RELATIONSHIP BETWEEN INTERNAL DISTRIBUTION OF EXOGENOUS AUXINS AND ACCELERATED RIPENING OF BANANA FRUIT

By M. VENDRELL*

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Summary

Bananas were dipped in aqueous solutions of 2,4-dichlorophenoxyacetic acid (2,4-D) or indoleacetic acid (IAA) at concentrations ranging from 10^{-5} to 10^{-2}M. Auxin, in proportion to its concentration, stimulated ethylene production; 10^{-2}M and 10^{-3}M IAA and all 2,4-D concentrations advanced ripening relative to control fruit. 2,4-D at concentrations of 10^{-2}M, 10^{-3}M, and sometimes 10^{-4}M stimulated the respiratory climacteric immediately after treatment, but ripening of the peel was delayed compared to the pulp.

These observations contrasted with those resulting from auxin treatment of banana slices by vacuum infiltration, where ripening was delayed.

Following treatment by dipping, a gradient of auxin concentration developed from the skin to the pulp, but the amount of auxin penetrating into the pulp was small. A small amount of 2,4-D was metabolized to CO_2, but 2,4-D did not contribute carbon to the increased ethylene production.

The advancement in the time of ripening in whole fruit dipped in solutions of auxins is attributed to the uneven distribution of auxin, which causes a localized production of ethylene. While ripening is delayed in cells containing a high concentration of auxin, ethylene diffusing from these cells triggers ripening in surrounding tissues. The effect of the delay in senescence resulting from auxin treatment of banana tissue can be observed in the difference in ripening times of peel and pulp.

I. INTRODUCTION

Ripening of fruit is known to be affected by treatment with plant hormones (Mitchell and Marth 1944; Hansen 1946; Freiberg 1955; Blake and Stevenson 1959; Coggins and Lewis 1962; Abdel-Kader, Morris, and Maxie 1966; Dostal and Leopold 1967). Auxins usually accelerate ripening in fruits of the climacteric type although indoleacetic acid (IAA) has been reported to cause small delays in ripening in bananas and tomatoes (Murata, Ku, and Ogata 1965; Abdel-Kader, Morris, and Maxie 1966).

The production of ethylene, the ripening hormone in fruits, has been observed to increase in many plant systems after treatment with auxins (Hansen 1946; Morgan and Hall 1962, 1964; Abeles and Rubinstein 1964; Burg and Burg 1966; Hall and Forsyth 1967; Holm and Abeles 1968). Several of the effects considered to be due to auxin are now attributed to this increased ethylene production and not directly to the auxin. Recently it was reported (Vendrell 1969) that when transverse slices of banana fruit were vacuum infiltrated with solutions of 2,4-dichlorophenoxyacetic acid (2,4-D) and IAA, respiration and ethylene production were increased but ripening was delayed. This delay was especially pronounced when slices previously treated with 2,4-D were treated with 10 p.p.m. ethylene for 24 hr, 1 or 3 days after

* Plant Physiology Unit, Division of Food Preservation, CSIRO, Ryde, and School of Biological Sciences, University of Sydney. Requests for reprints to P.O. Box 43, Ryde, N.S.W. 2112.

auxin treatment. This concentration of ethylene is sufficient to induce ripening in control slices treated with water. It was suggested that auxins may cause a reversion of banana tissue to a more juvenile state which is less sensitive to ethylene treatment.

These contrasting results indicated that the effects of auxins on the ripening of fruit depend strongly on the method of treatment and that the extent of penetration of auxin may be the critical factor which determines the types of response obtained.

This paper reports the effects on respiration, ethylene production, and ripening of dipping whole bananas in solutions of 2,4-D and IAA. The work also included a study of the penetration and distribution of [^{14}C]2,4-D in the banana tissue and the extent of its metabolism to CO_2 and ethylene.

II. Materials and Methods

(*a*) *Source of Fruit and Preparation and Treatment of Bananas*

Bananas of the Williams Hybrid strain of the Dwarf Cavendish variety were obtained from Avoca, N.S.W., and handled as described by Palmer and McGlasson (1969).

Whole bananas were treated by dipping for 30 min in sterile aqueous solutions of 2,4-D or IAA plus 0·025% wetting agent (Citowett),* then placed singly or in pairs in respiration jars at 20°C and ventilated with humidified air at the rate of 0·5–1 litre per hour per banana.

(*b*) *Analyses*

Carbon dioxide production was measured colorimetrically (Claypool and Keefer 1942) or with an infrared gas analyser, model SB2 (Grubb Parsons & Co. Ltd., England). Soluble solids were measured as described by Palmer and McGlasson (1969). Ethylene measurements were made with a gas chromatograph as described by McGlasson (1969).

A subjective measurement of yellowing of the skin (chlorophyll breakdown) was made using the colour index devised by the Fruit Dispatch Co. (Anon. 1961). The index ranges from 1–8. The fruits were scored only to index number 5 at which they are yellow with green tips.

(*c*) *Measurement of Internal Ethylene Concentration*

The bananas required 2 or 3 weeks to begin the respiratory climacteric. Ethylene production by such fruit is very low, and the concentrations in the ventilating air streams were near the detection limits of the gas chromatograph (about 5×10^{-3} p.p.m. in a 2·5-ml sample).

In long-term experiments with green fruits it is not desirable to let the ethylene accumulate because ripening could be hastened. Therefore, in some experiments, when a careful study of changes in ethylene levels was necessary, internal concentrations were measured as these are higher and can be measured more accurately.

Since frequent sampling was needed, apparatus similar to that described by Burg and Burg (1965*b*) was used. To minimize ethylene production caused by injury (McGlasson 1969) a 15-gauge syringe needle (Luer type) was used as both a borer and a gas-sampling tube. The needle was inserted into the fruit, withdrawn and cleared, lubricated with silicone grease, and replaced in the same hole. The needle was not inserted to the full depth of the initial puncture thus leaving a small cavity in the pulp. A syringe (2 ml vol.) closed with a rubber cap was fitted to the needle and 1-ml samples were taken through the rubber cap at intervals of 2 hr or more.

(*d*) *Measurement of the Internal Distribution of 2,4-D*

To determine the distribution of 2,4-D, bananas were treated with aqueous solutions of [1-^{14}C]2,4-D (0·5 mCi/ml). The solutions were adjusted to a certain concentration by the addition of unlabelled 2,4-D.

* Marketed by BASF Australia Ltd.

Solutions of radioactive compounds were applied by brush. The fruit were kept wet for the same time used in the dipping treatments (30 min).

After the incubation period, the bananas were rinsed with distilled water to remove unabsorbed 2,4-D. Transverse slices, about 2-mm thick, were cut and each slice was divided into skin and pulp. About 1 mm of the outer part of the skin was separated from the remaining 3–4 mm. The pulp was divided in two ways: (1) in half of the samples a central disk (8 mm in diameter) was cut from the remainder of the tissue; (2) in the remaining samples the three carpellary regions were cut from the rest of the pulp. The latter comprised the central disk (8 mm in diameter), and the conducting tissue between the carpels (septa) and between the pulp and the skin. By either method one slice yielded four subsamples. These were freeze-dried. The final product was oxidized and the evolved CO_2 containing $[^{14}C]CO_2$ was trapped and counted as described by Palmer and McGlasson (1969).

(*e*) *Measurement of the Extent of 2,4-D Metabolism to CO_2 and Ethylene*

Whole fruits were treated with [1-^{14}C]- and [2-^{14}C]2,4-D (0·5 mCi/ml) as described in Section II(*d*) and were then enclosed in respiration jars. $^{14}CO_2$ evolved by the fruit was measured after collecting the respired CO_2 in 9 ml ethanolamine–methoxyethanol (1 : 4 v/v) (Palmer and McGlasson 1969). To check the production of $[^{14}C]C_2H_4$ the effluent air streams were passed through traps containing 9 ml of 0·25M mercuric perchlorate in 2M perchloric acid (Young, Pratt, and Biale 1952). An equal volume of scintillator solution was added. It consisted of a mixture 2 : 1 (v/v) of toluene scintillator [4 g 2,5-diphenyloxazole and 0·1 g 1,4-bis(4-methyl-5-phenyloxazol-2-yl)benzene in 1 litre of toluene] and Triton X-100.* The samples were counted in a liquid scintillation spectrometer (Tricarb model No. 3325, Packard Instrument Co., Illinois, U.S.A.). Counting efficiency was 10%.

The order of the CO_2 and C_2H_4 traps was reversed to find if any cross-contamination had occurred.

(*f*) *Autoradiography of ^{14}C Distribution*

Bananas were treated with [1-^{14}C]2,4-D as described in Section II(*d*), and incubated for 1 or 4 days. After the incubation period, transverse slices were cut and freeze-dried. The slices were sand-papered to give a smooth surface, then jetted with air to remove fine particles. A piece of Ilfex X-ray film was placed on each side of the slices and clamped between two glass slides. The film was exposed in the dark for 20 days, then developed in Ilford Phenisol for 4 min.

III. Results

(*a*) *Effect of 2,4-D and IAA on Respiration and Ethylene Production*

Concentrations of 2,4-D and IAA ranging from 10^{-5} to 10^{-2}M were used; 10^{-3}–10^{-2}M 2,4-D stimulated ethylene production above rates normal for green fruit (Figs. 1(*a*) and 2). The effects of 5×10^{-3}M 2,4-D were usually detected 8–16 hr after dipping. The increase in external ethylene concentration (cf. rate of ethylene production curve) was detected at about the same time as the rise in internal concentration. This contrasts with the preclimacteric stages for the control fruits, where no simultaneous increases in internal and external ethylene were observed [Fig. 1(*a*)]. An increase in external ethylene was measured when the internal concentration had reached a level of about 0·2 p.p.m. Respiration rates were also stimulated (Fig. 3).

The rates of respiration or ethylene production between the time of treatment and the start of the climacteric were not measurably increased by IAA at concentrations of 10^{-5}–10^{-2}M and with 2,4-D at a concentration of 10^{-5}M and sometimes

* Supplied by Rohm and Haas Co., Philadelphia, Pa., U.S.A.

10^{-4}M. However, there was a significant rise in the internal ethylene concentration which was maintained until the climacteric started. The rises induced by 5×10^{-3}M IAA [Fig. 1(*b*)] and by 5×10^{-5}M 2,4-D were similar.

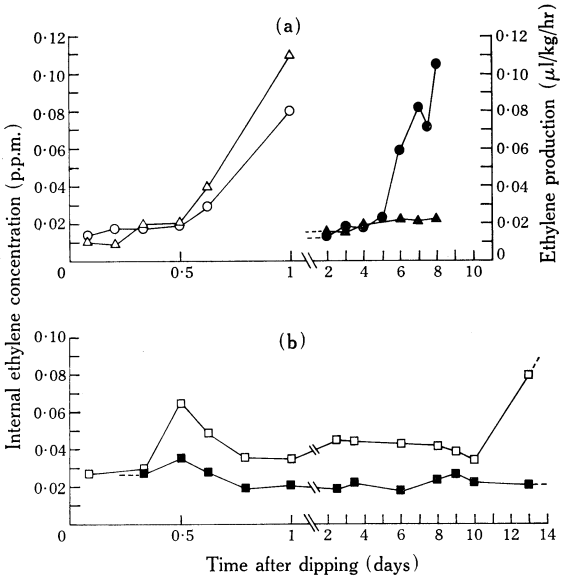

Fig. 1.—(*a*) Effect of dipping whole bananas in 5×10^{-3}M 2,4-D(○, △) and in water (●, ▲) on internal ethylene concentration (○, ●) and rate of ethylene production (△, ▲). (*b*) Effect of dipping whole bananas in 5×10^{-3}M IAA (□) and in water (■) on internal ethylene concentration. In both (*a*) and (*b*) each curve represents the average of four bananas. The bananas used in (*b*) are from a different lot to the ones used in (*a*).

(*b*) *Effect on Ripening*

All 2,4-D concentrations advanced ripening as indicated by the respiratory climacteric and ethylene production (Figs. 2 and 3) but the pattern was different to that which occurs during natural ripening.

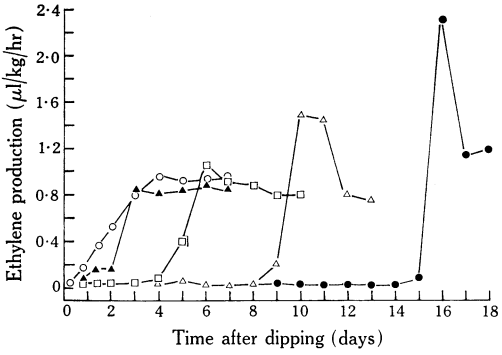

Fig. 2.—Ethylene production by bananas dipped in 10^{-2}(○), 10^{-3}(▲), 10^{-4}(□), and 10^{-5}M (△) 2,4-D solutions. ● Control. All fruits were from the same hand, and two fruits were used for each treatment.

In bananas treated with 2,4-D at a concentration of 10^{-3}M or higher, and sometimes 10^{-4}M, the stimulated respiration and ethylene production rates increased

steadily until they reached a peak as in natural ripening, but the time required to reach the maximum rate was longer than in the natural climacteric (Fig. 3) and the

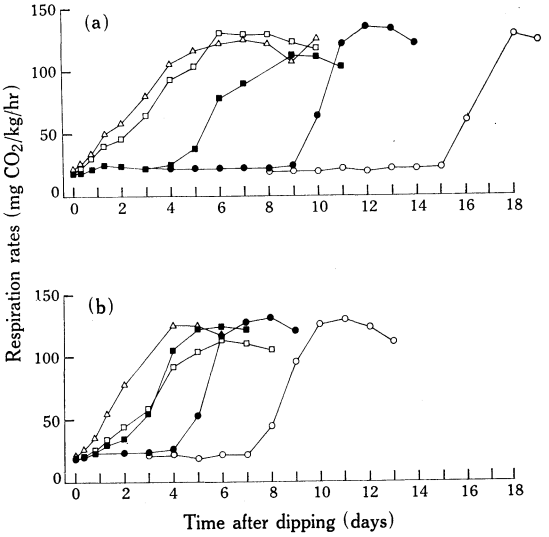

Fig. 3.—Respiration rates of bananas dipped in 10^{-2}(△), 10^{-3}(□), 10^{-4}(■), 10^{-5}M (●) 2,4-D solutions. ○ Control. All fruits in (*a*) and (*b*) were from the same hand. Two fruits were used per sample. The fruit in (*a*) is the same as that in Figure 2.

maximum rate of ethylene production was smaller (Fig. 2). Also, ripening of the pulp, as judged by softening, presence of volatiles, and increase in soluble solids [Fig. 4(*a*)] was delayed 1–2 days compared with natural ripening. Ripening of the peel, as indicated by yellowing [Fig. 4(*b*)] and changes in general texture, was delayed compared to the pulp. When yellowing developed in treated fruit it was not uniform.

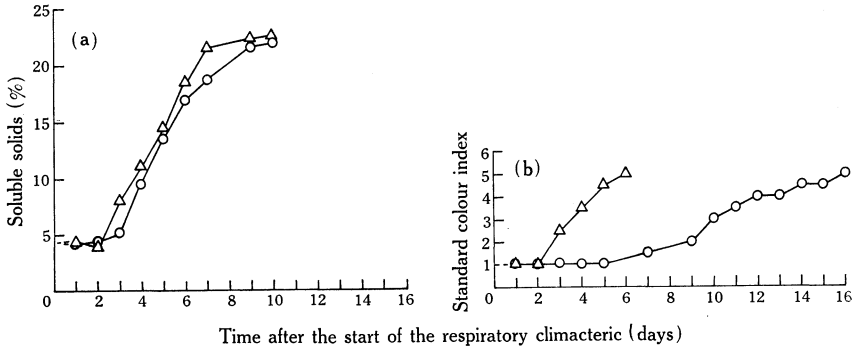

Fig. 4.—(*a*) Changes in soluble solids (as a measure of total sugars) and (*b*) skin yellowing (standard colour index, Anon. 1961) in bananas during the natural ripening (△) and in ripening induced by dipping in 5×10^{-3}M 2,4-D(○).

Although the smaller concentrations of 2,4-D did not promote measurable early increases in respiration, there was an advance in the start of the respiratory climacteric and ripening which was proportional to concentration (Fig. 3).

IAA also advanced ripening, but only treatments with concentrations of 10^{-3}M or higher gave significant results (Table 1). No damage was observed in the skin or pulp tissue of the fruit at any of the concentrations of 2,4-D or IAA used.

TABLE 1

EFFECT OF DIPPING WHOLE BANANAS IN IAA SOLUTIONS ON TIME TO COMMENCEMENT OF RIPENING

The data in each column were obtained with bananas from the same hand. Two bananas were used per sample

IAA Concn. (M)	Days to the Beginning of the Respiratory Climacteric*											
	1	2	3	4	5	6	7	8	9	10	11	12
0†	8	15	16	17	17	17	18	18	19	20	23	25
10^{-5}	—	—	16	—	17	18	18	17	15	22	—	23
10^{-4}	—	—	15	—	17	—	18	—	18	—	—	—
10^{-3}	9	11	16	14	15	15	15	16	15	19	14	23
10^{-2}	8	11	—	13	—	—	—	—	—	—	16	—

* The start of ripening was considered to coincide with the beginning of the respiratory climacteric.

† Water control.

(c) *Internal Distribution of 2,4-D*

Bananas were treated with aqueous solutions of [1-^{14}C]2,4-D adjusted to 10^{-3} or 10^{-5}M with unlabelled 2,4-D, incubated for 1 or 4 days, and the distribution of ^{14}C

TABLE 2

DISTRIBUTION OF [1-^{14}C]2,4-D IN BANANA TISSUE 1 AND 4 DAYS AFTER TREATMENT WITH 10^{-5}M 2,4-D

Sample A represents 1 mm of the outer part of the peel and B the remainder. Each value is the average of eight samples. Sample C represents the central part of the pulp (8 mm in diameter), D the remainder. Following an alternative method of cutting, E represents the carpellary area and F the central part (8 mm in diameter) of the pulp plus the conducting tissue. Each of the values for these four subsamples is the average of four determinations

Sample	^{14}C (%)		Disintegrations per Minute per Gram Fresh Weight	
	1 Day	4 Days	1 Day	4 Days
Peel A	58·6	44·1	2466	2911
B	34·0	37·9	894	1458
Pulp C	0·3	0·2	23	17
D	7·0	17·8	90	320
Pulp E	0·9	2·9	16	82
F	6·6	14·9	184	552

then evaluated. Similar results were obtained at the two concentrations, and only those for 10^{-5}M 2,4-D are shown in Table 2. After 1 day ^{14}C recovered from the

tissue was confined almost entirely to the skin (92·6%), and more than half of this radioactivity was found in the outer 1 mm. Small amounts of ^{14}C were found in the conducting tissue of the pulp but practically no radioactivity was recovered from the carpellary tissue or the centre of the pulp. Four days after treatment 2,4-D penetration had increased but 82% of the radioactivity remained in the skin. Autoradiography (Fig. 5) confirmed that, 4 days after treatment, little ^{14}C had moved past the inner regions of the peel.

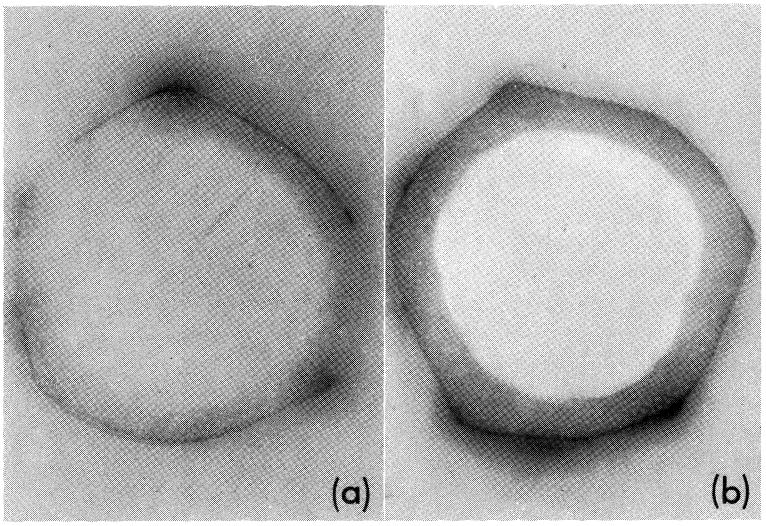

Fig. 5.—Autoradiograph of transverse section of banana showing the internal distribution of ^{14}C 1 day (*a*) and 4 days (*b*) after treatment of whole bananas with [1-^{14}C]2,4-D (0·5 mCi/ml). Natural size.

(d) Evolution of $^{14}CO_2$ and $^{14}C_2H_4$ from Bananas Treated with [1-^{14}C]- and [2-^{14}C]2,4-D

The evolution of $^{14}CO_2$ was measured following treatment of bananas with solutions of [1-^{14}C]- and [2-^{14}C]2,4-D adjusted to 10^{-3}M with unlabelled 2,4-D (Fig. 6).

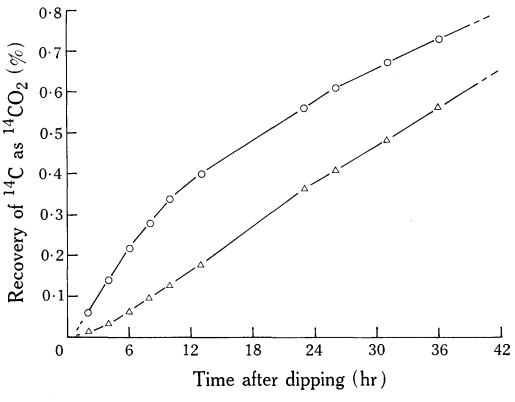

Fig. 6.—Percentage recovery of ^{14}C as $^{14}CO_2$ evolved from bananas dipped in solutions of [1-^{14}C]2,4-D (△) and [2-^{14}C]2.4-D (○) each with an activity of 0·5 mCi/ml and adjusted to 10^{-3}M by the addition of unlabelled 2,4-D.

During the first 12 hr $^{14}CO_2$ was evolved considerably faster from bananas that had been treated with [2-^{14}C]2,4-D than from those treated with [1-^{14}C]2,4-D. The

difference gradually decreased and after 3 days the total amount of $^{14}CO_2$ produced by each isotope was about the same. About 1% of the ^{14}C which penetrated the tissue in 3 days was recovered as $^{14}CO_2$.

No radioactivity was detected in the trapped ethylene.

IV. Discussion

It has been reported (Vendrell 1969) that ripening in banana tissue is delayed by vacuum infiltrating transverse slices with aqueous solutions of 2,4-D and IAA. Previous workers (Mitchell and Marth 1944; Freiberg 1955; Blake and Stevenson 1959; Murata, Ku, and Ogata 1965) had reported that auxins, applied by dipping or spraying, usually advance ripening in whole bananas. It was suggested that these contrasting results could be explained by the limited penetration of the auxins to be expected with the latter methods compared with the uniform distribution obtained by vacuum infiltration of slices (Palmer and McGlasson 1969). This paper confirms previous reports that treatment of whole fruit with auxins accelerates ripening. The present results show also that the dipping treatment gives a gradient in the concentration of auxin from the skin to the pulp, with little penetration into the pulp. Additionally, it is shown that even in whole fruit the senescence-delaying effect of auxins (Vendrell 1969) can still be observed. In fruit treated with 2,4-D the development of yellow colour lags behind the ripening of the pulp (Fig. 4).

These observations may be explained as follows. The application of auxins is known to stimulate ethylene production in many tissues, including bananas, and the effect is proportional to auxin concentration (Vendrell 1969). This effect is apparent in whole fruit treated by dipping. However, since the penetration of auxin is confined mainly to the skin, the initial increase in ethylene production and any senescence-delaying action will also be confined to the skin. Some of this ethylene diffuses directly to the atmosphere thus accounting for the measured increase in production, and some must diffuse into the pulp resulting in the measured increase in internal concentration [Figs. 1(*a*) and 1(*b*)]. When the internal concentration reaches a critical level, ripening of the pulp is triggered (Burg and Burg 1965*a*). The ripening tissue will produce an excess of ethylene (Pratt and Goeschl 1969) which will ultimately overcome the senescence-delaying effects of auxin in the skin (Vendrell 1969). Further observations explained by this theory are: (1) the skin remains rigid and green while the pulp is in an advanced state of ripening; (2) when yellowing of the skin occurs it is not uniform; and (3) the variations in the response of fruit of varying physiological ages to intermediate concentrations of 2,4-D. For example, Figure 3(*b*) shows that 10^{-4}M 2,4-D stimulated the onset of the respiratory climacteric soon after treatment, with control fruit ripening in 8 days, whereas in the set used in Figure 3(*a*), consisting of younger fruit, the climacteric did not begin until 4 days after treatment. It has been shown that the sensitivity of fruit to applied ethylene increases with age after harvest (Burg and Burg 1965*a*). IAA and the lower concentrations of 2,4-D increase the levels of ethylene in the tissue [Figs. 1(*a*) and 1(*b*)]. These concentrations are not sufficient to trigger ripening immediately, but they shorten the time taken by the fruit to enter the climacteric (Fig. 3; Table 1). Nonetheless, ripening may not take place for a considerable time after treatment.

These experiments do not distinguish between two possibilities: (1) that the time of ripening is advanced as long as sufficient auxin remains in the tissue to induce a threshold ethylene concentration at a certain age of the fruit; or (2) that, while the auxin is present, an increase in the internal ethylene concentration modifies the subsequent potential of the tissue to ripen. It has been observed (Vendrell, unpublished data) that bananas subjected to a temporary ethylene treatment ripen sooner than controls and this favours the second possibility.

The production of $^{14}CO_2$ from radioactive 2,4-D indicates that only about 1% is metabolized to CO_2 over a period of 3 days and that the direct contribution of the carbon of 2,4-D to the rise in respiration caused by treatment with 2,4-D is not significant. The initially greater production of $^{14}CO_2$ from [2-^{14}C]2,4-D treatment compared to that from [1-^{14}C]2,4-D treatment is unexpected because the C1 of the acetate side-chain seems likely to be more readily metabolized than C2.

The absence of measurable $^{14}C_2H_4$ confirms the report of Morgan and Hall (1962) that in cotton plants 2,4-D does not directly contribute to the increased ethylene production.

V. Acknowledgments

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