typical rates were 15 $\mu g\ O_2\ cm^{-2}\ hr^{-1}$. A simple method for measuring soil oxygen diffusion rates in the laboratory was then devised, utilizing an oxygen meter and a stream of N_2 gas. Soil conditions such as texture, bulk density, compaction around expanding tubers, oxygen sinks and water contents were studied with respect to their relative effects on limiting oxygen uptake by tubers. The minimum soil oxygen diffusion coefficient required for adequate tuber aeration is quite sensitive to the soil respiration rate and the depth of soil covering the tubers. Water contents of "field capacity" or a little wetter were found to not necessarily inhibit tuber aeration in loamy sand, silt loam, and silty clay soils provided the bulk densities were not excessive; i.e., greater than 1.6 or 1.7 $Mg\ m^{-3}$ in the silt loam. Reduced aeration due to compaction around growing tubers is a possibility in the silty clay, but probably not in well drained silt loam or loamy sand. The criteria for a minimum acceptable soil oxygen diffusion coefficient must be based on tuber periderm permeability, soil ethylene generation, and other anaerobic soil reactions, as well as tuber respiration per se.

Additional index words: **Oxygen diffusion, Ethylene, Soil compaction, Soil respiration.**

RECENT literature concerning the aeration of potatoes has been briefly reviewed by Holder and Cary (1984). It appears that the tubers may be more sensitive to oxygen stress than the roots. As a rule, for good production of many common crops, the soil pore size distributions should be such that the soil drains rapidly enough to provide an air filled pore volume fraction of at least 0.15 within an hour or two following rain or irrigation (Cary and Hayden, 1973). For potatoes, the oxygen diffusion rate as measured with platinum electrodes should be at least 0.5 $\mu g\ cm^{-2}\ min^{-1}$ (Jackson, 1962). Though these general criteria may be largely complied with, even on well-managed clay soils, potatoes (*Solanum tuberosum*), and particularly the Russet Burbank variety, are generally not grown on soils with textures finer than silt loam. The coarse textured, sandy soils are preferred because tuber quality is better. Perhaps this sensitivity to texture results from differences in aeration.

The oxygen relations of potato tubers may be quite different than those of the roots. The tubers create a relatively large oxygen sink. Moreover, their surfaces are not uniformly permeable to oxygen for most of it must enter through the lenticels. As the tubers grow, soil is pushed aside and, since the soil must be kept moist to achieve good tuber quality, there is potential for compaction at the soil-tuber interface. The purpose of the work reported here was to learn in more detail how this system operates, i.e.,

a) Measure the oxygen uptake by tubers under field conditions,
b) Determine the relative importance of lenticel spacing and soil compaction around the tubers in limiting oxygen availability,
c) And find the values of soil variables such as water content, bulk density, respiration, and texture that can limit tuber oxygen uptake.

MATERIALS AND METHODS

The oxygen uptake of potato tubers was measured in the field on a plot of Portneuf silt loam (coarse-silty, mixed, mesic Durixerallic Calciorthid). The plants, under the management of Dr. Dale Westermann, received current state-of-the-art best management for water, fertility, insect and disease control. "Pint" size plastic freezer bags were used in measuring the oxygen uptake. A 24 cm^2 rectangular section was cut from one side of each bag. The normal bag opening was gathered around a small glass tube and clamped to make an air tight seal. The soil was brushed away from the top of nine growing tubers without otherwise disturbing them. The exposed skin was rinsed with clean water and gently dried with absorbent paper tissue. The rectangular opening in the plastic bag was then placed over the exposed surface of the potato and held in place with a nontoxic electronics grade silicon rubber cement (Dow Corning 738 RTV)[3]. The soil was replaced leaving only the open end of the glass tube exposed. A rubber septum was placed on the glass tube so that gas samples could be drawn from the plastic bag with a needle and syringe. Enough cotton was placed in each bag so that they would hold 100 to 200 mL of air under the weight of the soil. Twenty-milliliter gas samples were taken (daily) from each bag and the amount of oxygen measured to the nearest 0.2% with a Beckman model C2 meter. This was compared to the oxygen in a reference bag that was in the soil near tubers but not attached to any of them. The difference between oxygen in this control bag and the bags attached to tubers varied from a few tenths of a percent to nearly 2% in some cases. At the end of the study, the tubers were brought into the lab with the bags still attached and tested for leaks. Two had developed leaks and the data obtained from them were discarded. The remaining bags were removed from the tubers, the rectangular holes covered with "duct" tape, and 300 mL of N put in the bags. This gas was sampled over the next few hours to determine the increase in oxygen and to subsequently calculate each bag's oxygen diffusion coefficient. This provided sufficient information to calculate the diffusion of oxygen from the soil into the bags when they were attached to the tubers. Since the oxygen content in the bags did not fluctuate very much during the day, steady state was assumed and the amount of oxygen that diffused into each bag from the soil was taken to be a good estimate of the uptake through the 24 cm^2 of tuber surface that each bag covered. Note that the humidity inside the bags must be kept high during the laboratory measurement of diffusion coefficients because the oxygen permeability increases as the plastic dries out.

Oxygen diffusion coefficients were measured over a range of water contents in the laboratory on three different textured soils packed to various bulk densities. This was done in a specially fabricated "soil oxygen diffusion cell." It was made

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[2] Soil scientist, Snake River Conservation Research Center, Kimberly, Idaho.

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[3] Trade names and company names are included for the benefit of the reader and do not imply an endorsement or preferential treatment of the product listed by the USDA.

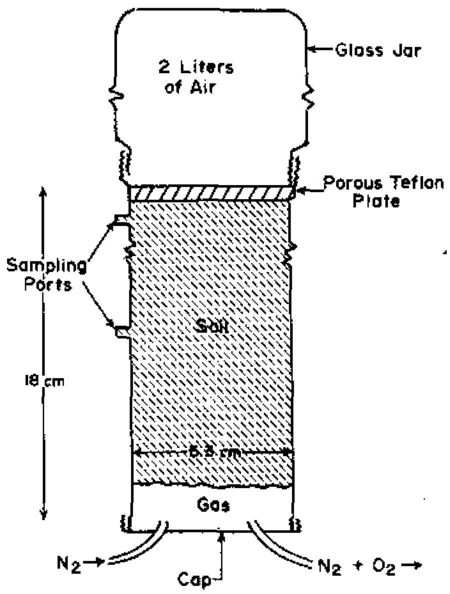

Fig. 1. Cross section diagram of the oxygen diffusion cell.

with a column closed on one end and with a porous teflon plate on the other end, Fig. 1. The end with the plate opened into a glass jar that held approximately 2 L of air. The porous teflon plate which separated the soil sample in the column from the reservoir of air was hydrophobic and so held the moist soil in place without creating a significant barrier to gas diffusion. The length of the soil samples in the columns could be varied from 1 to 16 cm by moving the porous plate. Nitrogen gas was passed through the closed end of the column over the surface of the soil sample at a rate of 40 mL min^{-1} and then analyzed for oxygen to the nearest $\mu L\ L^{-1}$ on a volume basis as described previously (Cary and Holder, 1982). Thus, the maximum rate of oxygen diffusion through the soil column from the air reservoir to the space at the closed end of the column was measured. Septum covered ports were provided along the sides of the soil column so that gas samples could be removed from oxygen measurements.

Oxygen measurements with this "diffusion cell" were used to find soil oxygen diffusion coefficients using a simple iterative process with basic language on a desk size personal computer. The problem was set up as cm^3 elements of soil between the air space at the closed end of the column and the soil-teflon porous plate interface. The oxygen flux through each element was accounted for in two steps expressed in the computer program as

$$J_i = D * (C_i - C_{i-1}) * l^{-1} \text{ and} \quad [1]$$

$$C_i = C_i + [J_{i+1} - J_i - (l * R)] * dt/V, \quad [2]$$

where J_i ($cm^3\ cm^{-2}\ h^{-1}$) is the oxygen flux across the boundary between element i and element i−1 with i being any element number starting with 1 next to the N_2 gas-soil interface, and increasing consecutively with each cm of soil toward the teflon plate. The time increment dt (h) was chosen small enough to provide stability, i.e., generally 10 to 60 s depending on the starting conditions. The remaining symbols are defined as: C, the volume fraction of oxygen in the gas phase; R, the soil oxygen consumption rate $cm^3\ cm^{-3}\ h^{-1}$; and V, the volume fraction of the soil gas phase (required because values of D, R, and J were based on the combined volume of all three soil phases). Since the elements were chosen as cm^3, $l = 1$ cm. Interpolation with this simple model gives the oxygen diffusion coefficient, D, for the soil. The steady state oxygen flux across the N_2 gas-soil interface at the capped end of the column must be measured and the oxygen concentration in the glass jar on the opposite end of the column must be known. The soil respiration rate and the soil air-filled pore space must also be given. The model was used to develop Fig. 2–4 in this paper. Other uses are the prediction of oxygen fluxes and concentrations under transient conditions at any point in the soil with constant or variable diffusion and respiration rates distributed in any pattern throughout the soil. The program is available upon request.

Table 1. Oxygen use, $\mu g\ cm^{-2}\ h^{-1}$, of three potato tubers growing in the field under high fertility conditions. Confidence in the values is $\pm$ 2 $\mu g\ cm^{-2}\ h^{-1}$.

Date	Time	Tuber no. 1	2	3
10 August	am	–	11	17
11	pm	12	15	15
12	am	–	15	12
	pm	12	15	12
15	am	16	19	14
16	pm	12	15	12
17	pm	8	15	12
31	pm	10	11	12
1 September	pm	6	13	11
2	pm	4	8	4
6	am	8	8	11
8	pm	12	15	14

RESULTS AND DISCUSSION

Typical oxygen uptake rates measured in the field are shown for three growing tubers in Table 1. The experimental uncertainty in these values is about ± 2 $\mu g\ cm^{-2}\ h^{-1}$. The data suggest a decrease in oxygen uptake on 2 September. The end of August through 2 September was a hot dry period and the soil water matric potential at the 15 cm depth fell to -180 kPa which is near the limit of water extraction that should be allowed for the Russet variety on the Portneuf silt loam. The plants were irrigated on 3 September, the weather cooled off and the oxygen uptake recovered to previous rates. Note, however, that so little is known about the relation between tuber oxygen uptake and potato plant water potentials under field conditions that no conclusions should be drawn from these preliminary data other than soil conditions should be such that at least 15 $\mu g\ O_2\ cm^{-2}\ h^{-1}$ can reach all tuber surfaces. This is in general agreement with data reported by Wigginton (1973) assuming one lenticel per cm^2 of tuber surface. It is only about one-third the rate suggested for potatoes when platinum wire electrodes are used to characterize the soil oxygen status (Holder and Cary, 1984); however, as will be pointed out, there are some additional aspects with respect to different geometries of the oxygen sensors and with the tuber's periderm permeability that must be considered when comparing these two methods.

The size of the soil oxygen diffusion coefficient required to provide 15 μg of $O_2\ cm^{-2}\ h^{-1}$ to the tuber surface depends on how deep the tuber lies below the soil surface. This is shown in Fig. 2 assuming a soil respiration rate of 2.5 $\mu g\ cm^{-3}\ h^{-1}$.

Table 2 shows some measured oxygen diffusion rates under relatively low air-filled porosities. The water contents in all cases were field capacity or wetter. Presumably for any given soil there is a single valued

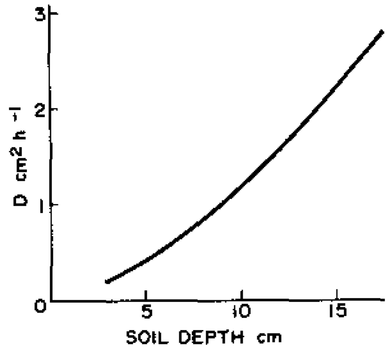

Fig. 2. The relation between tuber depth and the minimum oxygen diffusion coefficient required to transport 15 μg O_2 cm^2 h^{-1} when the soil respiration rate is 2.5 μg O_2 cm^{-3} h^{-1}.

functional relationship between air filled porosity and gas diffusion coefficients, see for example Sallam et al. (1984). This allows one to predict how the gas diffusion coefficients will change with water content. In the case of the Portneuf silt loam (Table 2), there is indeed a relation between oxygen diffusion and air-filled pores until the bulk density rises into the range of 1.7 or more. Normal field upper root zone bulk density for this soil is generally less than 1.45 Mg m^{-3}, but it can rise to 1.7 where compaction from wheel traffic occurs. At this high density many of the air-filled pores are evidently discontinuous (see also results reported by Currie, 1984).

The other obvious anomaly in the data shown in Table 2 occurs in the silty clay soil. The large oxygen diffusion coefficient of 10 cm^2 h^{-1} was due to very fine cracks that developed as the soil drained. Even hairline cracks are extremely effective in promoting oxygen diffusion in wet soil. They are also difficult to describe quantitatively and that is why only a few diffusion coefficient values for low soil bulk densities are shown in Table 2, i.e., the low density samples tended to develop cracks soon after wetting and their diffusion coefficients were relatively large and erratic.

Table 2. Measurements of soil oxygen diffusion coefficients as affected by bulk density, volumetric water, and soil air contents.

Air content	Diffusion coefficient	Bulk density	Water content
m^3/m^3	cm^2/h	Mg/m^3	$m^3/m^3/h$
	Silt loam		
0.17 ± 6%	7.33 ± 9%	1.13 ± 3%	0.40 ± 3%
0.11	4.06	1.43	0.35
0.10	1.09	1.80	0.22
0.08	0.06	1.78	0.28
0.08	5.85	1.47	0.37
0.08	5.10	1.47	0.37
0.07	4.87	1.44	0.39
0.07	3.25	1.44	0.39
0.06	2.53	1.47	0.39
0.05	0.03	1.75	0.31
0.02	1.60	1.47	0.43
0.02	0.01	1.82	0.31
	Silty clay		
0.23	4.80	1.12	0.36
0.17	10.00	1.20	0.38
	Loamy sand		
0.16	5.43	1.46	0.29
0.15	2.31	1.42 1.42	0.31

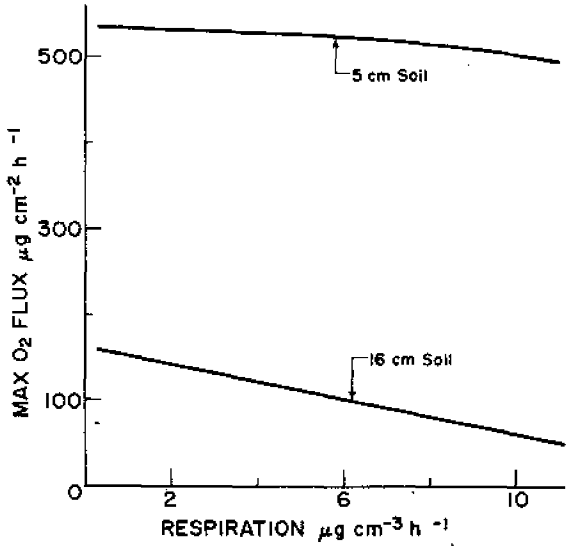

Fig. 3. The relationship between the maximum rate of oxygen diffusion through either 5 or 16 cm of soil as a function of soil respiration rates. The soil oxygen diffusion coefficient is assumed to be a constant 10 cm^2 h^{-1}.

Soil respiration can have a large effect on soil oxygen flux. In Fig. 3 the maximum rates of oxygen diffusion from the surface to the 5 and 16 cm soil depths are shown as a function of respiration rates. The oxygen diffusion coefficient was assumed to have a constant value of 10 cm^2 h^{-1}. The soil respiration rate can be quite dynamic. It rises abruptly when water is added to dry soil and then gradually declines. It is stimulated by tillage and certainly by the incorporation of fresh organic matter (Smith, 1974; Knapp et al., 1983). Even the soil's fertility and small changes in water content may effect it. The respiration rates used to find the oxygen diffusion coefficients in Table 2 were 2, 2.5, and 3 μg cm^{-3} h^{-1} for the loamy sand, the silt loam, and the silty clay, respectively, based on measurements of oxygen consumed by moist 100 g samples during the 1st week after wetting. The large effects that respiration may have on oxygen transfer through soil was demonstrated in the laboratory with the soil oxygen diffusion cell. The results are shown in Table 3. The addition of sucrose completely stopped the diffusion of oxygen through 12 cm of moist soil for at least 3 days even though they were only wet to "field capacity". These decreases in diffusion transport may result from the growth of organisms that fill pore space as well as create high respiration rates.

The effect of lenticel density on limiting oxygen uptake was also investigated with the soil column dif-

Table 3. Oxygen diffusion, μg cm^{-2} h^{-1}, through 12 cm of soil packed to bulk density of 1.45 Mg m^{-3} and wet to field capacity with water containing 6% sucrose.

Days after wetting	Loamy sand	Silt loam
1	16.0 ± 5%	0
3	9.1	0
4	0	–
6	0	37.1
10	15.2	–
13	--	93.6
20	84.4	--

fusion apparatus. The soil surface at the closed end of the column was covered with a layer of paraffin wax. One to three holes, each 1 mm in diameter, were punched through the paraffin to simulate the soil tuber interface. This seldom decreased the oxygen flux by more than 25%. On the other hand, when the soil was covered with a layer of silicone rubber cement and one or two small holes made through it, the passage of oxygen sometimes dropped by 90%. Evidently the paraffin shrinks away from the soil surface during cooling, leaving a thin gap between the soil surface and the paraffin. The oxygen concentration can then build up in this space and facilitate relatively rapid diffusion through the hole or holes in the paraffin. It seems to me that the potato tuber-soil interface probably behaves more like the paraffin than the silicone rubber layer because the tuber is rigid and shrinks a bit during the day as water stress develops in the plant canopy. If so, the lenticel's size and distribution may not be too important a factor in limiting oxygen uptake but their permeability to oxygen must be considered. Burton (1965) reported measurements of oxygen permeability suggesting a drop of 4% in the oxygen concentration across the periderm is required to drive the diffusion of 15 $\mu g\ cm^2\ h^{-1}$ into the tuber.

It is possible that meeting an oxygen demand of 15 $\mu g\ cm^{-2}\ h^{-1}$ at the soil tuber interface may not always insure proper growth. Incubation of the Portneuf silt loam has shown that when the oxygen level drops below 2%, ethylene forms (my unpublished data). There is some information in the literature that suggests ethylene affects tuber development (Campbell and Moreau, 1979; Catchpole and Hillman, 1969). Thus, criteria for proper tuber aeration may require that the oxygen concentration in the layer of soil surrounding the tuber be kept high enough to reduce ethylene formation as well as to meet the oxygen demand of the tuber.

Figure 4 may be used to assess the impact of such a requirement. In the case of the Portneuf silt loam Fig. 2 shows that the minimum value for the oxygen diffusion coefficient that will meet the tuber requirements at a depth of 16 cm is 2.5 $cm^2\ h^{-1}$. Fig. 4 shows

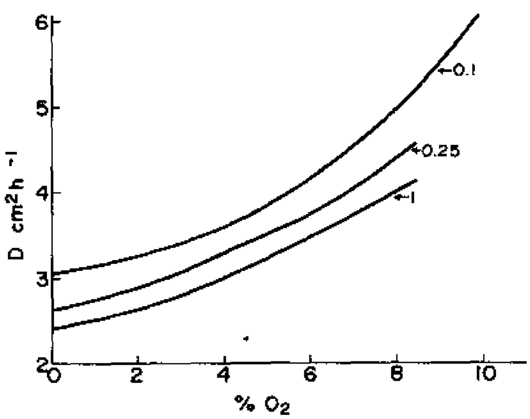

Fig. 4. The relation between the soil oxygen diffusion coefficient and the oxygen concentration around a potato tuber at the 16 cm soil depth when the soil respiration is 2.5 $\mu g\ cm^{-3}\ h^{-1}$ and the tuber uptake is 15 $\mu g\ cm^2\ h^{-1}$. The parameters on the three curves are the ratio of the oxygen diffusion coefficient in first cm of soil surrounding the tuber to the oxygen coefficient of the remaining 15 cm of soil.

that this would insure an oxygen level of only 1% in the soil surrounding the tuber. Therefore, the minimum diffusion coefficient should be at least 2.7 to hold the oxygen above 2% if one wishes to avoid ethylene production around the tuber in this particular soil. However, due to periderm permeability, one needs at least a 4% oxygen atmosphere surrounding the tuber. The periderm permeability then becomes the critical factor, requiring a soil diffusion coefficient of at least 3 $cm^2\ h^{-1}$, according to Fig. 4.

Figure 4 also shows the relative effects of compaction in the first centimeter of soil surrounding the tuber. If compaction or puddling due to tuber growth decreased the oxygen diffusion coefficient in this first centimeter of soil by a factor of 10, then the diffusion coefficient in the remaining 15 cm of soil should be at least 3.5 to maintain a 4% oxygen atmosphere around the tuber. In soils where ethylene production occurs at oxygen concentrations above 4%, the minimum permissible level around the tuber would be raised accordingly. Other anaerobic soil reactions may also need to be considered.

The potential for soil compaction to restrict oxygen around the tuber was studied with the soil oxygen diffusion cell in the laboratory. Enough water was added at the closed end of the column to wet about 10 cm of soil. The maximum oxygen flux from the air reservoir through the soil was then measured. The cap on the closed end was removed and a few milliliters of water added so the soil surface could be puddled. After 3 or 4 h the oxygen flux was measured again. Typical results are shown in Table 4. The flux across the puddled silty clay interface remained zero until drainage into dry soil ahead of the wetting front caused the puddled surface to crack. If the cracks were then sealed with a bit of grease, the oxygen flux remained very small for at least 24 h. It appears that packing around the tubers is not likely to be a major problem in well-drained silt loam and sandy soils but it could create oxygen or ethylene stress in clay textured soils.

In closing, note that most of the examples presented here are for steady state. Soil oxygen changes in response to transient conditions such as irrigation or rain are often relatively slow, at least below the wetting front. For example, a tuber's "high" rate of oxygen use (15 $\mu g\ cm^{-2}\ h^{-1}$) consumes only about 0.01 mL of oxygen gas per hour. Viewing this as a decrease in concentration of 1% oxygen per milliliter of soil air per hour gives one some feeling for the potential rates of oxygen depletion and emphasizes the importance of air-filled pore space in forestalling the onset of anaerobic conditions.

Table 4. The effect of puddling at the soil-tuber interface on the amount of oxygen that can diffuse across the interface when the soil is in a wetting cycle.

Soil texture and depth of wetting	Bulk density	Water content	Oxygen flux
	Mg/m^3	$m3/m^3$	$\mu g/(cm^2\ h)$
Loamy sand, 9 cm	1.41 ± 3%	0.34 ± 3%	92.6 ± 5%
After puddling			79.3
Silt loam, 10 cm	1.44	0.46	78.9
After puddling			37.1
Silty clay, 14 cm	1.12	0.39	71.5
After puddling			0

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