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PHYSIOLOGY OF ETHYLENE PRODUCTION,
USE, AND REACTIONS IN PLANTS

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Although the high physiological activity of ethylene has been known since the work of Neljubov¹ in 1901, it was not until 1924 that Denny² discovered that ethylene in concentrations of less than 100 ppm in air greatly accelerated the removal of chlorophyll from the peel of lemon. Later, in 1926, R. B. Harvey³ showed that ethylene exerted a marked effect in hastening the ripening of many fruits and vegetables.

A number of workers at that time investigated the changes in composition of ethylene treated fruits. In general, they agreed that ethylene treatment hastened the removal of green color and accelerated the rate of softening and of the hydrolytic processes involved in ripening, although the final composition of ethylene treated fruits was about the same as that of fruits picked at the same time and ripened with heat alone. The advantage of ethylene treatment lay in the shortened time required to reach the ripe stage and the concomitant decrease in shrinkage losses.

Then in 1932 Elmer⁴ observed that ripe apples produced an emanation which had a high power to influence the growth of other tissues, particularly the sprouting of potatoes. The chemical and physiological properties of this emanation were very similar to those of ethylene. Finally Gane⁵ in 1934 was able to demonstrate conclusively that ethylene was produced in apples, and in sufficient quantity to produce the observed effects.

Hansen and Hartman⁶ have concluded from chemical and biological tests of the active emanation from pears that it also is ethylene or a substance of as high activity.

Denny and Miller⁷ have tested a great variety of tissue for active emanations using as a test the epinastic reaction of the potato plant. They obtained responses from the fruits of apple, pear, banana, tomato, cantaloupe, squash, eggplant, avocado, and

¹Neljubov, D. Über die horizontale Nutation der Stengel von *Pisum sativum* und einiger anderen Pflanzen. *Beih. Bot Centralbl.* 10 128 (1901).

²Denny, F. E. Hastening the coloration of lemons. *Jour. of Agr. Research.* 27 757 (1924).

³Harvey, R. B. Artificial ripening of fruits and vegetables. *Minnesota Agr. Exp. Sta. Bull.* 247 (1928).

⁴Elmer, O. H. Growth inhibition of potato sprouts by the volatile products of apples. *Science* 75 193 (1932).

⁵Gane, R. Production of ethylene by some ripening fruits. *Nature* 134 1008 (1934).

⁶Hansen, E. and H. Hartman. Occurrence in pears of metabolic gases other than carbon dioxide. *Ore. Agr. Exp. Sta. Bull.* 342. (1935).

⁷Denny, F. E. and L. P. Miller. Production of ethylene by plant tissues as indicated by the epinastic response of leaves. *Contrib. Boyce Thompson Inst.* 7 97 (1935).

loquat; from the partially mature seeds of pea and lima bean; from the leaves, stems, roots, and flowers of dandelion; and from leaves and stems of rhubarb, hollyhock, peony, and asparagus.

Evidently a considerable variety of tissues and species produce physiologically active gaseous emanations. It thus becomes of interest to determine what part these emanations play in the functioning of the plant.

The apple is a particularly desirable fruit for such investigation since epinastic tests indicate that it produces a relatively larger quantity of ethylene than any other tissue.

The author's method for the determination of the quantity of ethylene present in plant tissues has been described in the literature, but it will be discussed briefly at this time. It depends upon the ability of dilute solutions of potassium permanganate to oxidize ethylene to ethylene glycol, and the estimation of ethylene is done by determining the quantity of permanganate unreduced.

Plugs of tissue are removed from the fruit, and the gas is extracted from them by boiling with water in a closed system. The gases are collected in an evacuated gas sampling bulb, and substances other than ethylene which reduce permanganate, and would thus interfere with the determination, are removed with sodamide. The purified gases, containing the ethylene, are passed into a flask, and permanganate solution is introduced and agitated for an hour to facilitate the oxidation. An aliquot of permanganate is removed at the end of this time and titrated with a microburette. In this way it is possible to estimate 0.04 mgm. of ethylene to 1 per cent.

The fact that ethylene is present in relatively large amounts in the apple, together with the fact that the apple is our longest keeping fruit, makes it of interest to determine the relation between ethylene content and storage life of apples. Six varieties of apples were chosen ranging from those which mature on the tree and have a relatively brief storage life, like Wealthy and Patten Greening, to MacIntosh which has a somewhat longer storage life, and to Malinda, Haralson, and Northwestern Greening, which mature only after some months of storage.

Apples of these varieties were wrapped in oiled paper and placed on trays in a chamber held at a temperature of 2° C. The apples were placed in storage on the twelfth of October and the first analyses were run about November first, thus allowing sufficient time for the fruit to come to equilibrium at that temperature.

The progressive changes of ethylene content of these stored fruits may be seen in Figure 1. It will be observed that at the beginning of their storage life the ethylene content of Wealthy and Patten Greening was high. However, since other observers, using the epinastic test for ethylene, agree that the ethylene content of ripe fruits is always much greater than that of green, it may be assumed that the content of the immature fruits was low and that it rose when the fruit ripened to a level equal to or greater

than that here observed, in which case a curve of shape similar to that observed for the other varieties would be expected.

In the other varieties, simultaneous with rising ethylene content there appeared a softening of the tissue, increased sweetness, heightened flavor, and the taste of acetaldehyde, all of which indicated that the fruit was attaining maturity. In summation it may be said of a hypothetical composite variety that the ethylene content increased markedly upon ripening, that this increase was followed by a rapid decrease, then a slight increase, and finally a gradual falling off of ethylene content in the senescent period of the fruit.

Further it will be observed that those varieties which mature later are characterized by a lesser capacity to produce ethylene, that is, there is an inverse relationship between ethylene production and keeping quality. This is quite in accord with a concept of ethylene as a catalyst or regulator of ripening.

Kidd and West⁸ have studied the course of respiratory activity in the apple. They observed that the respiratory rate fell off as the fruit reached mature size. Then, when ripening began, there was a rapid increase of respiratory rate, followed successively by a period of decreasing respiratory rate, a short but marked increase in rate, and finally decreasing respiration during the senescence of the fruit. It will be observed that there is a marked resemblance, qualitatively at least, between the course of respiratory activity and that of ethylene content of the fruit. The well-known effect of ethylene as a stimulant of plant respiration suggests strongly that ethylene may be a regulator of respiratory activity in the mature fruit.

This point of view has been tested out on the banana, a fruit which behaves in ripening in a manner somewhat similar to the apple. Green bananas were taken off the car at Minneapolis, and 4.35 kg. of fruit were placed under a bell jar in which also was placed 100 cc. of 5 N sodium hydroxide to absorb the carbon dioxide produced by the fruits in respiration. To the bell jar was con-

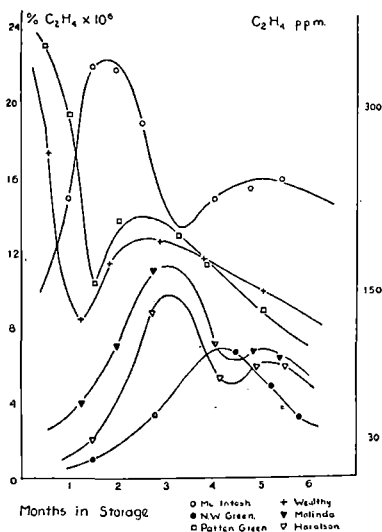


FIGURE 1

Ethylene content of apple varieties in storage.

⁸ Kidd, F. and C. West. The course of respiratory activity throughout the life of the apple. Food Invest. Bd. Rept. 1924.

nected a source of oxygen supply at a low constant pressure, in such a manner that all carbon dioxide absorbed was replaced by oxygen, thus maintaining at all times an atmosphere with approximately the composition of air as regards carbon dioxide and oxygen content. The bananas were held in the dark at 19° to 20° C., the recommended temperature for ripening bananas. At the end of each day a sample of the air in the bell jar was analyzed for ethylene, and the volumes of carbon dioxide produced and of oxygen absorbed were measured.

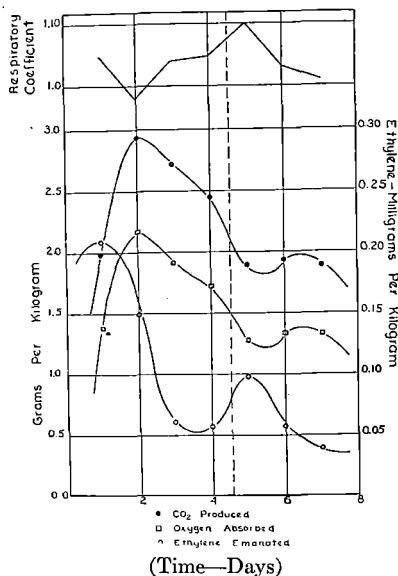


FIGURE 2

Ethylene production by ripening bananas.

consumed by the fruit, since production falls off rapidly when the respiration is at a maximum, stays low while the respiration is high, and when the respiration falls off as ripeness is reached, the ethylene production again jumps up, only to fall off again as fruit becomes senescent.

Further evidence for the consumption of ethylene during the ripening process may be found in the work of Wolfe⁹ who has found that with bananas as they reach Chicago, small but consistent increases in the ripening rate are caused by ethylene treatment although such treatment did not materially hasten the approach of the climacteric.

The earlier workers were more of the opinion that the effect of ethylene was on hydrolyses, but no such effect of ethylene on

⁹ Wolfe, H. S. Effect of ethylene on the ripening of bananas. *Bot. Gaz.* 92 337 (1931).

enzymatic processes *in vitro* has been found. Nord¹⁰ has suggested that the effect of ethylene is on permeability, but the effect of ethylene on the water permeability of potato tuber tissue and on the permeability of cabbage petiole to thiourea has been found to be only about 15 per cent, which hardly seems able to account for the effects observed.

Lynch¹¹ was perhaps the first to suggest that the effect of ethylene was on the oxidative processes in ripening. Lynch, however, laid emphasis on the oxidase and peroxidase systems of the fruits rather than on simple respiratory activity and has stated that only those fruits which contain oxidase or peroxidase activity uniformly distributed should be amenable to ethylene treatment. But peroxidase activity is characteristic of all living tissue, so it can constitute no criterion, and the cucurbits, which contain no oxidase system, not only respond to ethylene treatment but also produce ethylene themselves. Evidently this viewpoint is not entirely satisfactory.

In any case, it seems that ethylene is concerned with the respiratory processes, being produced by them and perhaps acting as a regulator of them. More than this cannot positively be said at the present.

A SURVEY OF FATHER JOHN KATZNER'S HORTICULTURAL WORK

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A pioneer country is one whose potentialities are unknown, and a pioneer settler is an experimenter finding and realizing the potentialities of the country he inhabits. It seems incredible to us, surrounded as we are with numerous varieties of productive fruit trees, that Minnesota was once regarded by intelligent men as a land where "apples can't be grown."¹ As for pears, grapes and cherries—their domestic growth was hardly given a thought. The climate, with its severe winters, its late spring frosts and its frequent years of drought, was simply considered as an insurmountable barrier for fruit crops.

To some of the pioneers, however, accustomed as they were to childhood environments abounding in fruit, such a condition was not only seriously annoying but also, they rightly thought, perhaps not quite true. Experiments and tests began. The year 1870

¹⁰ Nord, F. F. *Physikalisch-chemische Vorgänge bei Enzymreaktionen Ergebnisse der Enzymforschung* 1 77 (1932).

¹¹ Lynch, L. J. A suggested coenzyme hypothesis for the ripening of fruits by ethylene gas treatment. *Proc. Roy. Soc. of Queensland* 47 18 (1936).

¹ History of Stearns County. Mitchell W. B. Vol. II, p. 739. 1915.