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Dual Effects of Ethylene on Potato Dormancy and Sprout Growth[1]

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ABSTRACT

Dormant potato tubers (*Solanum tuberosum* L.) of two cultivars were treated with various concentrations of ethylene gas for various exposure periods. As has been shown by others, ethylene caused a rapid but transient increase in respiration rate, which appeared to be independent of any effects on dormancy. All concentrations tested caused accelerated sprouting, 2 microliters per liter being the most effective. Ethylene exerts a dual effect on potato tubers: it markedly shortens the duration of rest, but it inhibits elongation of the sprouts during extended treatment. Comparing these results with published work on seeds, bulbs, and corms suggests that ethylene must have a significant but as yet unexplained role in rest and dormancy. However, since the most effective ethylene treatment did not equal the response elicited by treatment with ethylene chlorhydrin, other factors must also contribute to termination of rest.

The initiation of sprouting in potato tubers is accompanied by a variety of biochemical changes which are usually reflected in changes in hormonal concentration, respiration rate, and the onset of nucleic acid synthesis and cell division and enlargement (16, 21, 24–26, 30, 31). A number of reports have supported the hypothesis that the rest period in potato tubers is regulated by gibberellins and ABA (24, 26, 30). However, the significance of other hormones, particularly of ethylene, has not been investigated adequately.

That ethylene is an endogenous growth hormone for plants and a potent growth regulator is well established (1, 23), but its role in the dormancy of potatoes and other plant organs has remained unclear. The older works on potato present conflicting evidence (4, 5), and there has been little clarification in recent work. Terminating dormancy in freshly harvested potatoes is an important practical problem, to which much attention has been given, and many chemical treatments have been tried (5, 22). Rosa (28) was first to try ethylene; concentrations of 10, 200, and 1000 μl/l were applied for 28 days giving substantial increases in the stand obtained 1 month after planting. On the other hand, Denny (8, 9) tried ethylene, propylene, and acetylene at 1000 and 10,000 μl/l for 4 and 7 days and found them to be ineffective. In studies by Vacha and Harvey (32), ethylene treatments with 1000 μl/l at 20 C for 6 days gave earlier sprouting and faster growth with some potato cultivars. Rosa (29) reported further tests with ethylene, using treatments of 455 and 2500 μl/l for 2, 3, or 4 weeks at 22 C; the 2- and 3-week treatments inhibited sprouting, whereas a 4-week treatment promoted sprouting (no difference between the concentrations was observed). In a better planned experiment with 800 μl/l, ethylene accelerated emergence, especially in the shorter treatments. Another experiment with 500 μl/l gave improved sprouting; propylene was as good or better.

Denny reported (8–10) that certain chemical derivatives of ethylene (including ethylene chlorhydrin, ethylene dichloride, and trichloroethylene) were particularly effective in stimulating sprouting of freshly harvested tubers, but since they are not naturally occurring, these chemicals should not be confused with ethylene in evaluating their physiological roles (23).

Other works describe ethylene as an inhibitor of sprouting in potato (18). During studies on the effect of ethylene on potato metabolism, Huelin (17) had noted effects on the sprouts, and when Elmer (11, 12) reported that emanations from ripe apples and pears caused inhibition of sprouting and abnormal sprouts, Huelin realized that the ripe fruits must be producing ethylene gas, the explanation of Elmer's observations. Barker (2) introduced ethylene into commercial scale field storage piles; ethylene reduced sprouting initially, but the effect seemed to lessen as storage was prolonged. On the other hand, when Furlong (13) took old potatoes from a field pile and stored them at 7 C in an atmosphere of about 100 μl/l ethylene for several additional months, sprouting was retarded.

Effects of ethylene on potato respiration under carefully controlled conditions have been reported recently (27). Since the earlier studies of effects of ethylene on potato sprouting are conflicting and most experiments were conducted with unphysiologically high concentrations of ethylene, long exposure times, and sometimes poorly controlled conditions, it was decided to re-examine this problem.

MATERIALS AND METHODS

In one experiment potato tubers (*Solanum tuberosum* L. cv. Russet Burbank) were harvested at Tulelake, California, 110 days after planting and cleaned with a soft brush. Triplicate samples, averaging 2.8 kg in weight and consisting of 19 carefully selected tubers, were placed in 25-liter metal chambers, which were ventilated continuously with about 10 liters air/hr. All operations were conducted in rooms controlled at 20 C. The relative humidity in the chambers was 68 to 72%. After 3 days storage (during which time the respiration rate stabilized), the tubers were treated for 72 hr with ethylene or ethylene chlorhydrin. The ethylene, in concentrations of 0, 0.02, 0.2, 2.0, and 20 μl/l, was supplied continuously in a gas stream from a pressure cylinder through a reduction valve and appropriate capillary flowmeters. The final concentrations of the gas were verified with flame-ionization gas chromatography. Res-

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piration was determined by measuring the concentration of carbon dioxide in the sample effluent using the colorimetric method of Claypool and Keefer (7). For the ethylene chlorhydrin treatments, the air flow through the sample containers was discontinued. The chemical (0.6 ml/l) was placed in a small dish in each container, and the containers were sealed for 72 hr. The regular air flow was restored after the ethylene chlorhydrin was removed.

The rate of sprouting (Table I), derived from the data of Figure 1, was determined according to the method of Harrington (15). It was calculated as follows:

$$\frac{N_1T_1 + N_2T_2 + N_3T_3 \cdots + N_nT_n}{N_1 + N_2 + N_3 \cdots + N_n} = \text{Rate}$$

wherein N_1 equals the number of tubers sprouted at time T_1; N_2 equals the increase in number of sprouted tubers observed between T_1 and T_2, etc. This formula gives a value for rate of sprouting in mean days and is the reciprocal × 100 of Kotowski's formula (20).

In another experiment 'White Rose' potato tubers from the same region were used. After harvest the tubers were washed and dried in air. Later handling procedures were similar to those of the first experiment; 10 tubers weighing about 2.3 kg were used per sample. The effects of treatment for 72 hr with concentrations of 0, 2, 10, and 20 μl/l of ethylene were tested, as was a concentration of 2 μl/l ethylene applied for 0, 8, 24, and 72 hr. In addition, the effect of a continuous treatment with ethylene for 40 days was determined.

Growth of sprouts was determined with 'Russet Burbank' potato tubers that had been stored for 5 months at 4 C. They were transferred to 20 C to promote sprouting. Tubers, with sprouts 20 to 25 mm in length, were treated in light-tight jars with 2 and 20 μl/l ethylene for 3 and 14 days. Sprout elongation was measured on an average of 15 to 20 tubers (1 sprout being measured per tuber) in four replicates per treatment. Sprout length and fresh weight were measured after 14 days of treatment when the experiment was terminated.

RESULTS

Effect of Ethylene Treatment on the Respiration Pattern of Potato Tubers. The respiratory pattern of 'Russet Burbank' potato tubers treated with different concentrations of ethylene is shown in Figure 1. After a time lag of only a few hours, the respiration rate of ethylene-treated tubers increased rapidly and reached a peak after about 28 hr. The height of the respiratory peak was proportional to ethylene concentration over the range 0.02 to 2 μl/l, but the peak at 20 μl/l concentration was somewhat lower than that at 2 μl/l. Interestingly, the initiation of the respiratory rise occurred almost simultaneously, irrespective of concentration. The rate of respiration of 'White Rose' tubers (Fig. 2) was similar for all concentrations of ethylene investigated in the experiment. However, the magnitude of the response was markedly greater with 'White Rose' than with 'Russet Burbank'. The rapid response to ethylene by treated tubers is indicated by the increased respiration detected after only 8 hr treatment (Fig. 3). Maximum rates were obtained by 24 hr, although longer exposures led to progressively higher rates of respiration even after the ethylene treatment was terminated.

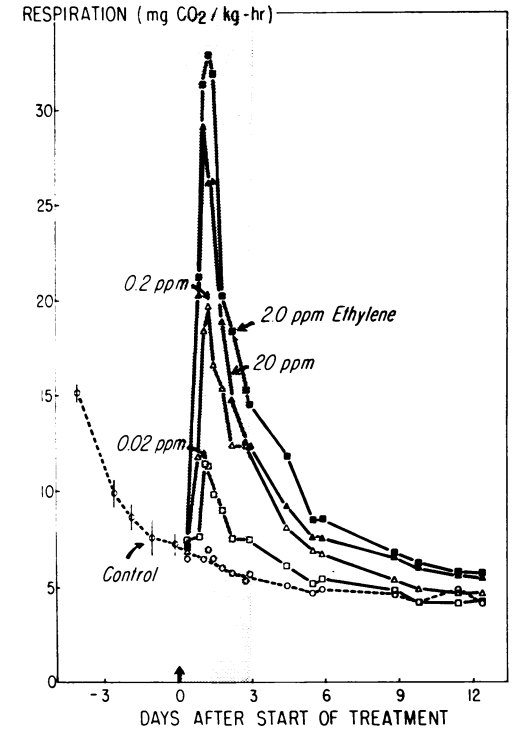

FIG. 1. Effect of various ethylene treatments for 72 hr on respiration of 'Russet Burbank' potatoes.

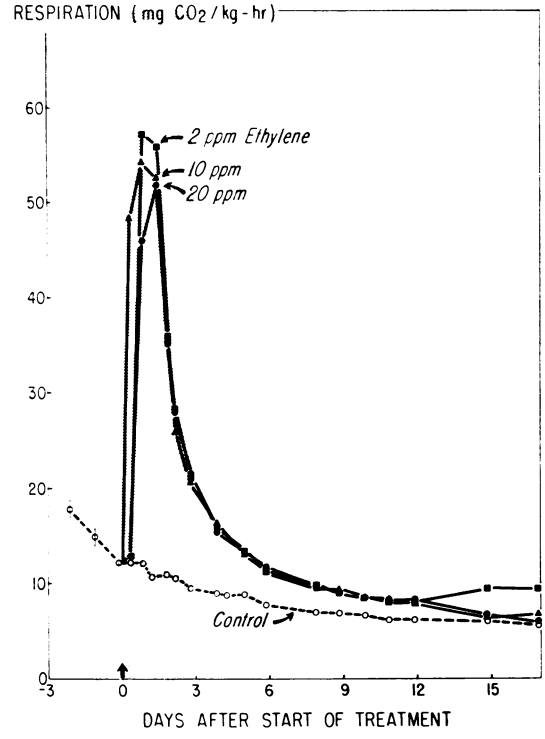

FIG. 2. Effect of various ethylene treatments for 72 hr on respiration rate of 'White Rose' potatoes.

Effect of Ethylene Treatment on Sprouting of Potato Tubers. Figure 4 and Table I show the effect of different concentrations of ethylene, in comparison with ethylene chlorhydrin and air, on sprouting of 'Russet Burbank' tubers. Ethylene, at all concentrations tested, accelerated the onset of sprouting; 2 μl/l ethylene was the most effective. Ethylene treatment was less effective than ethylene chlorhydrin which elicited 100% sprouting within 20 days. In contrast, 70% of the tubers sprouted when treated with 2 μl/l ethylene, the optimal concentration, and only 9% of the control tubers sprouted in the same time.

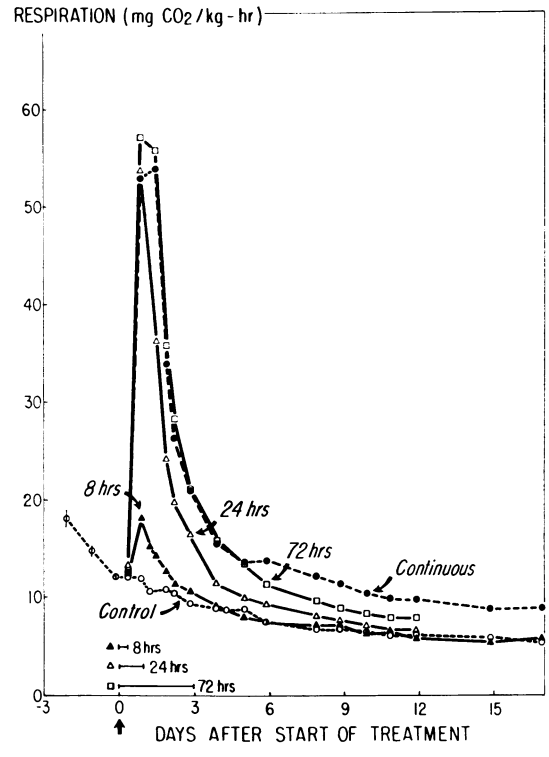

FIG. 3. Effect of treatment for varying lengths of time with 2 μl/l ethylene on the respiration rate of 'White Rose' potatoes.

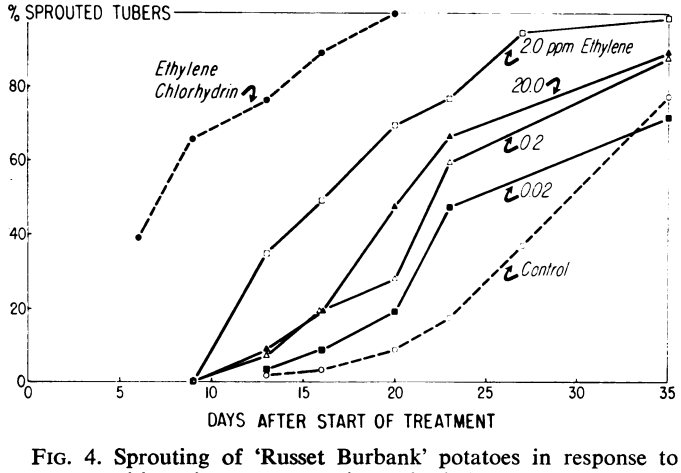

FIG. 4. Sprouting of 'Russet Burbank' potatoes in response to treatment with various concentrations of ethylene or with ethylene chlorhydrin.

Sprouting in the controls was typically delayed over the entire period of the experiment. In 'White Rose' tubers, sprouting was markedly accelerated by ethylene chlorhydrin and less so by ethylene. Sprouting of 'White Rose' tubers treated with 2 and 10 μl/l ethylene was similar over a 28-day period; thereafter those treated with 2 μl/l ethylene sprouted slightly faster (Fig. 5).

In an experiment to determine the effect of the duration of exposure to ethylene on sprouting, treatment for as short a period as 8 hr (Fig. 6) was found to stimulate sprouting; maximum effect of ethylene was achieved after a 24-hr exposure to ethylene. Continuous treatment with ethylene completely inhibited sprouting, but after treatment was discontinued, sprouting ensued at a rate apparently identical to that in tubers that had received brief exposures to the gas. The comparative effects of ethylene and ethylene chlorhydrin on sprouting are summarized in Table I. Clearly, ethylene chlorhydrin markedly promoted rapid sprouting in comparison with the untreated controls or with ethylene at any concentration tested. Moreover, 100% of the tubers sprouted by the time the experiment was terminated, a value that was closely approached only by the 2 μl/l treatment. The rate of sprouting in the different treatments, as measured by Harrington's (15) calculation method, also reveals the stimulation produced by all treatments in comparison with air or continuous ethylene.

Table I. *Effect of Differing Concentrations of Ethylene on Rate of Sprouting of 'Russet Burbank' Potato Tubers*

The values are averages of three samples.

Treatment (3 days)	Days to 50% of Sprouting	Sprouted		
		After 20 days	Final	Rate
		%		*mean days*
Air	29	9	77	31.8
Ethylene, 0.02 μl/l	24	19	72	25.6
Ethylene, 0.2 μl/l	22	28	88	29.8
Ethylene, 2.0 μl/l	16	70	98	20.4
Ethylene, 20.0 μl/l	20	47	89	23.3
Ethylene chlorhydrin	4	100	100	17.6

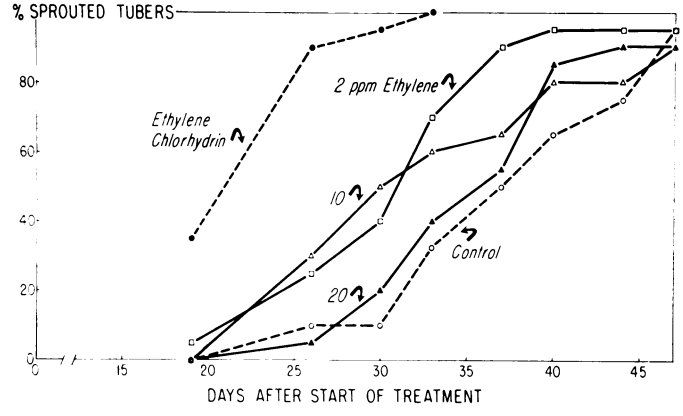

FIG. 5. Sprouting of 'White Rose' potatoes in response to treatment with various concentrations of ethylene or with ethylene chlorhydrin.

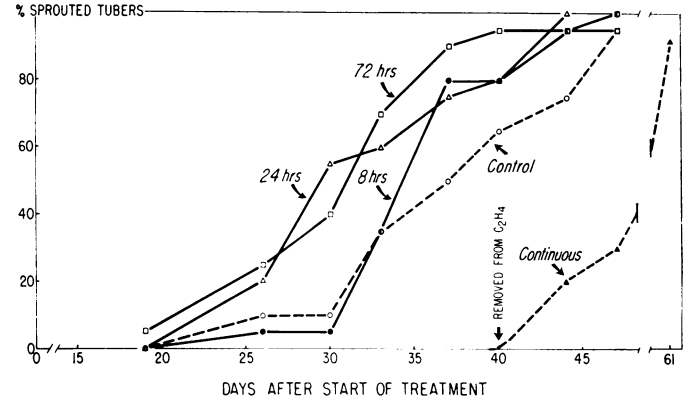

FIG. 6. Sprouting of 'White Rose' potatoes in response to treatment with 2 μl/l ethylene for various lengths of time.

Effect of Ethylene Treatment on Sprout Growth. The effects of two concentrations of ethylene on growth of the sprouts is shown in Table II. The elongation rate was inhibited in ethyl-treated sprouts in both concentrations in comparison to the control. The extended treatment caused greater inhibition of sprout elongation; the shorter, ethylene-treated sprouts were thicker than the controls, but the weight of the sprouts in all treatments was similar.

Table II. *Effect of Differing Concentrations and Duration of Ethylene Treatment on 'Russet Burbank' Potato Sprout Growth*

Treatment	Sprouts	
	Growth in length[1]	Final weight
	mm	*mg*
Control	27.5	667
2 μl/l—72 hr	8.8	619
20 μl/l—72 hr	8.1	578
2 μl/l—14 days	4.5	648
20 μl/l—14 days	4.4	595

[1] Average elongation per sprout in 14 days.

DISCUSSION

Treatment with ethylene resulted in a rapid increase in respiratory activity with peaks that essentially coincided at all concentrations and regardless of duration of exposure. The respiration results agree well with those of Reid and Pratt (27). The time of the appearance of sprouts was related closely to concentration of the gas; all concentrations of ethylene tested accelerated sprouting, and 2 μl/l was most effective. Respiration rate of potatoes during ethylene chlorhydrin treatment was not determined, but after transfer to air the respiration rate was higher in comparison to ethylene-treated tubers, possibly reflecting injury induced by this chemical. The maximum effects of ethylene on respiratory activity and on sprouting in the present experiments were attained as a result of 72 hr exposure to the gas. Exposure to ethylene gas for 40 days stimulated respiration (Fig. 3) but inhibited sprouting. The respiration rate of control tubers remained low throughout these experiments, so it appears that ethylene effects on sprouting and respiration are independent. It is of interest, in this connection, that Burton (6) reported that the respiration rate of tubers falls during the storage period and increases only after sprouting begins. Therefore, despite the rapid respiratory response to ethylene, it is unlikely that termination of rest period is linked to respiration.

From the experimental findings, it is clear that sprouting is promoted by short (up to 72 hr) exposures to ethylene. On the other hand, exposure to the gas inhibits sprout elongation when already elongating sprouts are treated for as little as 72 hr with concentrations as low as 2 μl/l. Hence it may be that both extended and short term ethylene treatments terminate rest, but that long term exposures to ethylene inhibit bud elongation, even though the rest is broken. This speculation is supported by the observation that tubers sprouted rapidly when transferred from continuous ethylene treatments to air. It may be concluded, therefore, that ethylene exerts a dual effect on potato tubers; it markedly shortens the duration of rest, whereas it inhibits elongation of the sprouts.

The significance of these results for an understanding of the regulation of the rest period is not clear. Burton (4) reported the occurrence of volatiles that suppressed sprouting of potatoes in storage. In view of the nature of the ethylene effects reported here, and of the very low concentrations of ethylene detected (less than 0.1 μl/l) in potato tubers thus far, ethylene cannot be considered an endogenous inhibitor of sprouting. On the other hand, if ethylene is a factor responsible for shortening dormancy, an increased production of ethylene preceding the onset of sprouting might be expected. Such an increase has not as yet been detected in potatoes. It is evident, however, that if the cultivars we tested produced even 2 μl/l ethylene, this alone could not account for the maximal potential sprouting elicited by ethylene chlorhydrin. In other words, it would appear that another factor or factors are required, in addition to ethylene, to produce the maximal response. While further investigation of changes in internal ethylene concentration are necessary to provide a more complete understanding of the action of this gas in dormancy, it is increasingly apparent that ethylene does play a role in dormancy of other storage organs, such as bulbs and corms (14) and seeds (3, 19). Considering that the effect of ethylene on dormancy of potatoes is elicited by relatively low concentrations of the gas (as low as 0.02 μl/l) and short exposures (8 hr), failure to detect a significant change in ethylene production does not preclude the possibility that ethylene plays a significant role in regulating dormancy.

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LITERATURE CITED

1. Abeles, F. B. 1972. Biosynthesis and mechanism of action of ethylene. Annu. Rev. Plant Physiol. 23: 259–292.
2. Barker, J. 1934. Sprouting in clamped potatoes. Great Britain Dept. Sci. Indus. Res., Food Invest. Bd. Rep. 1933: 80–82.
3. Burdett, A. N. 1972. Ethylene synthesis in lettuce seeds: its physiological significance. Plant Physiol. 50: 719–722.
4. Burton, W. G. 1952. Studies on the dormancy and sprouting of potatoes. III. The effect upon sprouting of volatile metabolic products other than carbon dioxide. New Phytol. 51: 154–162.
5. Burton, W. G. 1957. The dormancy and sprouting of potatoes. Food Sci. Abstr. 29(1): 1–12.
6. Burton, W. G. 1961. The physiology of the potato: problems and present status. Proc. First Triennial Conf. E. A. P. R. 1960, Wageningen. pp. 79–117.
7. Claypool, L. L. and R. M. Keefer. 1942. A colorimetric method for CO_2 determination in respiration studies. Proc. Amer. Soc. Hort. Sci. 40: 177–186.
8. Denny, F. E. 1926. Hastening the sprouting of dormant potato tubers. Amer. J. Bot. 13: 118–125.
9. Denny, F. E. 1926. Second report on use of chemicals for hastening the sprouting of dormant potato tubers. Amer. J. Bot. 13: 386–396. 4 pl.
10. Denny, F. E. 1945. Synergistic effects of three chemicals in the treatment of dormant potato tubers to hasten germination. Contrib. Boyce Thompson Inst. 14: 1–14.
11. Elmer, O. H. 1932. Growth inhibition of potato sprouts by the volatile products of apples. Science 75: 193.
12. Elmer, O. H. 1936. Growth inhibition in the potato caused by a gas emanating from apples. J. Agr. Res. 52: 609–626.
13. Furlong, C. R. 1948. Summer potato storage in clamp and cool store. Agriculture (London) 55: 81–85.
14. Halevy, A. H., R. Shilo, and S. Simchon. 1970. Effect of 2-chloroethanephosphonic acid (Ethrel) on health, dormancy, and flower and corm yield of gladioli. J. Hort. Sci. 45: 427–434.
15. Harrington, J. F. 1962. The effect of temperature on the germination of several kinds of vegetable seeds. XVIth Int. Hort. Congr. 2: 435–441.
16. Hemberg, T. 1970. The action of some cytokinins on the rest-period and the content of acid growth-inhibiting substances in potato. Physiol. Plant. 23: 850–858.
17. Huelin, F. E. 1933. Effects of ethylene and of apple vapours on the sprouting of potatoes. Great Britain Dept. Sci. Indus. Res., Food Invest. Bd. Rep. 1932: 51–53.
18. Hughes, D. L., B. Takahashi, H. Timm, and M. Yamaguchi. 1974. Influence of ethylene on sprout development of seed potato. Amer. Potato J. In press.
19. Ketring, D. L. and P. W. Morgan. 1972. Physiology of oil seeds. IV. Role of endogenous ethylene and inhibitory regulators during natural and induced

afterripening of dormant Virginia-type peanut seeds. Plant Physiol. 50: 382–387.
20. KOTOWSKI, F. 1927. Temperature relations to germination of vegetable seed. Proc. Amer. Soc. Hort. Sci. 23: 176–184.
21. MILLER, L. P., J. D. GUTHRIE, AND F. E. DENNY. 1936. Induced changes in respiration rates and time relations in the changes in internal factors. Contrib. Boyce Thompson Inst. 8: 41–61.
22. PERLASCA, G. 1956. Chemical control of sprouting in white potatoes. Amer. Potato J. 33: 113–133.
23. PRATT, H. K. AND J. D. GOESCHL. 1969. Physiological roles of ethylene in plants. Annu. Rev. Plant Physiol. 20: 541–584.
24. RAPPAPORT, L. 1972. Mechanism of dormancy in storage organs. Proc. 18th Int. Hort. Congr. 5: 143–155.
25. RAPPAPORT, L. AND N. WOLF. 1968. Regulation of bud rest in tubers of potato, *Solanum tuberosum* L. *In:* T. Hirai, ed., Biochemical Regulation in Diseased Plants or Injury. Phytopathological Society of Japan, Tokyo. pp. 203–211.
26. RAPPAPORT, L. AND N. WOLF. 1969. The problem of dormancy in potato tubers and related structures. Soc. Exp. Biol. Symp. 23: 219–240.
27. REID, M. S. AND H. K. PRATT. 1972. Effects of ethylene on potato tuber respiration. Plant Physiol. 49: 252–255.
28. ROSA, J. T. 1925. Shortening the rest period of potatoes with ethylene gas. Potato Assn. Amer., Potato News Bull. 2: 363–365.
29. ROSA, J. T. 1928. Effects of chemical treatments on dormant potato tubers. Hilgardia 3: 125–142.
30. SHIH, C. Y. AND L. RAPPAPORT. 1970. Regulation of bud rest in tubers of potato, *Solanum tuberosum* L. VII. Effect of abscisic and gibberellic acids on nucleic acid synthesis in excised buds. Plant Physiol. 45: 33–36.
31. TUAN, D. Y. H. AND J. BONNER. 1964. Dormancy associated with repression of genetic activity. Plant Physiol. 39: 768–772.
32. VACHA, G. A. AND R. B. HARVEY. 1927. The use of ethylene, propylene, and similar compounds in breaking the rest period of tubers, bulbs, cuttings, and seeds. Plant Physiol. 2: 187–193.