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EFFECT OF WATER STRESS ON THE RESPIRATORY GAS EXCHANGE OF BANANA FRUIT AND TISSUE

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SUMMARY

When drying is effected in air, the respiration of water-stressed banana fruit tissue is increased in the preclimacteric phase, but reduced at the peak. This applies to the behaviour of whole fruit but not to that of tissue incubated in osmotic (mannitol) solutions.

The increased respiration rate of stressed preclimacteric tissue is reduced, when measured in air at 25°C, after cold or anaerobic incubation during drying. This reduction appears to be at the expense of both the developing and the unstressed respiration.

Variations in respiratory quotients suggest that changes occur in biochemical pathways when tissue is stressed.

I. INTRODUCTION

Although the effects of water stress on the physiology of plants have been extensively investigated (Vaadia, Raney and Hagan 1961; Kozlowski 1964, 1968) effects on post-harvest fruit physiology are not well documented, and the data which do exist are contradictory.

Tsalpatouros (1956), discussing the influence of relative humidity on the respiration and ripening behaviour of harvested bananas, showed diagrams relating low humidity with reduced green-life and with respiration rate, which is higher during the preclimacteric phase and lower at the climacteric peak. The figures are diagrammatic and no basic data are quoted. (Green-life of climacteric type fruits has been defined by Peacock and Blake (1970) as the time that elapses

between harvest and the onset of the respiratory climacteric. Gac (1956) consistently found lower preclimacteric respiration rates in fruits held at low humidities, conditions which, relative to high humidities, stimulated apples and pears to ripen, but which retarded the ripening of grapes. Wardlaw, Leonard and Barnell (1939) also reported lower respiratory peaks of bananas held at low humidities, but made no comparisons of preclimacteric rates at the humidities investigated. Littmann (1972) has reported a consistent loss of green-life at low humidities in harvested banana, pear and avocado fruits.

Reports of changes in respiration rates of water-stressed plants and tissues other than fruit are also variable. Both increased and decreased respiration may be found in the one tissue depending on the magnitude of the stress (Parker 1952; Brix 1962; Kaul 1966), and the effect may be different in plants of different ecological groups (Zholkevich 1961). However, most reports linking high water content with high respiration rate deal with awakening tissues (seeds, buds, etc.).

The experiments reported in this paper were designed to establish effects of water loss on the respiratory behaviour of banana fruit. The effect obtained with tissues depended on the means by which water stress was provided. Tissue was either dried in air or placed in osmotic solutions. The former conditions equated best with conditions applied in the whole-fruit experiments, where respiration rate increased with increasing stress. This respiratory increase was tested for its sensitivity to cold and anaerobic conditions, both of which are known to influence the development of induced respiration in fresh tissue slices (Hackett *et al.* 1960; ap Rees 1966).

II. MATERIALS AND METHODS

Whole-fruit experiments.—Preclimacteric banana fruit (*Musa acuminata* Colla cv. Giant Cavendish) were selected from a grower's property at The Gap, near Brisbane, and were received at the laboratory within an hour of harvest. Fruit were weighed individually, dipped in an aqueous fungicidal solution (600 p.p.m. 2-(4-thiazolyl) benzimidazole, marketed as "Thibenzole"), and held at 20°C in individual respiration jars ventilated with air. The air, scrubbed of carbon dioxide and ethylene, was passed over each fruit at 100 ml per min and at mean relative humidities (with estimates of standard deviations) of $13 \cdot 1 \pm 4 \cdot 0$ and $95 \cdot 0 \pm 1 \cdot 8\%$. Respiration rates were expressed as carbon dioxide evolved. The details of the methods for whole fruit are those used by Littmann (1972).

Tissue experiments.—The differences between the biochemistry of thin tissue slices in liquid bathing media and that of the parent plant organ from which they were taken have been investigated by Laties (1963, 1967), who showed that differences during the induced respiration phase could be reduced in potato tissue by increasing slice thickness. Palmer and McGlasson (1969) reported that transverse slices of banana fruit suffered less respiratory interference with increasing slice thickness up to 6 mm, where slices were closely representative of whole fruit. Plug size was therefore maximized, having regard to respirometer flask dimensions. Also, to minimize the metabolic changes due to cutting, and particularly those associated with induced respiration, all stressing and control conditions were applied over a period of 40–60 hr after removing plugs.

In experiments examining the effect of stress on respiration rate, tissue pieces were prepared as follows. Under aseptic conditions, plugs of 6 mm diameter were removed with a cork borer, and slices 6 mm thick cut from the pulp. The slices were rapidly rinsed with water, dried with tissue paper and placed under the required conditions. During ageing, water loss was obtained either by maintaining the plugs in air of different humidities or by incubating in a range of aerated mannitol solutions of different osmotic pressures.

For the air-drying experiments, sufficient material was taken to provide 50 tissue pieces for each set of conditions, and this necessitated pooling plugs from up to seven banana fruit from the one hand. Tissue pieces were randomized into five petri dishes which were placed in closed airtight containers (volume 1·5 l) over one of a series of NaCl solutions of different concentration (saturated NaCl to distilled water), providing a range of water vapour pressures. An ethylene absorbent ("Purafil") was included in the containers, which were then stored at 25°C for 40–60 hr.

On removal, two samples of eight pieces of tissue were taken from each treatment and placed in Warburg respirometer flasks. No liquid bathing medium was employed. The remainder of the tissue was used to determine its water potential, using the method of Chardakov (1953). Oxygen uptake and carbon dioxide evolution were determined by the direct method at 25°C. Readings were taken for a number of days to ensure that tissue was still preclimacteric. Ethylene was then added and measurements continued until the climacteric peak had occurred.

The second method of applying water stress to tissue plugs, by placing them in mannitol solutions of different osmotic pressures, was done in two ways. Tissue plugs prepared as above were either aged in moist air for 48 hr, after which they were added to the test mannitol solutions (pH 5·2 phthalate buffer) in Warburg respirometers, or they were incubated for 48 hr in the test aerated solutions, then transferred to the respirometers. Aseptic conditions were maintained, and incubating solutions were replaced after 1, 6 and 22 hr.

For anaerobic incubation, tissues were prepared in the same manner as the air-drying experiments except that air and N_2 were passed through the containers. The gases were brought to the water vapour pressure required by bubbling through the salt solutions over which the tissues were held. Extremes of humidity only were used. For incubation under cold conditions, the methods employed in the air-drying experiments were again used. Tissue samples were placed over water and saturated NaCl solutions at 1°C. At 25°C water was also used, and the concentration of the salt solution was chosen to provide the same rate of water loss as that provided by saturated NaCl at 1°C.

III. RESULTS

The effect of humidity of storage on the respiratory behaviour of whole fruit is shown in Tables 1 and 2. Mean preclimacteric rates of carbon dioxide production were increased under low humidity by from 14 to 35·5% (Table 1). Most differences were highly significant. This relationship was reversed at the climacteric peak (Table 2), stressed fruit having lower peaks which were reduced by from 15·2 to 40·4% of the unstressed levels. In three of the four pairs of means, differences were found to differ significantly.

TABLE 1

EFFECT OF STORAGE HUMIDITY (RH) ON THE MEAN PRECLIMACTERIC RESPIRATION RATE (RR) (mg CO_2/kg ORIGINAL FRESH WEIGHT/HOUR) OF WHOLE FRUIT

Experiment No.	RH = 95%			RH = 13%			—		
	No. of Fruit†	Mean RR	S.E. of Mean	No. of Fruit†	Mean RR	S.E. of Mean	Difference	S.E. of Difference	Percentage Increase‡
1a	8	15·67	± 0·68	7	21·24	± 0·23	5·57	± 0·72***	35·5
1b	7	15·61	± 0·22	7	20 62	± 0·16	5·01	± 0·27***	32·1
1c	6	15·68	± 0·29	7	21·14	± 0·16	5·46	± 0·32***	34·8
2	4	17·40	± 0·81	4	22·00	± 0·32	4·60	± 0·87**	26·4
3	7	20·60	± 0·70	7	23·49	± 0·74	2·89	± 1·02*	14·0
4	9	16·73	± 0·17	8	21·97	± 0·43	5·24	± 0·46***	31·3

† Final numbers. Data from fruit suffering rots or accidents before climacteric onset were rejected.

‡ Mean RR at 95% RH = 100%

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

TABLE 2

EFFECT OF STORAGE HUMIDITY (RH) ON THE PEAK RESPIRATION RATE (RR) (mg CO_2/kg ORIGINAL FRESH WEIGHT/HOUR) OF WHOLE FRUIT

Expt. No.	RH = 95%			RH = 13%			—		
	No. of Fruit†	Mean RR	S.E. of Mean	No. of Fruit†	Mean RR	S.E. of Mean	Difference	S.E. of Difference	Percentage Decrease‡
1a	7	80·66	± 1·84	5	54·78	± 3·74	25·88	± 3·80***	32·1
1b	6	82·97	± 5·26	6	51·98	± 3·00	30·98	± 6·06***	37·3
1c	5	84·32	± 5·39	7	71·51	± 5·15	12·81	± 7·62 NS	15·2
2	4	99·00	± 1·68	4	59·00	± 4·71	40·00	± 5·00***	40·4

† Final numbers. Data from fruit suffering rots or accidents before climacteric peak were rejected.

‡ Peak RR at 95% RH = 100%.

*** $P < 0.001$ NS Not significant.

The pattern of carbon dioxide production found in whole fruit was confirmed for both carbon dioxide and oxygen in air-stressed tissue pieces (Figures 1 and 2). For each decrease of 1 atm in water potential, preclimacteric oxygen consumption and carbon dioxide evolution both increased at a rate of approximately 1·8 ml/kg fresh tissue weight/hour. This represented an increase of 68% for oxygen exchange and 78% for carbon dioxide exchange, between —7 and —27 atm. The reduction of peak gas exchange with increasing stress is shown in Figure 2. For each decrease in water potential of 1 atm, oxygen uptake was reduced by approximately 2·1 ml and carbon dioxide by 1·3 ml/kg fresh tissue weight/hour. Over the range of water potential examined, this represented a fall to 77% of the unstressed oxygen uptake, and 83% of unstressed carbon dioxide production. The regression coefficient of peak carbon dioxide against water potential was significant at $P < 0{\cdot}01$. For the other three regression coefficients, significant levels of $P < 0{\cdot}001$ were established.

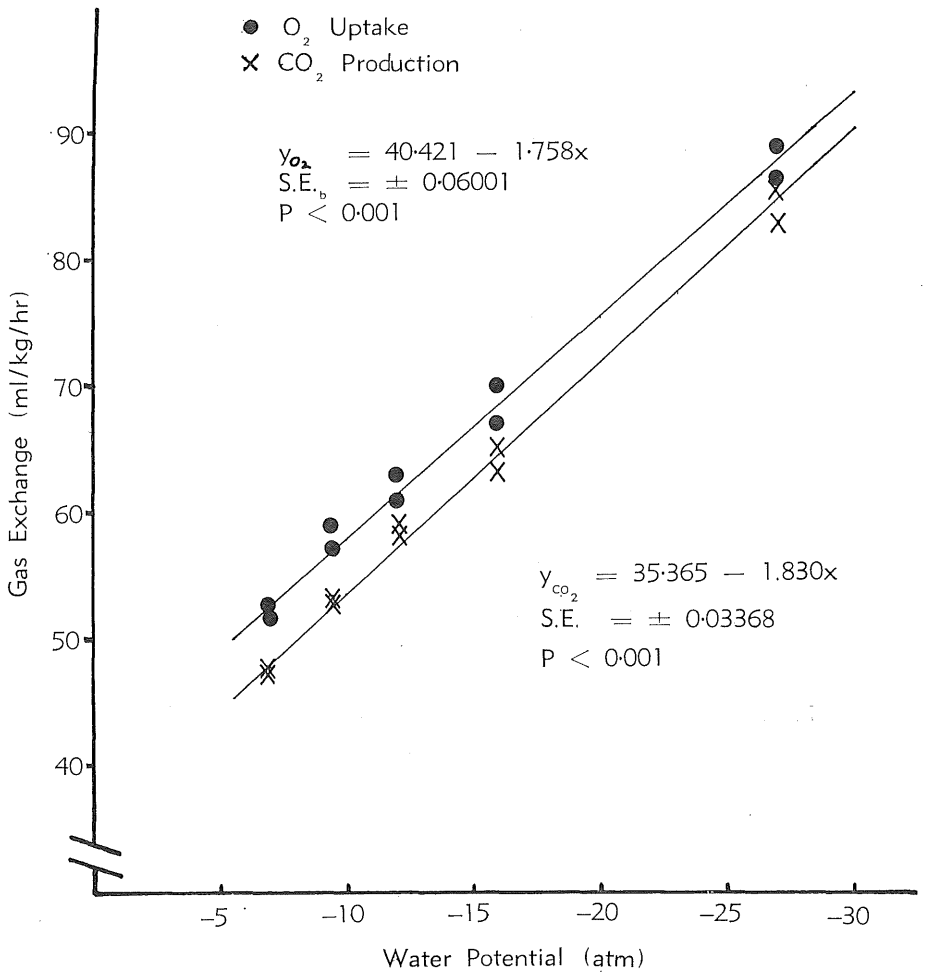

Fig. 1.—Effect of water stress on preclimacteric respiration rate.

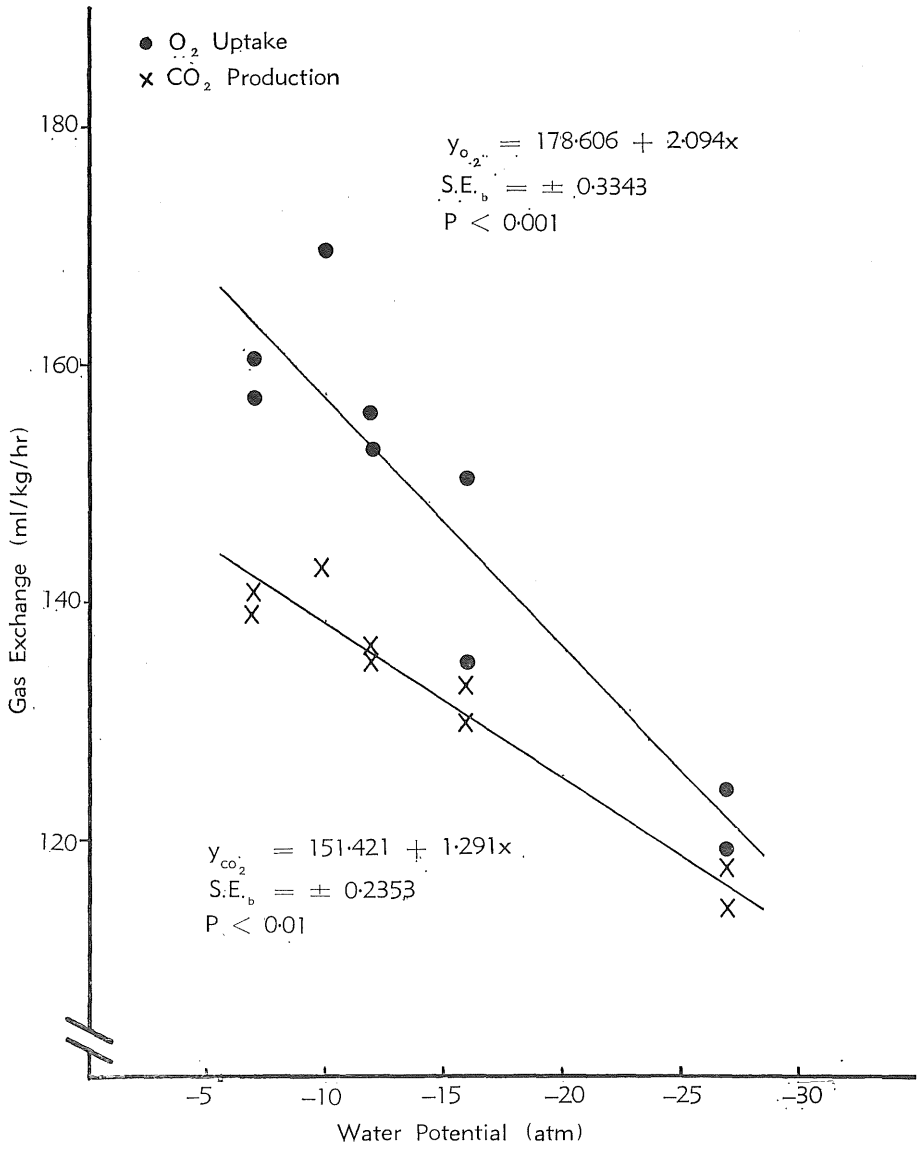

Fig. 2.—Effect of water stress on respiration rate at climacteric peak.

Respiratory data of water-stressed banana fruit were used by Littmann (1972) to estimate time to ripen. These data are combined with data from this paper in Figure 3, which illustrates diagrammatically the differences between the shapes of the respiratory curves of stressed and unstressed fruit. The main differences lie in time to onset of climacteric rise, preclimacteric respiration rate and peak respiration rate.

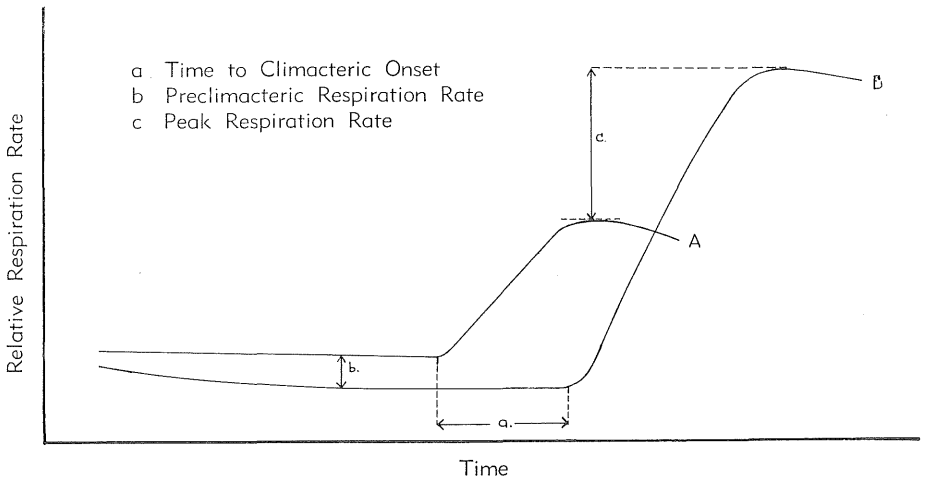

Fig. 3.—Diagrammatic representation of relative respiration rates of water-stressed (A) and unstressed (B) banana fruit.

The effect of water stress on respiratory quotient (RQ) is shown for both preclimacteric and peak respiration rates in Figure 4. Both regressions are significant ($P < 0{\cdot}01$). No difference between the regressions was able to be shown; however, the RQ values at the climacteric peak were significantly lower than preclimacteric levels ($P < 0{\cdot}01$).

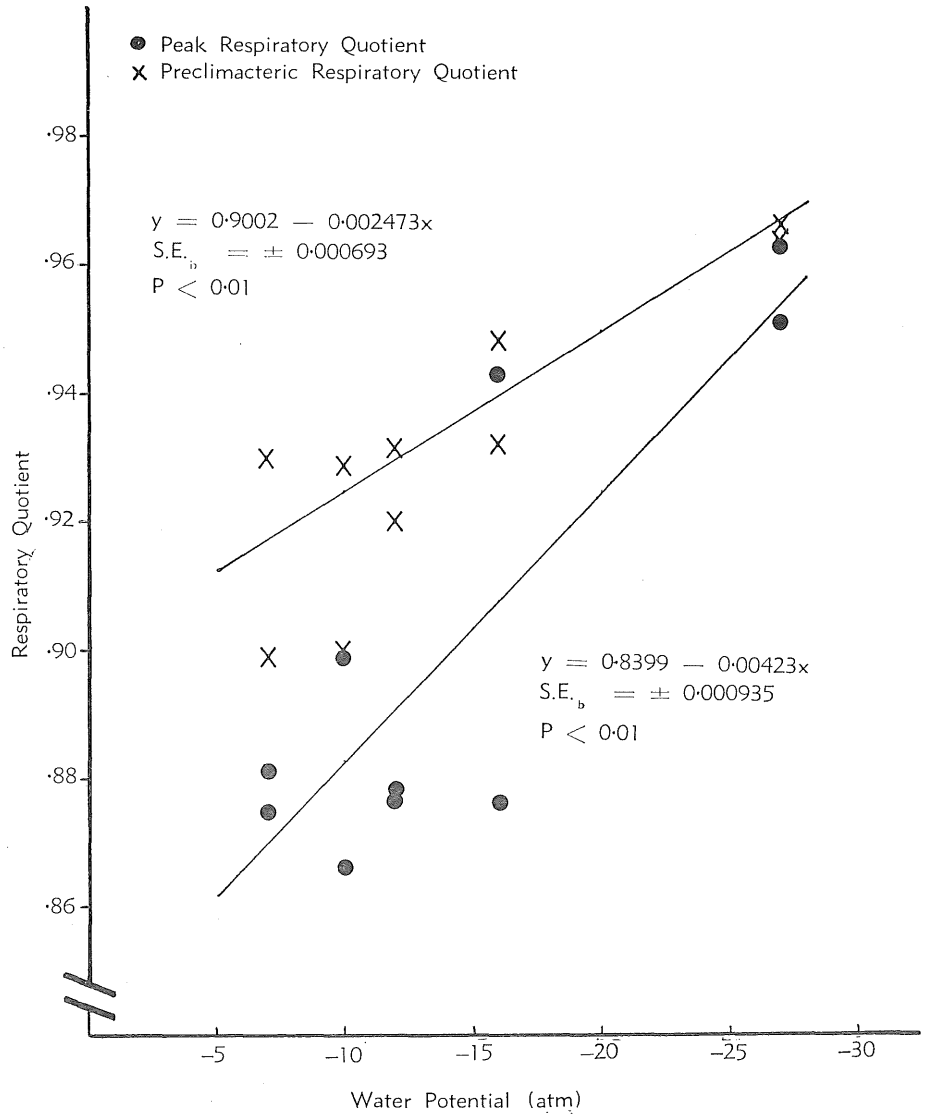

Fig. 4.—Effect of water stress on respiratory quotient.

Attempts to provide water stress in tissues by incubation in osmotic solutions gave respiratory data at variance with those obtained from air-dried tissue, in that respiration fell, instead of rising with increasing stress. Figure 5 illustrates the influence of mannitol in phthalate buffer (pH 5·2) on the preclimacteric respiration of tissue previously aged for 48 hr in air. The respiration rate of tissue incubated in mannitol solutions for 48 hr was also reduced with increasing stress. This was measured by transferring tissue to respirometers without liquid bathing medium.

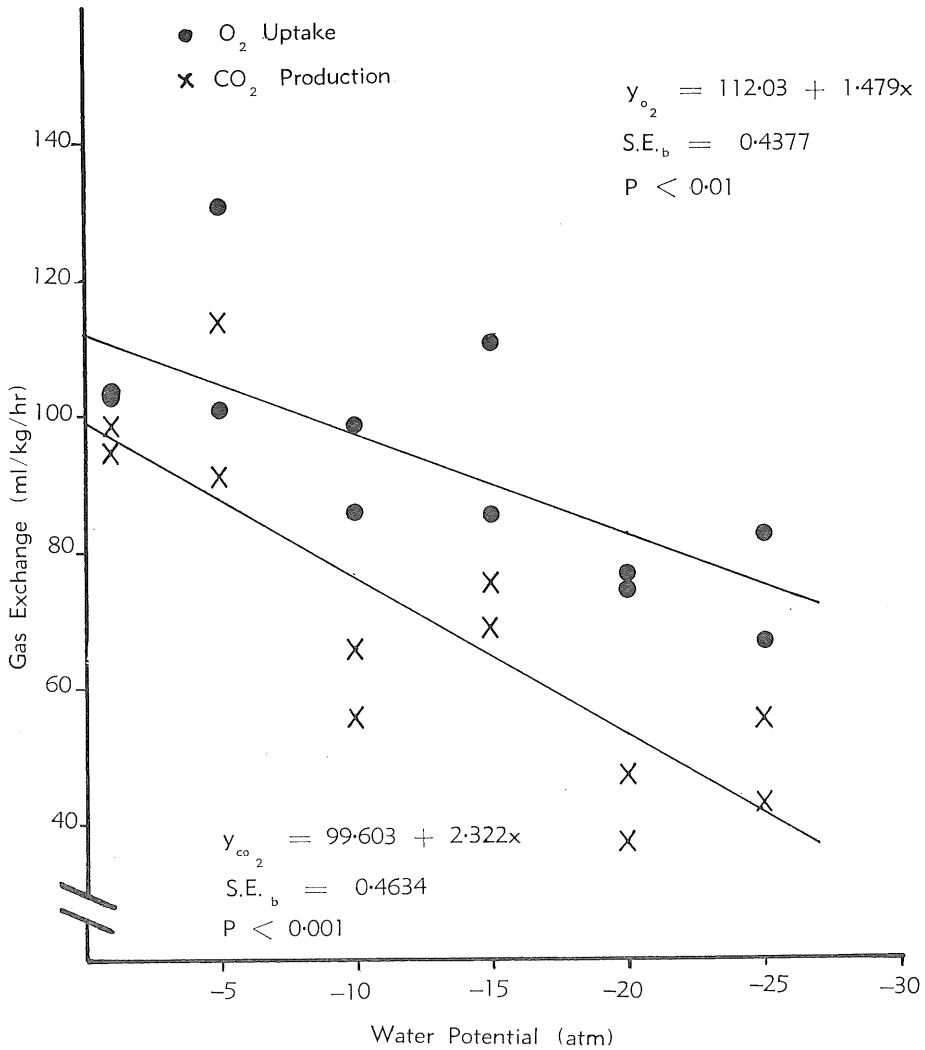

Fig. 5.—Effect of mannitol solutions of different water potential on tissue respiration rate.

The effects of anaerobic and cold incubation on various respiratory responses to water stress are shown in Tables 3 and 6 respectively. The term "stress" in this paper has been reserved for discussion of water stress only, and is not used to refer to the effects of cold or anaerobic treatments.

In the anaerobic experiment quoted (Table 3) there were four treatments: incubation in air and 100% nitrogen of both stressed and unstressed tissue. The respiratory oxygen uptake (QO_2) of tissue incubated in air was 88·5 (ml/kg/hr) when unstressed. When water potential was decreased (from −9·5 to −22·2 atm), QO_2 increased to 163·1, a rise of 84%. This level in stressed tissue was reduced by anaerobic incubation to 79·6 ml/kg/hr, which is 90% of the unstressed QO_2, and 49% of the total QO_2 of stressed tissue incubated in air. The effect of nitrogen incubation on unstressed tissue was to reduce the QO_2 from 88·5 to 51·4, a reduction to 58% of the value in air.

TABLE 3

EFFECT OF ANAEROBIC INCUBATION ON STRESS-INDUCED RESPIRATION RATE (25°C)

	Moist (Unstressed)		Dry (Stressed)	
	Air	Nitrogen	Air	Nitrogen
Mean percentage weight loss	0·12	0·43	27·1	26·6
Mean water potential (atm)	− 9·5	− 8·5	− 22·2	− 18·3
Mean O_2 uptake* ± S.E.	88·52 ± 1·263	51·39 ± 2·120	163·12 ± 5·150	79·62 ± 2·130
Relative rate O_2 uptake	1·000	0·581	1·843	0·899
Mean RQ ± S.E.	0·853 ± 0·0215	0·480 ± 0·0241	0·917 ± 0·0012	0·535 ± 0·0204
Mean CO_2 production*	75·58 ± 2·827	24·66 ± 1·348	149·47 ± 3·664	42·53 ± 2·502
Relative rate CO_2 production	1·000	0·326	1·978	0·563

* ml/kg/hr

The significance of differences between the various treatments on oxygen uptake levels is shown in Table 4. RQs were also compared and the significances of differences between RQs of the various treatments are shown in Table 5. Among the treatments, increasing QO_2, increasing QCO_2 and increasing RQ are all related, so that differences in CO_2 production between the treatments were generally more marked than differences in oxygen uptake.

TABLE 4

SIGNIFICANCE OF DIFFERENCES BETWEEN OXYGEN UPTAKE MEANS OF EACH TREATMENT OF ANAEROBIC INCUBATION EXPERIMENT (VALUES > *P*)

——	Moist Air	Moist N_2	Dry Air
Dry N_2	·05	·001	·001
Dry air	·01	·001	..
Moist N_2 ..	·001	..	..

TABLE 5

SIGNIFICANCE OF RQ DIFFERENCES BETWEEN MEANS OF EACH TREATMENT OF ANAEROBIC INCUBATION EXPERIMENT (VALUES > *P*)

——	Moist Air	Moist N_2	Dry Air
Dry N_2	·001	N.S.	·01
Dry air	N.S.	·01	..
Moist N_2 ..	·001	..	..

In Table 6 are quoted the results of an experiment in which cold is shown to inhibit the respiration of stressed tissue. In this experiment there were four treatments: incubation of stressed and unstressed tissue at both 25° and 1°C. At 25° the QO_2 of unstressed tissue was 66·1 ml/kg/hr. When stressed, water potential decreased from −7 to −12 atm approx. and QO_2 increased to 79·4, a rise of 20%. The effect of cold was to reduce the QO_2 in stressed tissue to 65·5, 99% of the unstressed and 82% of the stressed tissue respiration. Under these three treatments the QCO_2 behaved similarly. However, a feature of this experiment was the behaviour of the fourth treatment, where the QO_2 of tissue held over water at 1°C was greater (79·9) than that of unstressed tissue at 25° (66·1).

TABLE 6

EFFECT OF COLD (1°C) INCUBATION IN AIR ON STRESS-INDUCED RESPIRATION RATE

	Moist (Unstressed)		Dry (Stressed)	
	25°C	1°C	25°C	1°C
Mean percentage weight loss	3·05	0·52	15·5	14·8
Mean water potential (atm)	− 6·8	− 6·9	− 11·8	− 13·6
Mean O_2 uptake* ± S.E.	66·09 ± 1 369	79·94 ± 2·206	79·39 ± 3·051	65·48 ± 1·703
Relative rate O_2 uptake	1·000	1·209	1·201	0·991
Mean RQ ± S.E.	0·919 ± 0·0108	0·513 ± 0·0182	0·879 ± 0·0158	·771 ± 0·177
Mean CO_2 production* ± S.E.	60·73 ± 1·459	40·81 ± 0·898	69·85 ± 3·230	50·68 ± 1·661
Relative rate CO_2 production	1·000	0·672	1·150	0·835

* ml/kg/hr

For the same unstressed tissues QCO_2 at 1°C was less (40·8) than at 25°C (60·7). The carbon dioxide production thus followed the pattern found for both oxygen and carbon dioxide in the anaerobic experiment. The significances of differences of QO_2 means between the treatments is given in Table 7 and of RQ means in Table 8.

TABLE 7

SIGNIFICANCE OF DIFFERENCES BETWEEN OXYGEN UPTAKE MEANS OF EACH TREATMENT OF COLD INCUBATION EXPERIMENT (VALUES > *P*)

—	Moist 25°C	Moist 1°C	Dry 25°C
Dry 1°C	NS	·001	·01
Dry 25°C	·01	NS	..
Moist 1°C	·001	..	..

TABLE 8

SIGNIFICANCE OF RQ DIFFERENCES BETWEEN MEANS OF EACH TREATMENT OF COLD INCUBATION EXPERIMENT (VALUES > *P*)

—	Moist 25°C	Moist 1°C	Dry 25°C
Dry 1°C	·001	·001	·01
Dry 25°C	NS	·001	..
Moist 1°C	·001	..	..

IV. DISCUSSION

The diagrams in Figure 3, which summarize the main differences found between stressed and unstressed tissue and whole-fruit respiration rates, are at some variance with the results reported elsewhere (Gac 1956; Tsalpatouros 1956).

In the preclimacteric condition, whole banana fruit and tissues held in air exhibit an increase in respiration rate with increased water stress. This observation supports the trends shown in the illustrations presented by Tsalpatouros (1956), but is in conflict with data reported by Gac (1956) for apples and pears. The observation by the same authors that low humidity reduces the climacteric peak value is confirmed by the experiments reported here. It is notable, however, that the report relating increased water stress with decreasing time to climacteric onset of bananas (Littmann 1972) conflicts with the diagrams of Tsalpatouros (1956), where an opposite effect is illustrated.

Because of the failure of osmotic solutions to produce effects similar to those obtained with air-dried tissues and fruits, it may be inappropriate to consider osmotic characteristics of air-dried tissue and fruit as being causally related to the respiratory responses. However, the changes in biochemistry which result from cutting and washing tissue pieces are well documented (Laties 1963; MacDonald 1967; ap Rees 1966) and indicate the care required in interpreting tissue data in terms of whole organs. Because of the lack of agreement between the solution method and the air method of obtaining stress in tissue, and the similarity of results obtained by the air-drying method for whole fruit and tissue, air-dried tissue and its responses to stress are considered to be the more representative of whole fruit.

The reasons for the increase in respiration of preclimacteric tissue with increasing stress in air are not known, but may be suggested by consideration of possible sites of respiratory control. If control is exercised by the phosphate carrier system (Pearson and Robertson 1954; Chance and Williams 1957; Laties 1967), increase in respiration probably results from either an increase in ADP concentration through utilization of energy or the occurrence of uncoupling of oxidative phosphorylation. The involvement of energy metabolism in resistance of plants to heat and drought stresses was suggested by Bozhenco (1965), who found that added microelements which provide resistance to stress also increase ATP content in plant tissues. If ATP mediates this resistance, the mechanism possibly is that adaptive reactions to stress made demands on energy reserves, converting ATP to ADP, and thus reducing the restriction on rate of respiration. On the other hand, partial uncoupling of phosphorylation has been found in some tissues subjected to drought conditions (Zholkevich 1961). If ethylene production is stimulated by water stress, as it is by many other types of stress (Pratt and Goeschl 1969), uncoupling may be affected by adenosine triphosphatase, an enzyme found to be increased in activity by ethylene in rat liver and yeast mitochondria (Olsen and Spencer 1968).

Although diffusion phenomena may limit oxygen availability in some tissues (MacDonald 1967), oxygen did not appear to be limiting in the preclimacteric phase in these experiments, as exemplified by the climacteric rise to the level of the peaks shown in Figure 2. This rise is unlikely to result from a decline in diffusive resistance during fruit ripening, because of reports of opposite effects with apples (Kidd and West 1949; Hulme 1951), avocadoes (Ben-Yehoshua, Robertson and Biale 1963) and bananas (Wardlaw and Leonard 1940; Wardlaw, Leonard and Barnell 1939). However, Wilkinson (1965) reported an increased resistance to gas exchange with water loss in apples, and this may explain the lower respiratory peaks found in the stressed fruit and tissue.

The data obtained on RQs expressed in Figure 4 suggest that changes in biochemical pathways occur under water stress and that the influence of these changes extends into the period of the climacteric peak. Because both respiration rates and RQs are altered by stress, more than one site appears to be affected. The general fall of RQ at the peak, calculated over the whole stress range investigated, contrasts with other reports. Although Biale (1946) found no change in RQ during avocado ripening, increased RQ is found in ripening apples (Hulme, Jones and Wooltorton 1963) and involves an increase in pyruvic carboxylase activity. Increased carboxylase activity during ripening is also reported in persimmons (Rakitin 1946) and bananas (Tager and Biale 1957). The differing result reported here may arise from the use of tissue plugs, and the possibility of a change in their RQ with time, a possibility recognized by ap Rees 1966).

The influence of anerobic and cold conditions during drying in reducing the development of stress-induced respiration is similar to the influence of these factors on induced respiration of freshly cut tissue slices (Hackett *et al* 1960; ap Rees 1966). These conditions also altered both the respiration rates and the RQ values, so their influence appears to be felt at a number of sites, although not necessarily the same ones affected by stress.

The possibility of the development of additional or different respiratory pathways during stress raises the question of whether anaerobic and cold conditions are retarding the developing or the unstressed respiration. Under moist conditions, anaerobic incubation caused a fall of approximately 37 ml O_2/kg/hr and this indicates that part of the induced respiration may still have existed in the moist. air-treated tissue (cf. Hackett *et al.* 1960). However, anaerobic incubation of

stressed tissue retarded QO_2 by about 84 ml/kg/hr, indicating that these conditions retarded at least the greater part of the development of the stress-induced respiration. A similar situation occurred with QCO_2 where moist tissue was reduced by 51 ml/kg/hr and dry tissue by 107 ml/kg/hr when held under anaerobic conditions. Similar arguments cannot be applied to the results of the cold incubation experiment. However, although similar mechanisms of action of cold and anaerobic incubation cannot be claimed, from these results it may be noted that with the exception of oxygen uptake after cold moist conditions, where significant differences are found in the intensity of oxygen and carbon dioxide exchange, and the value of RQ in each experiment may be rated from highest to lowest in the order: dry air at 25°, moist air at 25°, dry treatment (cold or nitrogen), and moist treatment. The exception with oxygen in the cold may be an effect of chilling, a phenomenon which occurs in banana fruit at the temperature used.

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