AN ABSTRACT OF THE THESIS OF

Janice Rose Seibel for the degree of Master of Science

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Title: ETHYLENE PRODUCTION, VEGETATIVE MATURITY, AND WINTER DORMANCY IN RED-OSIER DOGWOOD

Abstract approved: Leslie H. Fuchigami

The stage of dormancy development at which deciduous nursery stock can be safely defoliated for harvest was investigated in red-osier dogwood (Cornus stolonifera Michx.). This stage, previously called "vegetative maturity," was found to correspond to the onset of winter dormancy in red-osier dogwood. A reduction in ethylene production by excised plant parts is associated with dormancy development, and occurs prior to this stage. This reduction occurs synchronously throughout the plant, though ethylene production by basipetal tissues prior to the decrease was lower than that by more acropetal tissues. The pattern of change in ethylene production by nodal tissue, which included the axillary buds and about 5 mm of petiole, seemed to be least affected by environmental growing conditions. The results obtained warrant investigation of the relationship between ethylene production and dormancy development in other woody plants.

Ethylene Production, Vegetative Maturity, and Winter Dormancy in Red-Osier Dogwood

by

Janice Rose Seibel

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INTRODUCTION

These studies were designed to investigate the stage of dormancy development in deciduous nursery plants at which they can be safely defoliated and harvested. The objectives were:

1. To find a method to assist growers in identifying the harvestable stage.
2. To relate the harvestable stage to some other, already recognized, stage in dormancy development.

The growing of deciduous nursery stock is a 20-30 million dollar industry in Oregon. Due to the long, warm summers and abundant water for irrigation, growers can obtain as much as 6 feet of new growth per season in the Willamette Valley. Trees are harvested mechanically, and after lifting they can be heeled in sawdust outside for winter storage.

The trees must be defoliated before digging for several reasons. Transpirational loss through leaves can lead to severe water stress. Leaves restrict air circulation and lead to disease and decay during storage. They add bulk during lifting and grading and create a clean-up problem in grading facilities (22). Most growers in the Willamette Valley wait to lift their deciduous nursery stock until natural defoliation is nearly complete.

Unfortunately, the environmental conditions in this area are such that leaf abscission in most deciduous plant species does not occur until late in the growing season, often well into the winter season. Consequently, growers are harvesting their trees from October to February (12). The rainy winter season usually begins in November, and the wet conditions greatly reduce harvest efficiency. Tree harvest can be 15 times more efficient before than after the onset of rain (12). Thus, it is in the interest of growers to hasten the process of defoliation. Many growers defoliate by hand in Washington State, but this process is very time-consuming and costly (21). Chemical defoliants offer a more efficient and economical means for early defoliation of trees.

The potential usefulness of chemical defoliants in the deciduous nursery industry has been recognized for some time (5, 24). Many chemical defoliants have been tested in recent years, including potassium iodide, bromodine, ethephon, DuPont-WK wetting agent, and others (6, 13, 14, 19-22, 30). Unfortunately, results with these chemicals have been erratic in many cases. Often the concentrations needed for successful defoliation damage the stems of the plants. The concentrations which are safe and effective vary between seasons and geographical areas (13, 20), and growers have been understandably reluctant to risk the use of chemical defoliants. Larsen has listed a number of factors which can affect plant response to chemical

defoliants (21). Fuchigami's results indicate that much of the unpredictability of defoliant effects from year to year can be attributed to the seasonal stage of development of the plants when the defoliant is applied (9, 10).

"Vegetative Maturity" and Defoliation

Continued manual defoliation of an actively growing deciduous plant will lead to tip dieback and in many cases death of the entire plant (10). Later in the growing season the effect of defoliation on the plants becomes less severe, and eventually the plants will suffer no damage from defoliation. This stage in the seasonal development of the plants occurs during dormancy development, after bud set and before natural leaf abscission in red-osier dogwood (10). There are no visual signs to distinguish a plant which can survive defoliation from one which cannot, and prior to the studies described here, no other stage of dormancy development had been found to correspond to this stage. Fuchigami has been using the term "vegetative maturity" to describe this stage of dormancy development (9, 10). By definition, it is the phase in the seasonal development of a deciduous plant when it can be maintained in a defoliated state without suffering visible damage. Hotze (12) studied the effects of hand defoliation on deciduous nursery stock, and showed that this stage of development can occur months before, or at the time of, natural defoliation,

depending upon the species and variety. Not surprisingly, the calendar date of vegetative maturity varies with species and variety. More significantly, in the 2 years she performed her studies Hotze found that the maturity date of a given variety could vary by more than a month.

This stage of dormancy development is a significant one to the deciduous nursery industry. Chemical defoliation using ethephon is more effective after plants reach this stage than before (9), and plants are less susceptible to damage by chemical defoliants after this time (12). Thus it should be possible to obtain successful defoliation without suffering tip dieback after the time of maturity development. It cannot be assumed that it would be impossible to damage plants with chemical defoliants after this stage is reached, but the risks involved would be greatly reduced. If the growers knew when their plants reached this stage, they could use chemical defoliants to allow early harvest and more efficient utilization of energy and labor.

Tip dieback from premature defoliation can take months to develop, and is therefore a useless index of seasonal development for the growers. What is needed is an immediately available (or nearly so), reliable index of maturity. Hotze suggested the use of xylem water potential as an indicator of this stage (12). This is a fairly rapid method, but additional field tests indicate that xylem water

potential alone is not a reliable predictor of vegetative maturity development (25). Thus the problem remains to find a practical, dependable test for the harvestable stage.

Ethylene Production as a Possible Index of the Harvestable Stage

Numerous studies have determined changes in endogenous plant growth regulators as they relate to bud formation and winter dormancy (23, 26, 33-36). In general, high levels of ABA and other inhibitors, along with low levels of GA's, auxins, and cytokinins (or substances with activities similar to these hormones) have been associated with winter dormancy. One plant hormone which has received less attention in connection with the formation of resting buds on woody plants is ethylene (1, 27), although the role of endogenous ethylene in seed (3, 4, 8, 15-17) and cormel (11) dormancy has been investigated. The function of ethylene in the dormancy of these propagules is unclear, but it is generally observed that low levels of ethylene production are associated with dormancy, while higher levels are associated with active growth. Other studies have linked exogenous ethylene with seed (2, 32) and corm (32) germination, tuber sprouting (29), and bud break (31, 32).

The development of vegetative maturity is intimately associated with dormancy development, and Fuchigami found that ethephon

sprays during dormancy development significantly delayed the development of vegetative maturity (10). These findings do not necessarily indicate that a reduction in ethylene production will occur during dormancy development, but when I compared ethylene production by stem sections from actively growing and dormant plants of red-osier dogwood, those from dormant plants produced drastically lower amounts of ethylene. These preliminary results indicated that ethylene production might be useful as an indicator of the harvestable stage in the seasonal development of the plants.

The next step was to determine if the timing of the reduction in ethylene production would make it useful as a predictor of vegetative maturity development, and whether environmental conditions could affect the relationship (if any) between ethylene production and vegetative maturity. For this study, red-osier dogwood plants were grown under 3 growing conditions. They were sampled weekly for ethylene production and defoliation tolerance. Ethylene production as affected by tissue type (i.e., leaf, node, or internode) and position was also investigated.

The Concept of Winter Dormancy and an Attempt to Relate it to Harvestable Stage

Discussion, understanding, and investigation of the "harvestable" or "vegetatively mature" stage would be greatly facilitated if

it could be shown to correspond to some other stage in the development of rest. The development of rest, also called true dormancy (18), innate dormancy (35), or dormancy (36), is a stepwise process. In the first stages of dormancy development in a deciduous plant, the newly formed terminal bud and the lateral buds will resume active growth if the leaves are removed, evidence that the buds are being inhibited by the leaves (7, 28, 31). This is a type of "correlative inhibition." Doorenbos (7) suggested the term "summer dormancy" to describe this type of dormancy. As the growing season progresses the plants reach a point at which defoliation will no longer stimulate bud break. At this point the buds have become innately dormant; they will not grow when the leaves are removed because conditions within the buds themselves prevent them from growing. When the plants reach the point at which defoliation no longer induces bud break, they have reached the end of summer dormancy. Doorenbos would say the plants have entered into a condition of "winter dormancy." This lab accepts the terminology of Doorenbos, and interprets the beginning of winter dormancy to be the onset of rest. The term "rest" is used in the most restrictive sense, to describe the deepest phase of winter dormancy (10).

Defoliation and subsequent observation of bud break and tip dieback allows determination of the relationship between winter dormancy development and the development of vegetative maturity.

Fuchigami performed such an experiment, leaving the plants under natural conditions after defoliation, and found the transition between summer and winter dormancy occurred 3 weeks prior to full vegetative maturity (10). Natural conditions in late summer and early autumn are not conducive to active growth, but rather are dormancy-inducing. It was hypothesized that growing conditions after defoliation would affect the apparent timing of the transition between summer and winter dormancy, and that the beginning of winter dormancy could be linked to vegetative maturity development when conditions were conducive to bud break after defoliation. The hypothesis was tested by placing defoliated plants in a warm greenhouse and observing subsequent bud break and tip dieback.

Explanation of Thesis Format

This thesis is written in the scientific manuscript format. The balance of the thesis text consists of 2 scientific papers, to be submitted for publication in HortScience and the Journal of the American Society for Horticultural Science, respectively. They describe the research performed and some of the results obtained. Additional results are presented in the Appendix.

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THE RELATIONSHIP OF VEGETATIVE MATURITY TO THE ONSET OF WINTER DORMANCY IN RED-OSIER DOGWOOD (*CORNUS STOLONIFERA* MICHX.)[1]

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Additional index words. Tip dieback, deciduous, bud break, dormancy, vegetative maturity

Abstract. The stage of dormancy development at which plants can be maintained in a defoliated state without suffering damage was found to correspond to the onset of winter dormancy in red-osier dogwood.

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Continued defoliation of an actively growing deciduous plant will cause death of part or all of the stem. During dormancy development a stage is reached at which defoliation no longer causes visible damage. This stage has been termed "vegetative maturity" and is also the stage of dormancy development in deciduous nursery trees at which they can be safely defoliated with chemicals for harvest (2, 4). Vegetative maturity has not been shown to correspond to any other stage of dormancy development, and this has complicated investigation and communication in this area.

Before attempting to relate the time of maturity development to other stages of seasonal development, it is necessary to have some understanding of the processes leading to the formation of buds and the development of rest, and to define the terms which one has chosen to describe these processes. The term "dormancy" will be used to describe a condition in which a tissue predisposed to elongate does not do so, whatever the reason might be. In the case of buds, then, this would include inhibition of growth by unfavorable environmental conditions, by other plant organs, or by factors internal to the buds themselves.

The first type of dormancy, that which is caused by unfavorable growing conditions such as low temperature or lack of moisture, has been termed "quiescence" (6) or "imposed dormancy." (8). This type of dormancy can be removed by simply changing the plants'

environment to one which is favorable for growth. The inhibition of lateral buds by the terminal growing point and the inhibition by the leaves of the terminal and lateral buds have been classified under the general term "summer dormancy" by Doorenbos (1). When the plants are in a state of summer dormancy, defoliation will result in bud break (1, 5, 8). This type of dormancy would be the equivalent to "correlated inhibition" (5) or "correlative inhibition" (8) and it is the type of dormancy present in the buds when they are first formed (8). When defoliation will no longer stimulate bud break, it is assumed that bud break is being inhibited by some condition within the bud itself. According to Doorenbos the plant has then entered a state of "winter dormancy." Often this type of dormancy can be broken by exposure to cool temperatures for a period of time; the amount of chilling required to break winter dormancy varies greatly among species (5).

Defoliation tests for the transition from summer to winter dormancy in the past have been performed under natural photoperiod and temperature (5, 7). When defoliated plants of red-osier dogwood were checked for regrowth and tip dieback under natural conditions in Corvallis, Oregon, the transition between summer and winter dormancy was found to occur 3 weeks before the development of vegetative maturity (3). Natural conditions in late summer and early autumn in Corvallis are dormancy-inducing, rather than conducive to active growth. The purpose of this study was to determine the

relationship between bud break and vegetative maturity development when defoliated plants were placed in an environment conducive to active growth instead of dormancy inducing conditions.

Cuttings of the Wayland, Massachusetts, clone of red-osier dogwood used in previous studies (2-4) were taken in the spring of 1976. Once rooted, they were transplanted into 5-inch paper pots in a 1:1:1 sand: soil:peat mix, and were placed in a lathhouse until the start of the experiment, at which time the average plant height was about 40 cm.

On July 6, 1976, 2 groups of 50 plants each were moved into controlled environment chambers under 10-hour (short-day) conditions to induce dormancy development. One chamber was maintained at a constant 21°C and the other chamber at 12° and 7°C during the light and dark periods, respectively. Light intensity was 3634 $\mu w/cm^2$ 15 cm above pot height. Another group was left in the lathhouse. An initial group of 5 plants was defoliated on July 6, and 5 plants from each controlled environment chamber were randomly selected and defoliated at approximately weekly intervals thereafter for 10 weeks. Defoliation of 5 plants a week from the lathhouse began on August 19. After defoliation the plants were moved into a greenhouse in which temperatures were no lower than 20°C during the day and no lower than 18°C at night. Plants were checked daily for regrowth after defoliation and new leaves were removed.

On December 1, final observations were taken on percent bud break; only the top 7 nodes and the growing point were considered in this determination. Percent tip dieback (100 x length of dead shoot/ total shoot length) was recorded in mid-March.

The pattern of percent bud break was very similar to that of tip dieback within each growing condition (see Fig. 1) except for the unexpected recurrence of tip dieback in plants from the warm chamber and the lathhouse. The date on which defoliation no longer induced bud break was August 24 in the warm chamber, September 7 in the cool chamber, and September 28 in the lathhouse. These dates correspond to the time of vegetative maturity development in all three cases. In a separate study performed with the same clone in the same season, plants which were left outside after defoliation stopped refoliating several weeks before the development of vegetative maturity[1] which is consistent with Fuchigami's results (3).

The growing conditions into which defoliated plants are placed, then, do have an effect on the relationship between defoliation-induced bud break and tip dieback in red-osier dogwood. When plants are left under dormancy-inducing (natural) conditions after defoliation, refoliation stops several weeks prior to vegetative maturity development (3). When the defoliated plants are placed

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[1] Nissila, unpublished results.

in a warm greenhouse, bud break continues until the time of vegetative maturity development.

The period during which defoliation stimulates bud break under natural conditions is clearly summer dormancy. When defoliation stimulates bud break under greenhouse conditions, but not natural conditions, the plants could still be considered to be in a state of summer dormancy. Since environmental conditions are responsible for holding the buds in check, the buds could be considered to be quiescent under natural conditions during this period. Leaves are still necessary at this time for the development of vegetative maturity, and plants defoliated during this period suffer sever tip dieback (3). When defoliation will not stimulate bud break under conditions conducive to active growth, plants are in a state of winter dormancy. Using this terminology, the development of vegetative maturity corresponds to the onset of winter dormancy in red-osier dogwood.

This discovery provides a much simpler means to determine vegetative maturity experimentally. The original method requires daily re-defoliation of test plants and observation of resultant tip dieback after bud break the next spring. Using defoliation-induced bud break in the greenhouse as an index of seasonal development, it is necessary to defoliate only once and then observe plants for regrowth over the course of the next few weeks. This method will save time and space in studies related to vegetative maturity development.

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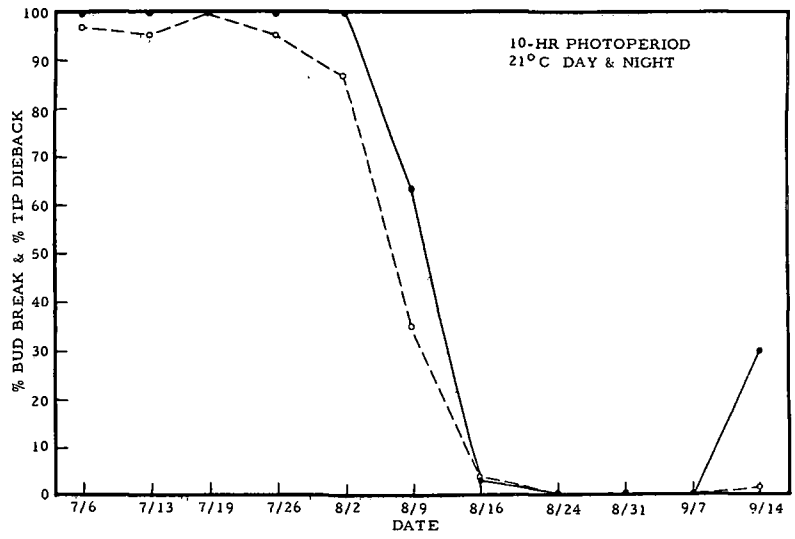
Fig. 1. Bud break and tip dieback of defoliated plants which had been growing in 3 different environments prior to defoliation. ●——● , tip dieback; o--o, bud break.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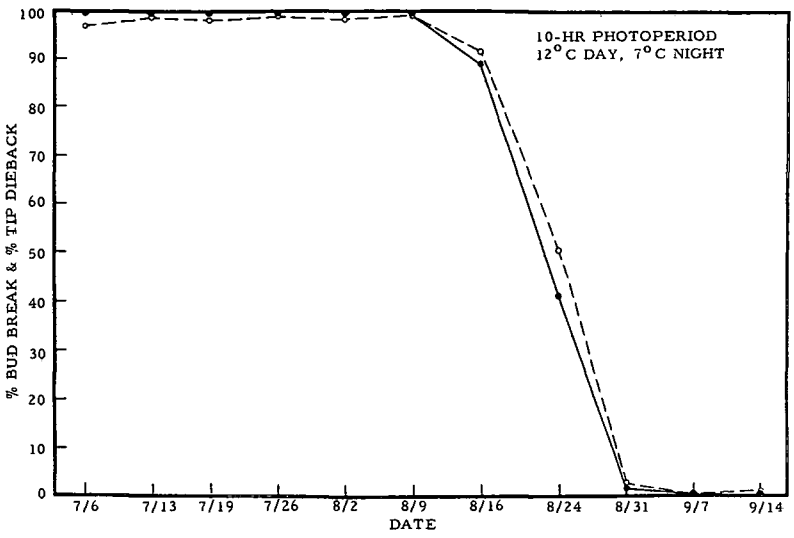
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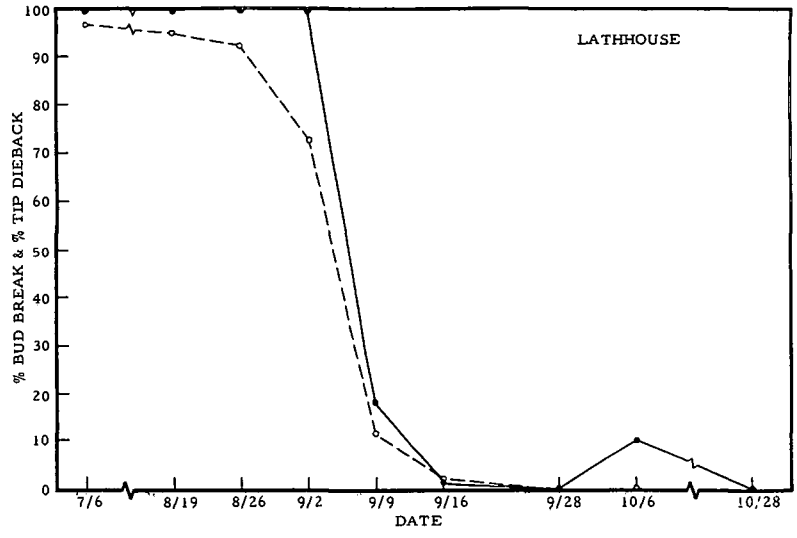
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ETHYLENE PRODUCTION AS AN INDICATOR OF SEASONAL DEVELOPMENT IN RED-OSIER DOGWOOD (*CORNUS STOLONIFERA* MICHX.)[1]

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Additional index words. Dormancy, vegetative maturity, deciduous, nursery stock, tip dieback

Abstract. Ethylene evolution from excised plant parts was tested as an indicator of stage of seasonal development in red-osier dogwood. A reduction in ethylene production occurs several weeks prior to the time when defoliation can be safely accomplished. This reduction occurs synchronously over the length of the plant, though ethylene production by basipetal tissues prior to the decrease was lower than that by more acropetal tissues. The pattern of change in ethylene production by nodal tissue, which included the axillary buds and about 5 mm of petiole, seemed to be least affected by environmental growing conditions. Ethylene could be used as a predictor for the harvestable stage of deciduous nursery plants.

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Introduction

Deciduous nursery stock must be defoliated before harvest and winter storage, but chemical defoliants applied at a premature stage of dormancy development may cause damage. The stage at which deciduous plants may be safely defoliated and harvested has been termed "vegetative maturity" by Fuchigami (7). There are no visual signs to distinguish a "mature" plant from one that is "immature," and the results of defoliation tests for stage of development are not available until months after testing. The deciduous nursery industry needs a rapid, reliable indicator of harvestability. These studies were initiated to find such a test.

The development of vegetative maturity is intimately associated with dormancy development (7). A concurrent study has shown vegetative maturity to correspond to the onset of winter dormancy in red-osier dogwood, if winter dormancy is defined to be the state when defoliation does not stimulate bud break under conditions conducive to active growth (16). The relationship between ethylene and dormancy (not necessarily winter dormancy) in seeds (2-5, 10-12), corms (8, 18), tubers (15), and buds (17, 18) has been investigated. Generally low levels of ethylene have been associated with dormancy and higher levels with active growth. Preliminary research in this lab comparing ethylene production by stem sections from actively

growing and dormant plants of red-osier dogwood showed much less ethylene production by dormant plants. It was not known when this change occurred, and the following study was performed to ascertain whether the reduction in ethylene production could be used to predict vegetative maturity in red-osier dogwood. The effects of tissue type and position on ethylene production were also investigated.

Materials and Methods

A clone of red-osier dogwood native to Wayland, Massachusetts, was propagated from single node stem cuttings in the spring of 1976. Once the cuttings were rooted they were planted in 5-inch paper pots in a 1:1:1 sand:soil:peat mix and placed in a lathhouse until the start of the experiment. The plants had 1 or 2 leaders and the average height was about 40 cm when the study began. A few days before the start of the experiment, plants were sorted into pairs of similar size and growth habit.

On July 6, 1976, 2 groups of 50 plant pairs each were moved into controlled environment chambers under 10-hour (short day) conditions to induce dormancy development. One chamber was maintained at 21°C day and night. The other was 12°C when the lights were on and 7°C when the lights were off. Light intensity in the chambers was 3634 $\mu w/cm^2$ 15 cm above pot height. A third group, containing 40 pairs of plants, was left under natural photoperiod and

temperature in the lathhouse. Five pairs of plants were sampled at the start of the experiment, and at approximately weekly intervals thereafter for 10 weeks, 5 plants from each controlled environment chamber were randomly selected and sampled. Sampling of the plants in the lathhouse (5 pairs per week) began on August 19, and continued through October 28.

Defoliation test for winter dormancy and maturity. At the time of sampling, 1 plant from each pair was defoliated and moved into a greenhouse where temperatures were no lower than 21°C during the day and 18°C at night. After defoliation, plants were checked at least once a day for regrowth, and newly expanded leaves were removed. On December 1, final observations were taken on percent bud break. Plants were then returned to the lathhouse, which had been covered with 4 mil clear polyethylene to prevent freezing temperatures (this was verified with a hygrothermograph). Percent tip dieback (100 x length of dead shoot/total shoot length) was determined in mid-March after spring growth was evident.

Ethylene production. The other plant from each pair was used for the determination of ethylene production. The evening before a test was to be run, 1 plant from each pair was brought into a controlled temperature room maintained at about 23°C. The following morning the plant parts were excised and placed in vials, which were then sealed with sleeve-type serum stoppers, and incubated in the

dark in the controlled temperature room. Approximately 6 hours later a 1 ml sample of the atmosphere in each vial was injected into a Carle 210 analytical gas chromatograph equipped with a 1.22 m x 3.18 mm 80/100 mesh activated Alumina column and a flame ionization detector, maintained at 100°C with a flow rate of 20 ml/min. The ethylene peak was identified by co-chromatography with authentic ethylene on the Alumina column and a Porapak N column. The tissues were weighed after forced air drying at 60°C for 48 hours.

Leaves, nodes (including the axillary buds and approximately 5 mm of the petioles), and internode sections were sampled from each of 3 positions on the longest leader of each plant. These positions included the first and second node below the growing point (Positions 1 and 2, respectively) and the third node from the bottom of the leader (Position 3) on plants grown in the controlled environment chambers. The first, second, and third nodes below the growing point were sampled on lathhouse-grown plants. The leaf petiole was cut with a razor blade approximately 5 mm from the abscission zone. Nodes and a section from the internode below each node were cut with razor blades arranged at a fixed distance of 7.5 mm.

Ethylene production by leaves from the first and second positions was averaged and called "leaves," and likewise "nodes" and "internodes" refer to ethylene production averaged across the first two positions.

Results and Discussion

Based on the defoliation test, plants grown in the 21°C controlled environment chamber were vegetatively mature and in a state of winter dormancy on August 24, those in the 12/7°C chamber on September 7, and those growing under natural photoperiod and temperature on September 28.

There was a reduction in ethylene production by all tissues at all positions prior to the development of winter dormancy. When ethylene production by leaves and internode sections was plotted against time, the pattern of ethylene production in relation to dormancy development differed between growing conditions (15). Therefore, it was not possible to choose a threshold value of ethylene production by leaves or internode sections to predict winter dormancy and harvestability. On the other hand the pattern of change in ethylene production by nodes was very similar in the 3 growing conditions (see Fig. 1). Such consistency under very dissimilar growing conditions indicates that the pattern could be expected to be the same in different growing seasons. This is essential if ethylene production is to be used as a predictor of harvestability. Based on the data shown in Fig. 1, we would expect plants to be harvestable a month after ethylene production by nodal tissue has dropped below 10 nl/mg dry wt/hr. Ethylene production could probably be used to approximate

the date on which plants would be harvestable, but not to predict it precisely.

Fig. 2 shows the pattern of ethylene production by the nodes at Position 1, which was near the top of the plant, compared to Position 3 which was near the bottom of the leader for plants grown in the controlled environment chambers. In both growing conditions, ethylene production prior to the decrease tended to be greater in the more acropetal tissues. The same pattern occurred in lathhouse-grown plants (16), and was generally apparent in all types of tissue, though it was most pronounced in internode tissue (16).

Leaf abscission began in the tenth week in the $12^{o}/7^{o}$ chamber, concomitant with an increase in ethylene production by nodes and leaves. Ethylene production by internode sections was unaffected (16). Leaves at Position 3 had abscised early in the experiment, and no increased ethylene production can be observed at this position during the tenth week (see Fig. 2).

The cause of the apparent slow-down in ethylene production cannot be determined from this study. The method employed almost certainly involves the measurement of wound-induced ethylene in addition to normal endogenous ethylene production (1). Saltveit[1] found a temporary increase in ethylene production by stem sections

[1]Personal communication.

of several woody plants beginning about $\frac{1}{2}$ hour after excision, with the peak occurring about 2 hours after excision. Preliminary tests in this lab compared ethylene production by stem section of the 3 different lengths from actively growing and dormant plants. The greater the ratio of cut surface to volume, the more ethylene was produced per mg dry weight. The decrease in ethylene production observed during dormancy development could have been caused by a reduction in the capacity of the plants to produce ethylene, an increase in tolerance to stress by wounding, or both.

Leopold et al. (13) have used a method which allows the measurement of internal levels of ethylene before the response to wounding has occurred. Leopold and Brown[2] measured ethylene content of white pine stems in the autumn and spring using this method. Ethylene content was low in September and not detectable in October. After bud elongation began in the next spring, ethylene levels increased until the beginning of June, after which it decreased to a steady state around 0.1 or 0.2 ppm. These results indicate a seasonal pattern of ethylene production in white pine. Such a pattern may exist in red-osier dogwood and be responsible at least in part for the changes observed. Ethephon treatments prior to the vegetatively mature stage postpones the development of vegetative maturity (6). It is

[2]Unpublished results.

possible that a reduction in ethylene production is not only coincidental with, but also necessary for, normal dormancy development.

Studies performed by Nissila (14) indicate there are other tests which show more promise than ethylene production for the prediction of harvestability. However, it is probable that seasonal patterns of ethylene production occur in other woody temperate zone species. Investigation of such patterns could provide additional understanding of the processes occurring during dormancy development.

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Fig. 1. The relationship between winter dormancy development and the reduction in ethylene evolution by nodes of red-osier dogwood. Ethylene curves were shifted in time and superimposed to show their similarity. ●——●, lathhouse; ●—●, 21°C chamber; ●- - -●, 12/7°C chamber. Arrows indicate the time of dormancy development corresponding to each curve; a = 12/7° chamber, b = 21° chamber, c = lathhouse. Bars indicate standard deviations. Each point is the mean of 5 observations.

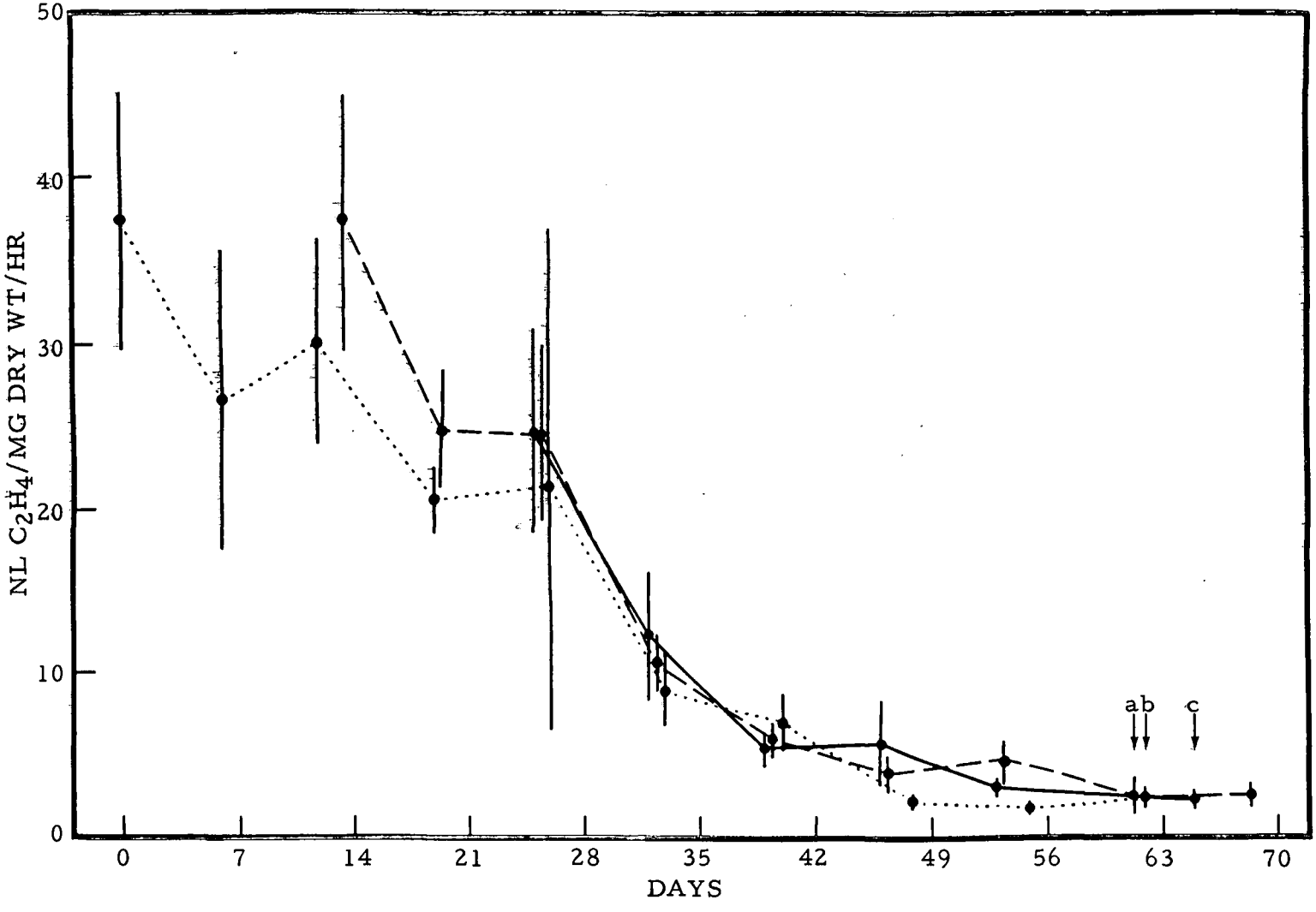
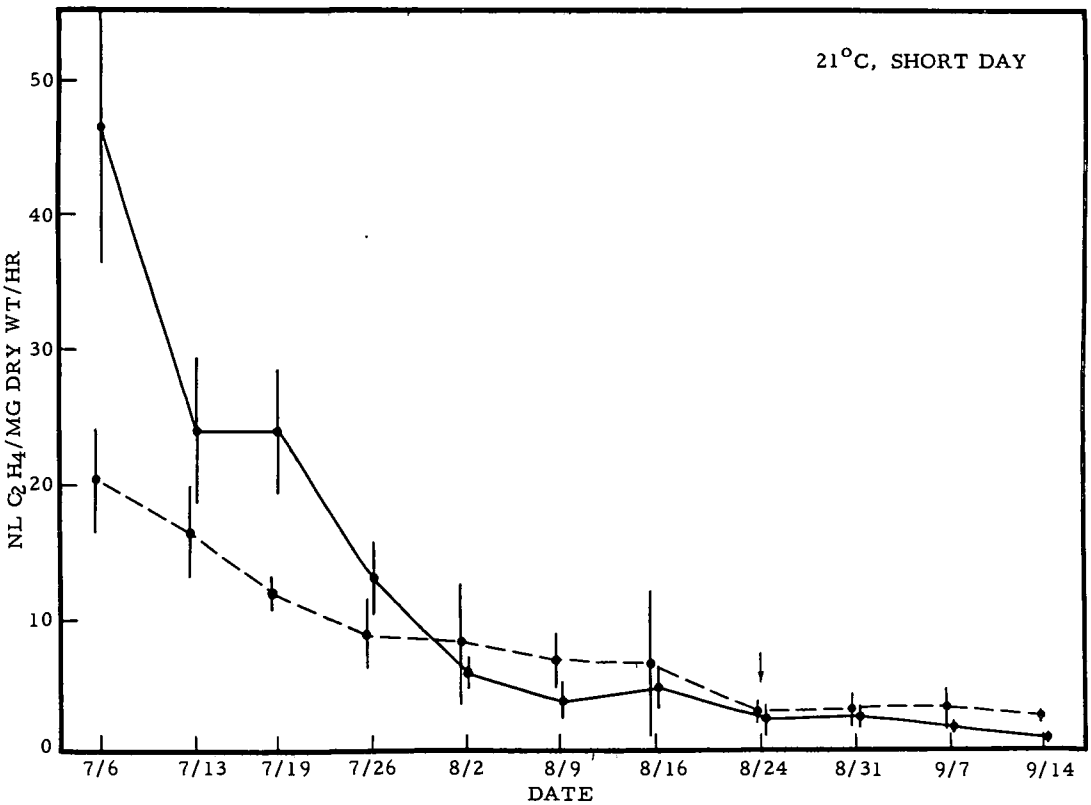
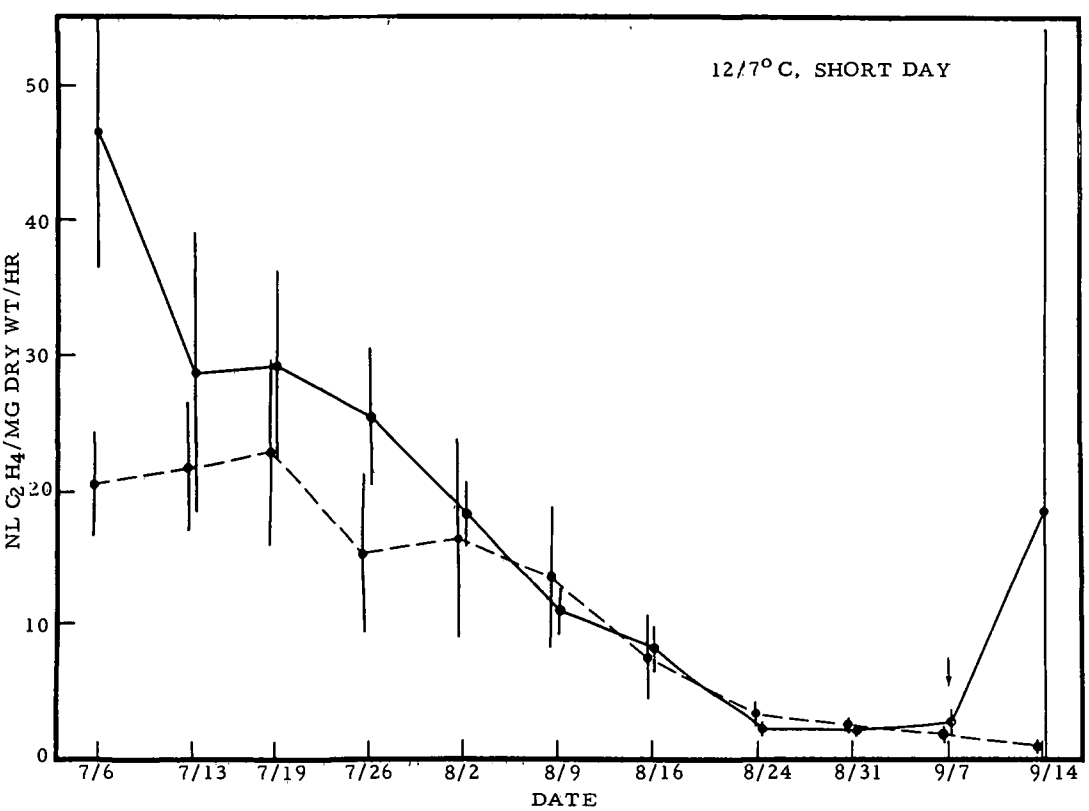

50
40
30
20
10
0
NL C_2H_4/MG DRY WT/HR
0
7
14
21
28
35
42
49
56
63
70
DAYS
a
b
c

Fig. 2. Average ethylene production by nodes from 2 positions on the plants. ●——●, Position 1; ●– –●, Position 3. Bars indicate standard deviations for 5 observations. Arrows indicate the date of maturity and winter dormancy development.


21°C, SHORT DAY
NL C2H4/MG DRY WT/HR
50
40
30
20
10
0
7/6
7/13
7/19
7/26
8/2
8/9
8/16
8/24
8/31
9/7
9/14
DATE


12/7°C, SHORT DAY
NL C2H4/MG DRY WT/HR
50
40
30
20
10
0
7/6
7/13
7/19
7/26
8/2
8/9
8/16
8/24
8/31
9/7
9/14
DATE

APPENDIX

TABLE 1. Average ethylene production by plant parts (nl/mg dry wt/hr) ± one standard deviation.

Trt. -Date	L1	L2	N1	N2	N3	I1	I2	I3
Initial-7/6	16.1 ± 10.8	7 6 ± 1.3	46.5 ± 10.1	28.2 ± 6.7	20.4 ± 3.8	37.3 ± 10.7	24.5 ± 3.3	15.0 ± 4.5
21°C- 7/13	10.2 ± 3.0	6.4 ± 0.7	24.0 ± 5.6	25.4 ± 8.0	16.5 ± 3.3	33.2 ± 5.3	28.8 ± 14.7	13.2 ± 5.1
7/19	17.8 ± 8.2	10.8 ± 9.2	23.9 ± 4.6	25.2 ± 7.8	11.9 ± 1.3	37.6 ± 10.5	19.4 ± 6.4	16.5 ± 8.3
7/26	3.3 ± 1.1	2.2 ± 0.5	13.1 ± 2.8	8.1 ± 1.3	8.8 ± 2.8	9.7 ± 2.7	8.1 ± 3.3	6.8 ± 3.0
8/2	2.5 ± 1.3	2.3 ± 1.1	6.1 ± 1.1	5.5 ± 0.8	8.2 ± 4.5	7.7 ± 3.6	6.2 ± 2.6	6.0 ± 2.7
8/9	1.7 ± 0.8	1.8 ± 0.8	3.8 ± 1.5	3.7 ± 0.8	7.0 ± 2.0	5.6 ± 2.4	4.4 ± 1.8	6.6 ± 3.3
8/6	1.4 ± 0.7	1.5 ± 0.6	4.8 ± 1.6	3.9 ± 1.5	6.6 ± 5.5	2.6 ± 1.1	4.6 ± 1.4	5.5 ± 1.3
8/24	1.0 ± 0.3	1.2 ± 0.7	2.3 ± 1.2	2.4 ± 1.1	3.0 ± 0.9	2.0 ± 1.1	1.9 ± 0.8	3.8 ± 2.0
8/31	1.3 ± 0.5	1.6 ± 0.8	2.6 ± 1.0	2.5 ± 0.4	3.1 ± 1.3	2.6 ± 0.9	2.3 ± 1.0	3.0 ± 0.8
9/7	0.9 ± 0.2	1.0 ± 0.2	1.9 ± 0.2	1.7 ± 0.3	3.4 ± 1.5	1.7 ± 0.4	1.9 ± 0.7	2.7 ± 0.9
9/14	0.7 ± 0.2	1.4 ± 1.6	1.0 ± 0.2	1.7 ± 1.6	2.7 ± 0.5	1.3 ± 0.4	1.2 ± 0.4	3.1 ± 1.5
12/7°-7/13	15.8 ± 10.6	5.9 ± 3.6	28.7 ± 10.5	24.7 ± 10.0	21.7 ± 4.8	30.2 ± 7.7	20.8 ± 6.1	20.1 ± 9.7
7/19	24.5 ± 9.0	11.0 ± 4.3	29.1 ± 7.1	31.1 ± 7.2	22.8 ± 7.0	44.4 ± 9.4	34.7 ± 9.3	15.7 ± 3.1
7/26	17.1 ± 7.6	7.3 ± 3.2	25.4 ± 5.1	15.6 ± 1.5	15.1 ± 6.0	27.7 ± 10.0	14.6 ± 7.8	12.0 ± 5.3
8/2	13.1 ± 5.8	5.8 ± 1.0	18.2 ± 2.5	24.8 ± 31.6	16.4 ± 7.5	20.6 ± 4.1	8.0 ± 1.8	11.2 ± 3.3
8/9	12.1 ± 6.3	4.7 ± 0.8	10.9 ± 1.8	6.8 ± 3.2	13.5 ± 5.4	16.0 ± 5.4	9.0 ± 2.4	10.4 ± 4.3
8/16	8.3 ± 4.4	4.4 ± 1.6	8.1 ± 1.8	5.8 ± 1.7	7.4 ± 3.2	15.1 ± 2.9	8.0 ± 1.6	7.0 ± 1.3
8/24	2.1 ± 0.6	1.4 ± 0.6	2.1 ± 0.7	1.9 ± 0.5	3.0 ± 1.0	2.3 ± 0.7	2.2 ± 0.6	2.8 ± 1.3
8/31	2.1 ± 0.6	1.0 ± 0.5	2.0 ± 0.3	1.5 ± 0.2	2.2 ± 0.5	1.8 ± 0.6	1.8 ± 0.5	3.0 ± 1.4
9/7	2.2 ± 0.8	2.4 ± 1.2	2.6 ± 0.9	2.1 ± 0.4	1.8 ± 0.6	2.2 ± 0.8	1.7 ± 0.6	1.7 ± 0.8
9/14	6.3 ± 10.8	1.8 ± 2.4	18.7 ± 35.9	1.0 ± 0.5	0.8 ± 0.2	1.4 ± 0.6	1.0 ± 0.2	0.9 ± 0.4
LH- 8/19	9.8 ± 6.3	3.6 ± 1.2	31.8 ± 7.7	17.6 ± 6.1	15.1 ± 2.5	25.7 ± 14.8	12.6 ± 4.2	9.6 ± 2.0
8/26	5.6 ± 4.2	2.2 ± 0.8	14.6 ± 4.4	9.8 ± 3.7	7.6 ± 3.0	10.2 ± 3.6	7.0 ± 2.4	6.7 ± 2.6
9/2	1.7 ± 0.5	1.5 ± 0.5	5.8 ± 1.0	4.5 ± 1.4	4.9 ± 1.8	5.3 ± 1.2	4.3 ± 1.7	3.7 ± 1.4
9/9	2.1 ± 0.7	1.6 ± 0.7	6.6 ± 3.6	4.6 ± 1.8	5.5 ± 2.2	6.3 ± 5.4	4.7 ± 1.7	4.1 ± 1.4
9/16	1.7 ± 0.5	1.7 ± 0.8	3.1 ± 0.9	2.9 ± 0.8	3.0 ± 0.8	3.0 ± 0.6	2.5 ± 0.3	2.5 ± 0.4
9/28	1.1 ± 0.4	1.1 ± 0.3	2.3 ± 0.5	2.2 ± 0.9	2.1 ± 1.0	2.1 ± 1.5	1.5 ± 0.6	1.8 ± 0.8
10/6	1.7 ± 0.5	1.6 ± 0.6	2.5 ± 0.6	2.0 ± 0.7	1.9 ± 0.7	2.2 ± 0.9	1.7 ± 0.8	1.6 ± 0.6
10/28	0.9 ± 0.1	0.9 ± 0.3	2.7 ± 0.6	2.3 ± 0.6	1.7 ± 0.9	1.0 ± 0.3	0.8 ± 0.2	0.8 ± 0.2

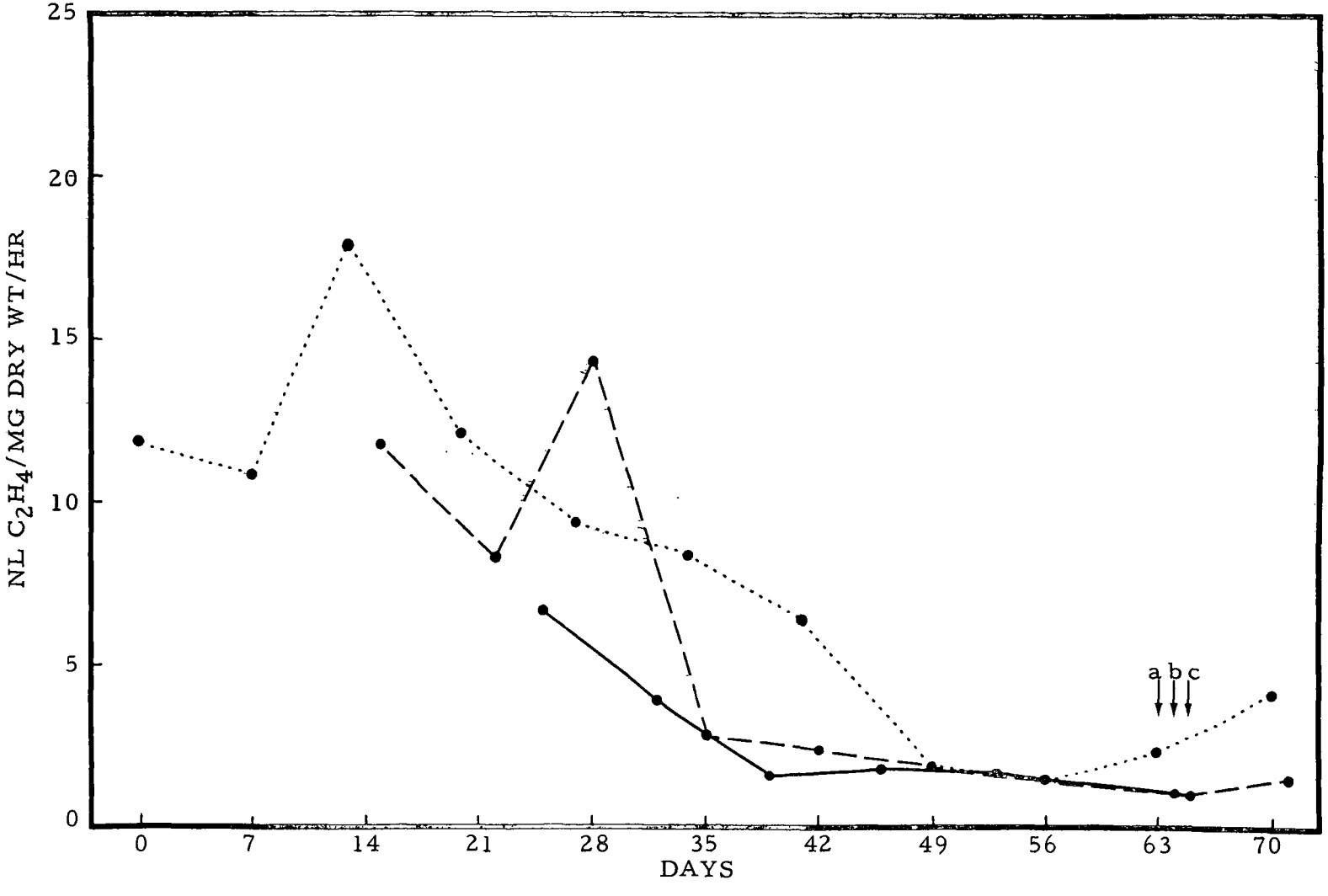
TABLE 2. Average ethylene production (nl/mg dry wt/hr) by different tissues and positions ± one standard deviation.

Trt. -Date		Leaves	Nodes	Internodes	Pos. 1	Pos. 2	Pos. 3
Initial-	7/6	11.8 ± 5.2	37.3 ± 7.7	30.9 ± 4.4	41.9 ± 9.5	26.4 ± 4.9	17.7 ± 4.1
21° -	7/13	8.3 ± 1.7	24.7 ± 3.6	31.0 ± 8.4	28.6 ± 4.6	27.1 ± 11.1	14.8 ± 3.5
	7/19	14.3 ± 6.9	24.5 ± 5.4	28.5 ± 7.7	30.8 ± 6.4	22.3 ± 6.9	14.2 ± 3.7
	7/26	2.8 ± 0.7	10.6 ± 1.7	8.9 ± 2.9	11.3 ± 1.9	8.1 ± 2.1	7.8 ± 2.8
	8/2	2.4 ± 1.2	5.8 ± 0.9	7.0 ± 3.1	6.9 ± 2.3	5.8 ± 1.5	7.0 ± 3.5
	8/9	1.8 ± 0.8	3.8 ± 1.2	5.0 ± 2.0	4.7 ± 2.0	4.1 ± 1.1	6.8 ± 1.9
	8/6	1.5 ± 0.6	4.4 ± 1.5	5.0 ± 1.2	5.2 ± 1.2	4.2 ± 1.4	6.0 ± 4.7
	8/24	1.1 ± 0.5	2.4 ± 1.1	2.0 ± 0.9	2.2 ± 1.1	2.2 ± 0.8	3.4 ± 1.4
	8/31	1.5 ± 0.5	2.5 ± 0.7	2.5 ± 0.9	2.6 ± 1.0	2.4 ± 0.7	3.0 ± 1.3
	9/7	1.0 ± 0.2	1.8 ± 0.2	1.8 ± 0.5	1.8 ± 0.3	1.8 ± 0.3	3.1 ± 1.2
	9/14	1.0 ± 0.9	1.4 ± 0.7	1.2 ± 0.4	1.2 ± 0.3	1.4 ± 0.7	2.9 ± 0.9
12/7° -	7/13	10.8 ± 5.8	26.7 ± 9.4	25.5 ± 5.0	29.5 ± 8.5	22.8 ± 7.0	20.9 ± 6.7
	7/19	17.8 ± 3.2	30.1 ± 6.3	39.6 ± 6.2	36.8 ± 7.3	32.9 ± 6.2	19.3 ± 4.8
	7/26	12.2 ± 4.8	20.5 ± 2.2	20.8 ± 5.2	26.2 ± 6.1	15.1 ± 4.4	13.6 ± 5.5
	8/2	9.4 ± 2.4	21.5 ± 15.3	14.0 ± 2.7	19.1 ± 3.1	16.4 ± 15.4	13.8 ± 5.4
	8/9	8.4 ± 3.2	8.9 ± 2.2	12.5 ± 3.7	13.5 ± 3.6	7.9 ± 2.3	12.0 ± 3.5
	8/16	6.3 ± 2.4	6.9 ± 1.7	11.6 ± 1.3	11.6 ± 1.6	6.9 ± 1.5	7.2 ± 2.3
	8/24	1.8 ± 0.5	2.0 ± 0.6	2.3 ± 0.6	2.2 ± 0.6	2.0 ± 0.5	2.9 ± 1.1
	8/31	1.5 ± 0.3	1.8 ± 0.2	1.8 ± 0.5	1.9 ± 0.4	1.6 ± 0.3	2.6 ± 0.8
	9/7	2.3 ± 0.9	2.3 ± 0.6	2.0 ± 0.7	2.4 ± 0.8	1.9 ± 0.4	1.8 ± 0.6
	9/14	4.1 ± 5.6	9.9 ± 18.1	1.2 ± 0.4	10.0 ± 17.8	1.0 ± 0.3	0.8 ± 0.3
LH -	8/19	6.7 ± 3.6	24.7 ± 6.2	19.1 ± 9.5	28.8 ± 10.0	15.1 ± 4.8	12.4 ± 2.2
	8/26	3.9 ± 2.4	12.2 ± 3.9	8.6 ± 2.8	12.4 ± 3.8	8.4 ± 3.0	7.2 ± 2.6
	9/2	1.6 ± 0.4	5.2 ± 1.0	4.8 ± 1.4	5.6 ± 1.0	4.4 ± 1.6	4.3 ± 1.5
	9/9	1.8 ± 0.6	5.6 ± 2.6	5.5 ± 3.5	6.4 ± 4.2	4.6 ± 1.7	4.8 ± 1.7
	9/16	1.7 ± 0.5	3.0 ± 0.6	2.7 ± 0.4	3.0 ± 0.5	2.7 ± 0.5	2.8 ± 0.6
	9/28	1.1 ± 0.2	2.3 ± 0.6	1.8 ± 1.0	2.2 ± 0.8	1.9 ± 0.8	1.9 ± 0.9
	10/6	1.6 ± 0.4	2.2 ± 0.6	1.9 ± 0.9	2.3 ± 0.8	1.8 ± 0.7	1.8 ± 0.6
	10/28	0.9 ± 0.2	2.5 ± 0.5	0.9 ± 0.2	1.9 ± 0.3	1.5 ± 0.4	1.2 ± 0.5

TABLE 3. Percent (± one standard deviation) and incidence of bud break and tip dieback in defoliated plants.

Trt. -Date		Bud Break		Tip Dieback	
		Percent	Incidence	Percent	Incidence
Initial -	7/6	96.6 ± 4.8	5	100.0 ± 0.0	5
21° -	7/13	95.4 ± 5.5	5	100.0 ± 0.0	5
	7/19	100.0 ± 0.0	5	100.0 ± 0.0	5
	7/26	95.2 ± 5.4	5	100.0 ± 0.0	5
	8/2	86.6 ± 10.1	5	100.0 ± 0.0	5
	8/9	34.6 ± 35.0	4	63.2 ± 37.9	5
	8/6	4.0 ± 8.9	1	1.6 ± 1.5	4
	8/24	0.0 ± 0.0	0	0.0 ± 0.0	0
	8/31	0.0 ± 0.0	0	0.0 ± 0.0	0
	9/7	0.0 ± 0.0	0	0.0 ± 0.0	0
	9/14	1.4 ± 3.1	1	29.6 ± 41.6	2
12/7° -	7/13	98.6 ± 3.1	5	100.0 ± 0.0	5
	7/19	98.0 ± 3.1	5	100.0 ± 0.0	5
	7/26	99.4 ± 1.3	5	100.0 ± 0.0	5
	8/2	98.0 ± 3.1	5	100.0 ± 0.0	5
	8/9	98.6 ± 3.1	5	100.0 ± 0.0	5
	8/16	91.4 ± 11.6	5	89.0 ± 11.4	5
	8/24	50.6 ± 47.2	3	41.0 ± 33.2	5
	8/31	2.6 ± 4.3	2	1.6 ± 3.0	2
	9/7	0.0 ± 0.0	0	0.0 ± 0.0	0
	9/14	0.6 ± 1.3	1	0.2 ± 0.8	1
LH -	8/19	95.0 ± 4.7	5	100.0 ± 0.0	5
	8/26	92.4 ± 13.4	5	100.0 ± 0.0	5
	9/2	72.6 ± 37.7	5	100.0 ± 0.0	5
	9/9	11.2 ± 10.8	4	18.2 ± 35.6	3
	9/16	2.0 ± 4.5	1	1.3 ± 2.1	2
	9/28	0.0 ± 0.0	0	0.2 ± 0.4	1
	10/6	0.0 ± 0.0	0	10.2 ± 22.8	1
	10/28	0.0 ± 0.0	0	0.0 ± 0.0	0

Fig. 1. The relationship between maturity development and ethylene evolution by leaves. Ethylene curves were shifted in time and superimposed. ●——●, lathhouse; ●—·—●, 21° C chamber; ●- - - -●, 12/7° C chamber. Arrows indicate the time of maturity development corresponding to each curve; a = 12/7° C chamber; b = 21° C chamber, c = lathhouse.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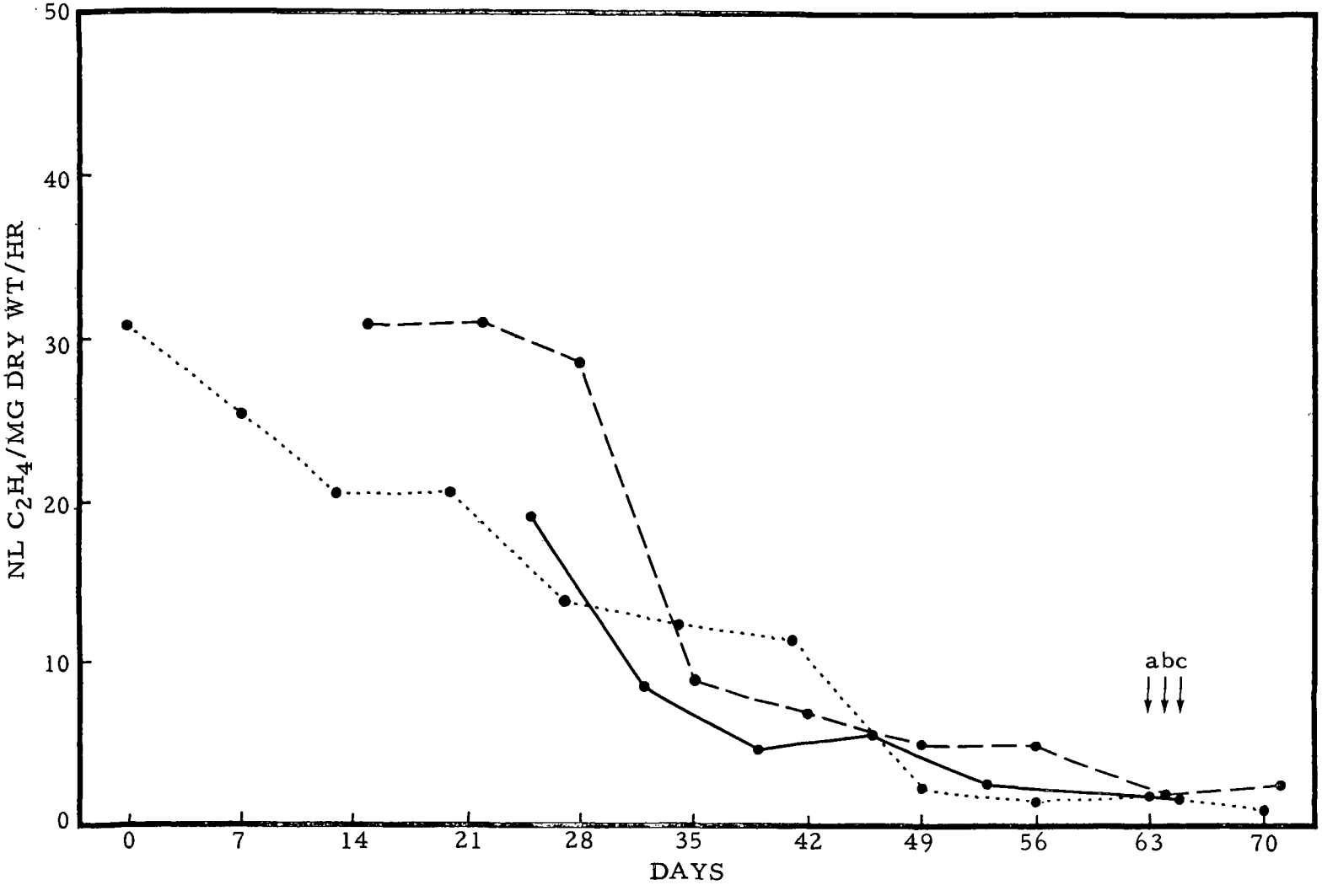
20
15
10
5
0
NL C_2H_4/MG DRY WT/HR
0
7
14
21
28
35
42
49
56
63
70
DAYS
a
b
c

Fig. 2. The relationship between maturity development and ethylene evolution by internode sections. Ethylene curves were shifted in time and superimposed. ●——●, lathhouse; ●— —●, 21° C chamber; ●- - - - -●, 12/7° C chamber. Arrows indicate the time of maturity development corresponding to each curve; a = 12/7° C chamber, b = 21° C chamber, c = lathhouse.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7
14
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42
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63
70
DAYS
abc