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STUDIES ON THE STORAGE OF POTATOES

III. THE COMPOSITION OF THE ATMOSPHERE IN A POTATO CLAMP

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(With One Text-figure)

The atmosphere in a potato clamp would be expected to differ in composition from the external air, because oxygen is continually being removed and CO_2 added by the respiration of the potato tubers. This might be a factor determining the storage behaviour of the potatoes, for the starch-sugar relationship and sprouting are both dependent on CO_2 concentration (Barker, 1936), and sprouting is also affected by oxygen concentration (Thornton, 1939). Apart from a reference by Barker & Wallace (1946) to unpublished work which showed that the CO_2 concentration in the atmosphere of a clamp of normal construction lay between 0·1 and 0·3%, there appears to be no information on the composition of the clamp atmosphere. The work described in this paper was therefore undertaken to find out how the concentrations of CO_2 and oxygen change throughout the storage period. As ethylene, in a concentration of 0·1% or less, has been shown to retard sprouting (Huelin, 1933), some determinations of the concentration of unsaturated compounds in the clamp atmosphere were also included.

METHODS

The clamp used had been constructed in several sections, isolated from each other by partitions of sisalkraft paper supported on wire-mesh and covered with straw, for testing various treatments intended to control sprouting. There was a central section about 5 yards long, kept as untreated control. The same clamp was used for an investigation of temperature changes during storage reported in a previous paper (Crook & Watson, 1950), where details of the history of the clamp and its dimensions are given. The potatoes were of the Majestic variety. The clamp was covered with earth on 7 December 1942, and the earth cover was continuous over the whole clamp without any straw ventilators at the ridge. From mid-February onwards there was a rapid rise in the temperature of the potatoes caused by bacterial rotting following blight infection. Eventually the rotting of the tubers proceeded so far that the clamp collapsed on 27 April 1943.

On 19 October 1942, soon after the clamp was made and while it was still covered only with straw, an iron tube of ½ in. internal diameter was introduced into the central section to allow samples of the clamp atmosphere to be withdrawn for analysis. The open inner end of the tube was placed on the middle line of the clamp about 15 in. below the ridge. The outer end was kept closed by a tightly fitting sealed glass tube and a rubber connexion. To withdraw a sample of the internal atmosphere for analysis, the glass tube was removed, and the iron tube was immediately connected to a glass bottle previously evacuated to a pressure of less than 0·01 mm. mercury by means of a rotary pump. By opening a screw clip, the bottle was filled with air from inside the clamp, and was then sealed again. The end of the iron tube communicated with the external air only for a moment while the bottle was being connected to it, and it was assumed that the air in the tube was in equilibrium with that inside the clamp. Three samples were taken on each occasion, two into litre bottles for estimation of CO_2 and unsaturated compounds, and one into a 250 ml. bottle for the determination of oxygen. Sampling began on 7 December 1942, just before the earth cover was applied, and continued usually at weekly intervals until 20 April 1943.

Oxygen in the gas samples was estimated by the method of Van Slyke & Sendroy (1932), in which oxygen is absorbed in alkaline hyposulphite solution and the diminution of pressure measured. CO_2 was estimated on another air sample by the method of Pettenkofer as modified by Letts & Blake (see Lunge & Keane, 1931). The bottles used for these samples were coated internally with paraffin wax. A known volume of standard baryta was introduced, the stopper replaced, and the bottle was allowed to stand overnight for absorption of CO_2 to be completed. The excess baryta was then titrated with standard acid using phenolphthalein as indicator. A similar method was used to determine unsaturated compounds. A known volume of 0·01 N-bromine in 2% KBr solution was pipetted into the bottle, which was allowed to remain overnight to complete the reaction of the unsaturated compounds with the bromine. A blank determination was carried out on laboratory air to allow for small losses of bromine by volatilization. The excess bromine was estimated by adding KI solution and titrating the liberated iodine with standard thiosulphate. Pyrex bottles without

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paraffin coating were used for this estimation, to avoid absorption of bromine. Unsaturated compounds were expressed as ethylene, though their actual nature is unknown.

RESULTS

The results of the gas analyses are given in Table 1; concentrations are expressed as percentage by volume. After the first ten sampling occasions, the determinations of oxygen were abandoned, because it became apparent that the sum of CO_2 and oxygen concentrations, and hence also the nitrogen concentration, was constant within the limits of estimation. This implies that the respiratory quotient of tion rate of the potatoes induced by rising temperature (Table 1), but there were wide fluctuations from a smooth trend. Comparison with anemobiagraph charts suggested that the fluctuations of CO_2 concentration were correlated with changes in wind velocity. Thus, the high CO_2 concentrations on 18 January and 15 March (Table 1) followed windless periods, while the low values on 25 January, 1 February and 3 March followed periods of high wind. One obvious exception occurred on 15 February when high wind apparently did not reduce CO_2 concentration. At this time the direction of the wind was W.N.W., that is to say, it was blowing along the length of the clamp which was orientated in the direction W.N.W.–E.S.E.

Table 1. *Composition of the clamp atmosphere*

Date	Concentration (%)				Temperature (° C.)*	Wind†		
	CO_2	O_2	CO_2+O_2	Ethylene		Direction	Velocity (m.p.h.)	Component normal to clamp face (m.p.h.)‡
1942								
7 Dec.	0·03	21·0	21·0	—	—	—	—	—
8 Dec.	0·18	20·7	20·9	—	8·2	S.W.	3	3
21 Dec.	0·13	20·9	21·0	—	7·9	S.	9	8
1943								
4 Jan.	0·20	20·8	21·0	—	9·1	N.W.	1	0·5
11 Jan.	0·10	20·9	21·0	—	11·0	S.E.	3·5	1·5
18 Jan.	0·59	20·3	20·9	0·02	11·0	—	0	0
25 Jan.	0·06	20·9	21·0	0·01	12·1	S.S.E.	12	8·5
1 Feb.	0·06	20·9	21·0	0·004	8·8	S.S.W.	11	11
8 Feb.	0·06	20·8	20·9	0·009	9·9	S.	3	3
15 Feb.	0·21	20·5	20·7	0·025	9·1	W.N.W.	19	0
22 Feb.	0·27	—	—	0·006	14·2	W.	1	0·5
3 Mar.	0·15	—	—	0·005	19·6	E.N.E.	15	10·5
8 Mar.	0·29	—	—	—	19·6	S.S.W.	4	4
15 Mar.	0·65	—	—	—	21·3	—	0	0
22 Mar.	0·21	—	—	0·006	24·0	N.N.E.	2	2
5 Apr.	0·27	—	—	—	23·2	S.W.	10	9
12 Apr.	0·23	—	—	—	23·8	W.S.W.	6	4
20 Apr.	0·86	—	—	—	35·6	S.W.	1	1

* Temperature at time of sampling on centre line of clamp 9 in. from ground.
† Mean for 3 hr. period prior to time of sampling, estimated from anemobiagraph chart.
‡ To nearest 0·5 m.p.h.

the tubers was very close to unity, indicating that the principal respiratory substrate was carbohydrate, a conclusion in accordance with expectation.

Oxygen concentration varied only between 21·0 and 20·3 %. This range is too small to have any physiological significance.

The sample taken on 7 December, immediately before the earth cover was applied, had a CO_2 concentration of 0·03 %, equal to that of the external atmosphere. On the following day it had risen to 0·18 %, because of the restriction on gas exchange between the interior of the clamp and the external air due to the presence of the earth cover. Subsequent analyses gave values ranging from 0·06 to 0·86 %. There is an indication of a steady rise that can reasonably be attributed to increasing respira-

The effect of wind in reducing the CO_2 concentration inside the clamp is presumably due to dilution of the internal atmosphere with air that has passed through the clamp covers from outside. If this is so, only the component of wind velocity normal to the faces of the clamp can be effective in reducing the internal CO_2 concentration, for the component along the length of the clamp cannot cause air movement through the clamp covers. This explains why, in the period before the sampling on 15 February, the wind of high velocity blowing along the length of the clamp, that is, with zero velocity normal to the clamp face, did not cause a fall in internal CO_2 concentration.

A regression analysis was made to see how much of the variation of CO_2 concentration could be accounted for by the temperature and wind factors.

The temperature chosen was that at the centre of the clamp (position *L*, Crook & Watson, 1950) at the time when the gas samples were taken; temperature varies with position in the transverse section of the potato heap, but temperatures at different positions are highly correlated in their time trends. Wind velocity and direction were read from the charts of an anemobiagraph situated at Rothamsted laboratory, about ¾ mile from the clamp; eye estimates were made of mean velocity and direction over a period of 3 hr. before each time of sampling. This period was chosen arbitrarily, because nothing was known about the rate of equilibration of CO_2 concentration after a change in the wind conditions. The temperature, wind velocity and direction for each sampling time, excluding the first which preceded the application of the earth cover, are given in Table 1, together with the calculated magnitude of the component of wind velocity normal to the clamp face. Northerly and southerly components were not distinguished by opposite signs; the components had a southerly direction on eleven out of the seventeen sampling occasions. When CO_2 concentration was plotted against the normal component of wind velocity, it appeared that the relation was not linear, and this was allowed for by including a quadratic wind velocity term in the regression. The analysis therefore consisted in fitting a multiple regression of CO_2 concentration on temperature and on the normal component of wind velocity and its square.

The calculated regression coefficients were:

On temperature: $0{\cdot}018 \pm 0{\cdot}0043$ % CO_2 per ° C.

On normal wind velocity: linear, $-0{\cdot}098 \pm 0{\cdot}035$ % CO_2 per m.p.h.; quadratic, $0{\cdot}0069 \pm 0{\cdot}0033$ % CO_2 per m.p.h.^{2}.

The temperature and linear wind velocity terms were highly significant, but the quadratic wind velocity term just failed to reach significance at the 5 % level. The multiple regression accounted for 64 % of the variance of CO_2 concentration. Fig. 1 shows that values of CO_2 concentration calculated from the regression equation for each sampling occasion fitted the observed values reasonably well. Fig. 1 must not be taken as an accurate picture of the variation of CO_2 concentration in the clamp atmosphere with time, because the samplings were made at long intervals. A continuous record of CO_2 concentration would probably show wide fluctuations within short periods, corresponding to the changes in wind.

The negative linear and positive quadratic regression coefficients on normal wind velocity show that the reduction of CO_2 concentration caused by unit increase in velocity was smaller at high than at low velocities. It is probable that this curvature of the relation between CO_2 concentration and wind velocity is an expression of the fact that there is a lower limit to the CO_2 concentration inside the clamp, namely that of the external atmosphere, 0·03 %, and that, as wind velocity increased, the CO_2 concentration approached this value asymptotically. Accordingly, the parabola defined by the quadratic regression can only be a rough approximation to the actual relation between CO_2 concentration and wind velocity.

As respiration rate increases exponentially with rise of temperature it seems unlikely that the CO_2 concentration could in fact be linearly related to temperature. However, an attempt to detect any departure from linearity by including a quadratic temperature term in the regression equation was unsuccessful; the quadratic coefficient was smaller than its standard error, and hence was far from significant. The inadequacy of the fitted regression equation to represent accurately the relation of CO_2 concentration to wind velocity and temperature is illustrated by the impossible negative sign of the value for 21 December calculated from the regression equation (Fig. 1). Nevertheless, the analysis is sufficient to show that there was a close dependence of CO_2 concentration on these two factors.

Unsaturated compounds in the clamp atmosphere were determined on only eight of the eighteen sampling occasions; the concentration, expressed as ethylene, ranged from 0·004 to 0·025 % (Table 1). The later values tended to be lower than the early ones suggesting that, if temperature had any effect, it depressed the 'ethylene' content. Both CO_2 and 'ethylene' concentrations were higher on 18 January and 15 February than on the three intermediate sampling dates (25 January, 1 and 8 February), but otherwise there is little evidence of a correlation between CO_2 and ethylene such as would be expected if both were similarly affected by wind. Partial regression coefficients of 'ethylene' concentration on temperature and normal wind velocity were calculated, but neither of them was significant; their values were:

On temperature, $-0{\cdot}00062 \pm 0{\cdot}00049$ % 'ethylene' per ° C.

On normal wind velocity, $-0{\cdot}00049 \pm 0{\cdot}00041$ % 'ethylene' per m.p.h.

It does not necessarily follow that 'ethylene' concentration was independent of temperature and wind velocity. The failure to demonstrate a correlation may merely be a consequence of the small number of observations.

DISCUSSION

The highest CO_2 concentration recorded in the clamp atmosphere was 0·86 %. This occurred at a time when bacterial rotting of the tubers following blight infection had reached an advanced stage; the temperature had risen to 36° C., and because of this and the presence of bacterial infection, the rate of CO_2 production must have been far greater than in a clamp of healthy potatoes. The clamp was completely covered with soil with no straw ventilators. The wind velocity normal to the clamp face in the period before the time of sampling was only 1 m.p.h. All these circumstances suggest that the CO_2 concentration at this time was near the maximum, and 18 January was 11° C., and as similar temperatures were recorded in clamps of healthy tubers in April 1944, it is likely that CO_2 concentrations above 0·3 % may occur even in the absence of bacterial infection. Values below the lower limit of 0·1 % given by Barker & Wallace occurred on three occasions. Two of them, on 25 January and 1 February, were attributable to high wind, and there had been moderate

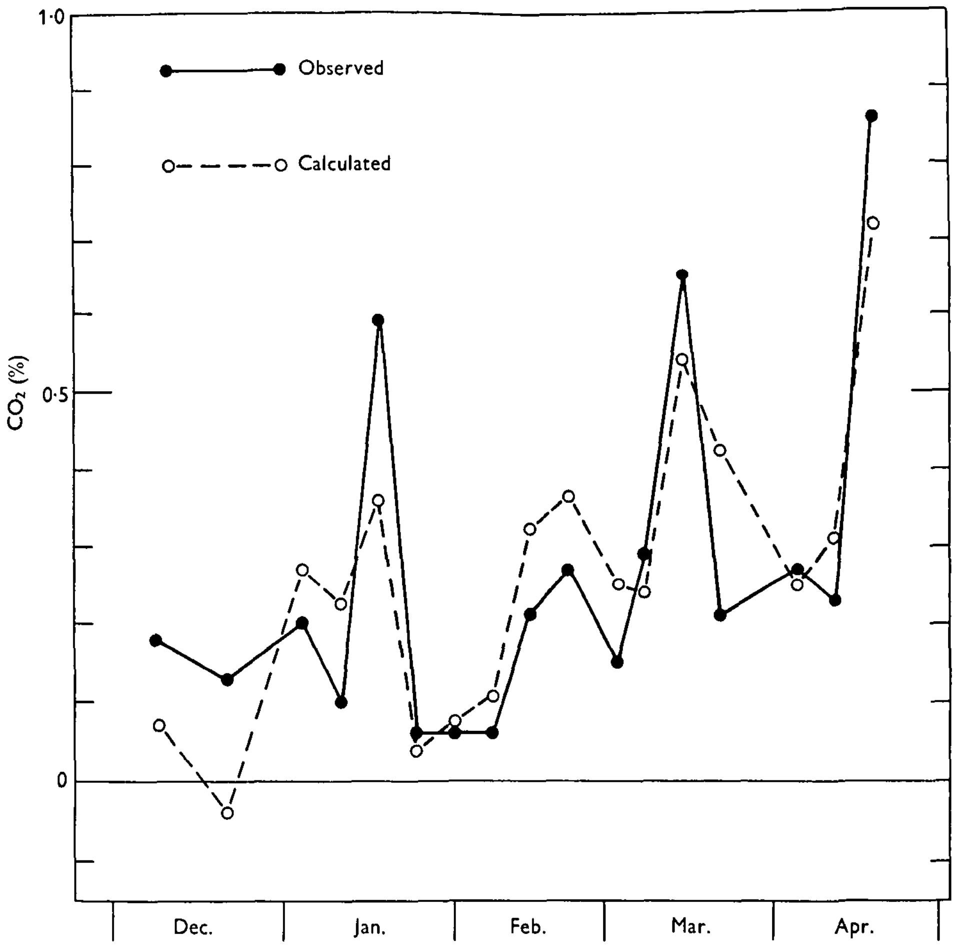

Fig. 1. Observed values of CO_2 concentration in the atmosphere of the clamp in 1942–3, and values calculated from the regression on temperature and the normal component of wind velocity.

that values higher than about 1 % are unlikely to occur.

Two other values fell above the upper limit, 0·3 %, of the range given by Barker & Wallace (1946) for CO_2 concentration in the atmosphere of a clamp. One of these, on 18 January, occurred on a calm day at a stage before the rotting of the tubers had proceeded far enough to affect the temperature drift appreciably; the sharp rise of temperature due to rotting began in mid-February (Crook & Watson, 1950). The temperature at the time of sampling on

wind (3 m.p.h. normal to the clamp face) before the third occasion on 8 February.

There appears to be no information on the effects of CO_2 concentrations as low as 1 % on sprouting and sugar content, but they are likely to be small and of no practical significance, judging from the effects of 5 % CO_2 described by Barker (1936) and Denny & Thornton (1941).

The reduction of CO_2 concentration by wind blowing in the direction normal to the clamp face supports the conclusion reached from a study of temperature variation in the same clamp (Crook & Watson, 1950), that wind can cause a flow of air through the clamp coverings. Wind caused large fluctuations of temperature from March 1943 onwards, but no wind effect was established in the earlier part of the storage period. This was attributed to drying of the soil cover; apparently the water content of the soil had fallen at the end of February to a critical value at which there was a sudden increase in the permeability of the soil to air flow. The effect of wind on CO_2 concentration, however, was not limited to the period from March onwards. Table 1 shows that CO_2 concentration was depressed by wind on 11 and 25 January, and 1 and 8 February. This implies that it was more sensitive than temperature to wind, and that a rate of entry of external air too small to produce detectable changes of temperature was sufficient to reduce CO_2 concentration appreciably. It was not possible to test whether the sensitivity of CO_2 concentration to wind increased after the end of February because the observations were not sufficiently frequent; the calculated regression coefficients on wind velocity measure only the average effect over the whole storage period.

The fact that so large a fraction of the variance of CO_2 concentration was accounted for by the regression on normal wind velocity during a period of only 3 hr. before the time of sampling indicates that equilibration of the internal CO_2 concentration with changed wind conditions was very rapid. After a transition from calm conditions to a period of continuous high wind, it was found (Crook & Watson, 1950) that about 2 days elapsed before the temperature throughout the heap of potatoes reached approximate equilibrium. This difference confirms the conclusion that CO_2 concentration was more sensitive than temperature to the entry of external air caused by wind.

The slow equilibration of temperature with change in wind is accounted for by the high specific heat of the tubers. To lower the temperature inside the clamp, far more heat has to be removed from the tubers than from the interstitial gas. If the CO_2 concentration in the clamp atmosphere is reduced, some CO_2 will come out of solution in the tubers, but the reserve of CO_2 in the tubers relative to that in the clamp atmosphere is probably much smaller than that of heat. If the whole of the internal atmosphere of the clamp were suddenly replaced by external air, the CO_2 concentration in the clamp atmosphere in the immediately following period would be very close to that of the external air, while the temperature of the potatoes would not fall appreciably. Thus the more rapid equilibration of CO_2 concentration than of temperature with wind changes is in accordance with expectation.

If the unsaturated compounds present in the clamp atmosphere were, in fact, ethylene, the concentration present in January and early February was sufficient to cause some retardation of sprouting. Huelin (1933) found that potato tubers treated continuously for a month with 0·001 % ethylene produced only 60 % of the weight of sprouts found on untreated tubers, but after treatment for a second month the retardation of sprouting ceased, and the treated tubers had a greater weight of sprouts than the controls. Higher concentrations of ethylene caused greater and more persistent reduction of sprouting; continuous treatment with 0·01 % reduced the weight of sprouts to 15 % of the control weight after 1 month, and to 79 % after 2 months.

The origin of the unsaturated compounds is not known. So far as we are aware, ethylene production by potatoes has never been reported. We have been informed by Dr J. Barker that when experiments were made at the Low Temperature Research Station, Cambridge, to determine non-CO_2 volatile carbon from potatoes respiring in air, by the furnace method, no trace was found. The unsaturated compounds, therefore, presumably did not come from the potatoes. It is possible that they were metabolites of micro-organisms in the earth or straw coverings or on the surface of the potatoes. Miller, Winston & Fisher (1940) have shown that *Penicillium digitatum* evolves a volatile substance, presumably ethylene, that causes epinasty in potatoes and other plants, and it is probable that other fungi and possibly bacteria have the same property.

The conclusion to be drawn from these results in relation to clamping practice is that no special precautions, such as the provision of straw vents through the earth cover, need be taken to prevent harmful accumulation of CO_2 or depletion of oxygen in the clamp atmosphere, for even in a clamp containing infected tubers at an abnormally high temperature, the magnitude of these changes was too small to affect the storage behaviour of the potatoes appreciably. Accumulation of unsaturated compounds may be of practical importance, but any effect of this is likely to be beneficial, leading to a retardation of sprouting.

SUMMARY

The CO_2 concentration in the atmosphere of a potato clamp varied between 0·06 and 0·86 %. The sum of CO_2 and oxygen concentrations remained approximately constant at 21 %. The CO_2 concentration increased with time from December to April. This was attributed to increase in the rate of respiration of the potatoes caused by rise of temperature. Wind blowing in the direction normal to the face of the clamp reduced the CO_2 concentration, presumably by causing external air to flow through the clamp coverings. A multiple regression of CO_2 concentration on temperature of the potatoes at the time of

sampling, and on the mean component of wind velocity normal to the clamp face estimated over a period of 3 hr. before the time of sampling, accounted for 64 % of the variance between sampling occasions.

Unsaturated compounds were detected in the clamp atmosphere by absorption in bromine; the concentration of these, expressed as ethylene, varied between 0·004 and 0·025 %.

The magnitude of CO_2 accumulation and oxygen depletion in the clamp atmosphere was too small to produce effects of practical importance on the storage behaviour of the potatoes. If the unsaturated compounds were ethylene, the concentration present was sufficient to cause appreciable retardation of sprouting.

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