Practical Application of Plant Growth Regulator on Horticultural Crops

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INTRODUCTION

Plant growth regulators have been an important component in agricultural production even prior to the identification of plant hormone. Plant growth regulators are now used on over one million hectares worldwide on a diversity of crops each year. However, most of these application are confined to high-value horticultural crops rather than field crops, although there are several significant exceptions.

Many plant growth regulators are now used for increasing crops yields. Nevertheless, most of the current uses for plant growth regulators in the high-value horticultural crops are not, however, for compounds that increase crop yield directly, either by increasing the total biological yield or the harvest index. Rather, compounds that provide economic benefit by enhancing crop quality or aid in more efficient crop management are more common.

Plant growth regulators that aid in crop yield and management fall into several categories. First, plant growth regulators are used to increase crops yield including horticultural crops. Second, plant growth regulators can be used as direct replacement for hand labor in horticultural crop production other than harvesting. Third, plant growth regulators can be used for manipulation of the harvest date in a wide range of crops. Fourth, reducing the fruit removal force by the application of growth regulator allowed the development and use of mechanical harvesting equipment.

Plant growth regulators are useful because they can in some way modify plant development. This may occur by interfering with the biosynthesis, metabolism, or translocation of plant hormone, or applied plant growth regulator may increase or decrease the endogenous levels of plant hormone when their endogenous levels are below or exceed that needed to change the course of plant development. Thus, the lecture will be focused on
the categories mentioned above.

**DEFINITION OF PLANT HORMONE**

Plant hormones play an integral role in controlling the growth and development of plants. A plant hormone is generally described as an organic compound synthesized in one part of the plant and translocated to another part, where in low concentrations (e.g., <1mM and often <1μM) it elicits a physiological response.

A problem with this definition is that in all cases plant hormones are not necessarily translocated. A prime example of such a case is the hormone ethylene which may bring about changes in the same tissue or even the same cell in which it is synthesized. Rather than to get caught up in semantics, perhaps a better idea is to outline what a hormone is not.

Inorganic compounds such as Ca^{2+} and K^{+} cause physiological responses and can be moved throughout the plant, yet they are not synthesized by the plant and are therefore not plant hormones. The same is the case for synthesized growth regulatory substances such as 2,4-D regardless of its structure being similar to that of auxin.

The definition states that the hormone must be translocated but mentions nothing about how or how far, or even whether it need only cause a response in the cells it is translocated to. Ethylene can affect the cells in which it is synthesized as well as cells to which it is translocated.

Sucrose is not a hormone even though it is synthesized, translocated, and stimulates a response (growth) because it is only at high concentrations that growth will occur. The same is the case for many other sugars as well as amino acids, organic acids, and other metabolites which are usually present in concentrations ranging from >1mM up to 50 mM and in some cases even higher than 50mM.

**THE NATURE, OCCURRENCE, AND EFFECT OF THE PLANT HORMONES**
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Auxins

\[
\text{N} \quad \text{H} \quad \text{CH}_2\text{-COOH}
\]

Nature of Auxins

Indole-3-acetic acid (IAA) is the main auxin in most plants. Compounds which serve as IAA precursors may also have auxin activity (e.g., indoleacetaldehyde). Some plants contain other compounds that display weak auxin activity. IAA may also be present 4-chloro-IAA has also been reported in several species (11), though it is not clear to what extent the endogenous auxin activity in plants can be accounted for by 4-Cl-IAA. Several synthetic auxins are also used in commercial applications.

Sites of biosynthesis

IAA is synthesized from tryptophan or indole primarily in leaf primordia and young leaves, and in developing seeds.

Transport

IAA transport is cell to cell. Transport to the root probably also involves the phloem.

Functions of Auxin

The following are some of the responses that auxin is known to cause.
1. Stimulates cell elongation
2. Stimulates cell division in the cambium and, in combination with cytokinins in tissue culture
3. Stimulates differentiation of phloem and xylem
4. Stimulates root initiation on stem cuttings and lateral root development in tissue culture
5. Mediates the tropistic response of bending in response to gravity and light
6. The auxin supply from the apical bud suppresses growth of lateral buds
7. Delays leaf senescence
8. Can inhibit or promote (via ethylene stimulation) leaf and fruit abscission
9. Can induce fruit setting and growth in some plants
10. Involved in assimilate movement toward auxin possibly by an effect on phloem transport
11. Delays fruit ripening
12. Promotes flowering in Bromeliads
13. Stimulates growth of flower parts
14. Promotes (via ethylene production) femaleness in dioecious flowers
15. Stimulates the production of ethylene at high concentrations

Gibberellins

Nature of GA

The gibberellins (GAs) are a family of compounds based on the ent-gibberellane structure. While the most widely available compound is GA₃ or gibberellic acid, which is a fungal product, the most important GA in plants is GA₁, which is the GA primarily responsible for stem elongation. Many of the other GAs are precursors of the growth-active GA₁.

Sites of biosynthesis

GAs are synthesized from mevalonic acid in young tissues of the shoot and developing seed. It is uncertain whether synthesis also occurs in roots.
Transport

GAs are probably transported in the phloem and xylem.

Functions of Gibberellins

Active gibberellins show many physiological effects, each depending on the type of gibberellin present as well as the species of plant. Some of the physiological processes stimulated by gibberellins are outlined below.

1. Stimulate stem elongation by stimulating cell division and elongation.
2. Stimulates bolting/flowering in response to long days.
3. Breaks seed dormancy in some plants which require stratification or light to induce germination.
4. Stimulates enzyme production (α-amylase) in germinating cereal grains for mobilization of seed reserves.
5. Induces maleness in dioecious flowers (sex expression).
6. Can cause parthenocarpic (seedless) fruit development.
7. Can delay senescence in leaves and citrus fruits.

Cytokinins

![Cytokinins](image)

Nature of Cytokinins

CKs are adenine derivatives characterized by an ability to induce cell division in tissue culture (in the presence of auxin). The most common cytokinin base in plants is zeatin. Cytokinins also occur as ribosides and ribotides.
Sites of biosynthesis

CK biosynthesis is through the biochemical modification of adenine. It occurs in root tips and developing seeds.

Transport

CK transport is via the xylem from roots to shoots.

Cytokinin Functions

A list of some of the known physiological effects caused by cytokinins are listed below. The response will vary depending on the type of cytokinin and plant species.

1. Stimulates cell division.
2. Stimulates morphogenesis (shoot initiation/bud formation) in tissue culture.
3. Stimulates the growth of lateral buds-release of apical dominance.
4. Stimulates leaf expansion resulting from cell enlargement.
5. May enhance stomatal opening in some species.
6. Promotes the conversion of etioplasts into chloroplasts via stimulation of chlorophyll synthesis.

Abscisic Acid

Abscisic acid is a single compound with the above formula. Its name is rather unfortunate. The first name given was "abscisin II" because it was thought to control the abscission on cotton bolls. At almost the same time
another group named it "dormin" for a purported role in bud dormancy. By a compromise
the name abscisic acid was coined. It now appears to have little role in either abscission or
bud dormancy, but we are stuck with this name. As a result of the original association with
abscission and dormancy, ABA has become thought of as an inhibitor. While exogenous
application can inhibit growth in the plants ABA appears to act as much as a promoter as
an inhibitor, and a more open attitude towards its overall role in plant development is
warranted.

**Sites of biosynthesis**

ABA is synthesized from mevalonic acid in roots and mature leaves, particularly in
response to water stress. Seeds are also rich in ABA which may be imported from the
leaves or synthesized *in situ*.

**Transport**

ABA is exported from roots in the xylem and from leaves in the phloem. There is some
evidence that ABA may circulate to the roots in the phloem and then return to the shoots
in the xylem.

**Functions of Abscisic Acid**

The following are some of the physiological responses known to be associated with
abscisic acid.

1. Stimulates the closure of stomata (water stress brings about an increase in ABA
   synthesis).
2. Inhibits shoot growth but will not have as much affect on roots or may even promote
growth of roots.
3. Induces seeds to synthesize storage proteins.
4. Inhibits the affect of gibberellins on stimulating *de novo* synthesis of \( \alpha \)-amylase.
5. Has some effect on induction and maintenance of dormancy.
6. Induces gene transcription especially for proteinase inhibitors in response to wounding
   which may explain an apparent role in pathogen defense.
Ethylene

\[
\begin{align*}
\text{H} & \text{C} \equiv \text{C} \\text{H} \\
\text{H} & \text{C} \equiv \text{C} \\text{H}
\end{align*}
\]

Nature of Ethylene

The gas ethylene (\(C_2H_4\)) is synthesized from methionine in many tissues in response to stress. It does not seem to be essential for normal vegetative growth. It is the only hydrocarbon with a pronounced effect on plants.

Sites of biosynthesis

Ethylene is synthesized by most tissues in response to stress. In particular, it is synthesized in tissues undergoing senescence or ripening.

Transport

Being a gas, ethylene moves by diffusion from its site of synthesis. A crucial intermediate in its production, 1-aminocyclopropane-1-carboxylic acid (ACC) can, however, be transported and may account for ethylene effects at a distance from the causal stimulus.

Functions of Ethylene

Ethylene is known to affect the following plant processes.
1. Stimulates the release of dormancy.
2. Stimulates shoot and root growth and differentiation (triple response)
3. May have a role in adventitious root formation.
4. Stimulates leaf and fruit abscission.
5. Stimulates Bromiliad flower induction.
7. Stimulates flower opening.
8. Stimulates flower and leaf senescence.
9. Stimulates fruit ripening.

**Salicylates**

![Salicylates structure]

Salicylates have been known to be present in willow bark for quite some time. They have only recently been recognized as potential growth regulators in plants. Salicylic acid is synthesized from the amino acid phenylalanine. It has numerous effects including:

1. Thermogenesis in Arum flowers.
2. Plant pathogen resistance-stimulates plant pathogenesis protein production.
3. Reported to enhance longevity of flower.
4. Reported to inhibit ethylene biosynthesis.
5. Reported to inhibit seed germination.
6. Blocks the wound response.
7. Reverses the effects of ABA.

**Jasmonates**

![Jasmonates structure]

Jasmonates are represented by Jasmonate and its methyl ester. They were first isolated from the jasmine plant in which the methyl ester is an important product in the perfume industry. Jasmonic acid is synthesized from linolenic acid which is an important fatty acid. Jasmonates have a number of effects such as:
1. Inhibition of many processes such as growth and germination.
2. Promotion of senescence, abscission, tuber formation, fruit ripening, pigment formation, and tendril coiling.
3. They appear to have important roles in plant defense by inducing proteinase synthesis.

PRACTICAL USE OF PLANT GROWTH REGULATORS

Auxins

The auxin-type plant growth regulators comprise some of the oldest compounds used in agriculture. Shortly after indole acetic acid (IAA) was identified, it was synthesized and became readily available. IAA was not found in itself to be useful in agriculture because it is rapidly broken down to inactive products by light and microorganisms. Nevertheless, a number of synthetic compounds were found to act similarly to IAA in the auxin bioassay tests. Indolebutyric acid (IBA) and NAA were found to increase root development in the propagation of stem cuttings. 2,4-dichlorophenoxyacetic acid (2,4-D) stimulates excessive, uncontrolled growth in broadleaf plants for which it is used as a herbicide. NAA is used to reduce the number of fruit that have set in apple, whereas 4-chlorophenoxyacetic acid (4-CPA) is used to increase fruit set in tomato. The auxins 2,4,5-trichlorophenoxypropionic acid (2,4,5-TP) and the dichlophenoxoy analog (2,4-DP) are used to prevent abscission of mature fruit in apple

Propagation

Rooting of stem cuttings was one of the first uses of auxins. The most common compound used is IBA, which has only weak auxin activity, but is relatively stable and insensitive to the auxin degrading enzyme systems. It is also not readily translocated. Other compounds such as NAA and 2,4-D will also promote root development, however, these compounds are more easily translocated to other parts of the stem cutting where they may have toxic effects. The auxins stimulate root development by inducing root initials that differentiate from cells of the young secondary phloem, cambium, and pith tissue.
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Stimulation of fruit set

One of the first recorded effects of auxins was the stimulation of fruit set in unpollinated ovaries of solanaceous plants. It is known that pollen was a rich source of auxin, and that in some species pollination alone was all that was required for fruit set to occur. In tomato, chemical stimulation of fruit set is all that is needed for fruit growth to take place as well. In addition, compounds that block the transport of auxin from the ovary to the pedicel of the flower also stimulate fruit set. It seems likely, therefore, that given environmental conditions somewhat inhibitory to fruit set, application of auxin to flowers could promote this process. In California, the early spring crop of tomatoes is treated with 4-CPA at 25-50 ppm to stimulate fruit set at a time of the year when cool night temperatures that inhibit fruit set in tomato are likely. This treatment results in an increase in yield and earlier harvest.

Chemical thinning

Removal of excessive numbers of young fruit from apple and pear trees is a common orchard management practice, although this results in drastic reductions in the total biological yield. There are two main reasons for removing as much as 80% of the flowers: first, to increase the total marketable yield by increasing the size of the remaining fruit, and second, to reduce the phenomenon of biennial bearing in order to maintain production levels from year to year. The effect of fruit thinning on fruit size is probably related to the leaf/fruit ratio. As this ratio is reduced below 30/1, fruit size is reduced as well. The time in which fruit thinning is done is as important to fruit size as the amount of fruit thinning. In order to improve flower bud production and fruit size in apple, thinning should take place within 30 days from full bloom. In apple, the period of cell division in the fruit is brief, ending approximately 20 days after full bloom. Removing excess fruit during this period can stimulate cell division within the remaining fruit. This early period is also of critical importance for floral initiation, the time when next year's crop will be partially determined. The two auxin-type compounds used in chemical thinning of apple and pear are NAA and NAAm (naphthalene acetamide). NAA is applied at 2-5ppm, 7-20 days after full bloom, whereas NAAm is effective during the same time period, but higher rates (17~34ppm) are used.

Several mechanisms have been proposed to explain the effect of auxins on fruit abscission.
Observations that auxin application reduced the early drop of flowers and fruit soon after the 
bloom period led to the suggestion that auxin first stimulated fruit set, and then due to 
increased competition between fruits for nutrients and assimilates, a greater percentage of fruit 
abscised during the June-drop period. This early increase in fruit set, however, is not always 
observed. It is proposed that fruit abscission occurs because NAA and NAAm induce embryo 
abortion. Without seed growth, fruit senescence and abscission take place prematurely. While 
the number of viable seeds is often correlated with fruit abscission, this is not always the 

case, suggesting that embryo abortion may not be the primary factor resulting in abscission. 
NAA does cause increased ethylene evolution from apple fruit within one day after 
application. Ethylene is known to reduce auxin transport from the leaf blade to the petiole, 
and to induce the synthesis of enzymes that degrade the abscission zone. Perhaps the 
induction of fruit abscission by NAA is mediated by ethylene, which stimulates abscission of 
fruit in a similar manner to its effect on the abscission of leaves.

While not strictly speaking an auxin, the compound carbaryl (1-naphthyl-N-methyl-
1-carbamate) is used commonly for chemical thinning in apple and is effective over a longer 
period of time than NAA. Carbaryl seems to induce abscission by interfering with assimilate 
or hormonal transport between the developing seeds and the fruit.

Prevention of fruit drop

Frequently, the mature fruit of apple, pear, lemon, and grapefruit will abscise prior to the 
time of commercial harvest. This obviously reduces the potential crop yield, and may result 
in the tendency to begin harvesting the crop earlier than is desirable, resulting in lower 
quality fruit. Under natural conditions, there seems to be an inverse relationship between 
auxin content of the fruit, and the tendency toward abscission. The role of auxin in 
abscission is complicated. Clearly, application of auxin soon after fruit set results in an 
acceleration of abscission, however, when auxins such an 2,4,5- DP, NAA, and 2,4-D are 
applied during the mid-stages of fruit growth, abscission is delayed or prevented. In addition, 
auxin application may decrease the response of fruit abscission zone to exogenously applied 
ethylene. NAA and 2,4,5-TP are used at 10-20ppm just prior to the beginning of fruit drop 
in apple. Repeat applications may be necessary with NAA or 2,4,5-TP prevent fruit drop for 
a longer period. In citrus, 2,4-D at 25ppm prevents premature fruit drop and allows an 
extension of the harvest season into the summer.
**Herbicidal action**

2,4-D and picloram (4-amino-3,5,6-trichloropicolinic acid) are two auxin-type herbicides that at low concentration bring about growth responses in plants similar to IAA. At higher concentrations they are herbicidal. 2,4-D is commonly used to control broadleaf weeds in grasses, and picloram is used for vegetation control on non-crop land because of its high activity and soil persistence. Both compounds cause epinastic bending in leaves, a cessation in growth in length, and increased radial expansion. After several days tumors may form, followed by a softening and collapse of the tissue. Epinastic bending and stem swelling are characteristic of ethylene effects on plants, and auxin induced ethylene biosynthesis may partially account for the effect of these compounds on plant growth. Treatment with inhibitors of ethylene synthesis or action in the presence of 2,4-D, however, do not reverse the herbicidal effects of the auxins. Auxin herbicides cause an increase in DNA, RNA, and protein levels in treated tissue. The greatest effect, however, is on RNA levels. Specific mRNAs are induced by auxin treatment, and ethylene apparently plays no role in the expression of these mRNAs. In addition, in resistant plants the level of RNAase activity is higher than in sensitive plants. One aspect of the herbicidal activity of the synthetic auxins seems clearly to be a disturbance in RNA metabolism of the cell.

**GIBBERELLINS**

Despite considerable enthusiasm for the potential uses for gibberellic acid in agriculture that existed when this compound was rediscovered by US and British scientists in the 1950's, major GA use remains limited to fruit crops, the malting of barley, and extension of sugarcane growth in certain production regions.

There are about 120 gibberellins found in both higher plants and the *Gibberella* fungus, although only two commercial products are available, GA₃ and a mixture of GA₄ and GA₇. Both are produced by fermentation cultures of the fungus. A formulation of GA₄/7 and benzyladenine is also available that is being used to induce apple fruit elongation, and to increase the extent of lateral branching in young trees.

*Increasing fruit size in grape*
GA is used extensively on seedless grape varieties to increase the size and quality of the fruit. Pre-bloom sprays of 20ppm induce the rachis of the fruit cluster to elongate. This creates looser clusters that are less susceptible to disease during the growing season. GA also reduces pollen viability, as well as decreasing ovule fertility in grape. Application of GA at bloom, therefore, results in a decrease in fruit set, which reduces the number of berries per cluster, but increases the weight and length of the remaining fruit. An additional application of GA during the late bloom to early fruit set period will further increase berry size. It has been suggested that this later application of GA increases the mobilization of carbohydrates to the developing fruit(Table 1, Fig 1).

Seeded varieties generally do not respond favorably to GA treatment. However, in Japan and Korea, the seeded variety 'Delaware', is cluster-dipped in 100ppm GA to induce parthenocarpic fruit development and increase berry size.

Table 1. Effects of GA3 applied at bloom and/or fruit set on fruit growth in 'Thompson Seedless' grapes.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Berry Number</th>
<th>Cluster compactness</th>
<th>Berry Wt. (G)</th>
<th>Berry length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>91</td>
<td>3.9</td>
<td>2.7</td>
<td>1.8</td>
</tr>
<tr>
<td>GA at bloom</td>
<td>61</td>
<td>2.8</td>
<td>3.3</td>
<td>2.3</td>
</tr>
<tr>
<td>GA at fruit set</td>
<td>90</td>
<td>4.1</td>
<td>4.0</td>
<td>2.3</td>
</tr>
<tr>
<td>GA at bloom+fruit set</td>
<td>64</td>
<td>3.0</td>
<td>4.8</td>
<td>2.6</td>
</tr>
</tbody>
</table>

Fig. 1. Effect of GA3 on the growth of Thompson seedless grape. Left; untreated check, Right; GA3 treated.
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Stimulating fruit set

Not all crops respond as positively as the tomato to auxin-induced fruit set. However, a number of deciduous fruit tree species such as apple and pear, as well as some citrus species, can be induced to set fruit with GA, or a combination of GA and auxin. In Europe, poor fruit set in apple and pear can drastically reduce crop yield. Consistently unfavorable weather during the pollination period has led to the development of a hormone mixture to induce parthenocarpic fruit set in apple. In pear, spring frost injury to the ovules or style can prevent fertilization and the stimulation for fruit set. Application of GA$_3$ at 15–30 ppm can induce parthenocarpic fruit and salvage what would have been a lost crop.

In citrus, fruit set of mandarin oranges is often light. Application of GA during full bloom can increase in endogenous GA-like substances in the region above the branch girdle.

Effects on fruit ripening

GAs are used to delay fruit ripening in lemon in order to increase the availability of fruit during the months of May–August when demand is high, but production is low. GA is applied in November or December in order to delay the harvest date, and increase storage life of the fruit (Table 2).

Delaying harvest is also important for a number of other citrus species including 'Navel' oranges and grapefruit. While fruit abscission can be controlled by 2,4-D, after maturity is attained, changes associated with the usefulness of holding the fruit on the tree longer in order to allow harvest to take place during the period of high consumer demand. GA application will reduce the occurrence of physiological rind disorders such as water spot, creasing, rind staining, and softening by delaying senescence of the rind tissue. GA$_4$ is registered for use on 'Golden Delicious' apple to reduce russetting, a physiological disorder that results from abnormal cell division in the epidermal layer of the fruit.
Table 2. Influence of gibberellic acid on lemon tree harvest patterns one year after treatment.

<table>
<thead>
<tr>
<th>GA Treatment (ppm)</th>
<th>March</th>
<th>May</th>
<th>June</th>
<th>August</th>
<th>October</th>
<th>January</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>9.2</td>
<td>46.3</td>
<td>23.7</td>
<td>12.3</td>
<td>5.8</td>
<td>2.5</td>
</tr>
<tr>
<td>5</td>
<td>10.0</td>
<td>40.6</td>
<td>24.1</td>
<td>16.9</td>
<td>5.8</td>
<td>2.6</td>
</tr>
<tr>
<td>10</td>
<td>10.1</td>
<td>39.4</td>
<td>23.7</td>
<td>170.</td>
<td>7.2</td>
<td>2.6</td>
</tr>
<tr>
<td>20</td>
<td>11.2</td>
<td>37.7</td>
<td>22.7</td>
<td>17.9</td>
<td>8.0</td>
<td>2.5</td>
</tr>
<tr>
<td>40</td>
<td>10.3</td>
<td>36.2</td>
<td>22.8</td>
<td>18.6</td>
<td>9.5</td>
<td>2.6</td>
</tr>
</tbody>
</table>

Increasing yield in sugarcane

Sugarcane growth is very sensitive to the reductions in average daily temperature normally experienced during the winter months in many cane producing regions of the world, especially Hawaii. GA application is used to overcome the reduced growth of the 3–5 internodes undergoing expansion during the cooler winter season. GA treatment has resulted in an increase in fresh weight of harvested cane of 10.9 ton/ha, and has increased sucrose yield by 1.1 ton/ha or 2.8%.

Malting of barley

GA is used to increase the yield of barley malt and to decrease the time required for this process to occur. Embryo growth and yield of malt extract are competitive processes, by increasing the rate of malting relative to embryo growth, a greater yield of malt extract occurs. Application of GA to germinating barley supplements the endogenous level of this hormone and accelerates the production and release of hydrolytic enzymes that degrade the storage proteins and carbohydrates of the endosperm into the sugars and amino acids that comprise the malt extract.

Controlling flower bud production

Spring application of GA is used extensively to accelerate flower bud production in artichoke to allow earlier harvesting dates. If treatment is delayed to coincide with the appearance of flower buds, increases in head size and number have also been reported.
Overcoming environmental constraints on growth

GA is used to break dormancy in plants that have not received an adequate chilling period for the resumption of growth to occur. For rhubarb crowns transplanted in the fall for forcing, GA application can substitute for the cold period normally required for bud development and subsequent petiole elongation. Potato tuber dormancy can also be broken by application of GA. This treatment is of value in the identification and screening of virus infected tubers. In warm climates, where it is possible to plant two crops in a single year, GA treatment can break dormancy of the seed tubers from the first crop in time for a second planting.

In celery production, GA is used to increase petiole elongation under cool weather conditions, where growth is reduced. GA is also being used as a seed treatment in rice to stimulate germination and initial elongation of semi-dwarf cultivars. This allows deeper planting, which improves germination and stand establishment.

Uses in plant breeding

GA can be used to induce precocious cone production in conifers. This may be an especially important aid to genetic improvement in silviculture. Douglas fir for example normally requires 20 years before seed production will occur, with GA4/7 6-year-old trees can be induced to produce seed.

GA has also been used to control flower sex expression in cucumbers and squash. GA application tends to promote maleness in these plants. When gynoecious cucumbers are treated with GA, staminate flowers are produced for breeding purposes.

Bolting and seed stalk formation are promoted by GA in many normally biennial vegetables. This facilitates hybrid seed production for commercial purpose as well as accelerating vegetable variety improvement.

GROWTH RETARDANTS

Plant growth retardants are synthetic compounds, which are used to reduce the shoot length of plants in a desired way without changing developmental patterns or being phytotoxic. This is achieved primarily by reducing cell elongation, but also by lowering the rate of cell division. In their effect on the morphological structure of plants, growth
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retardants are antagonistic to gibberellins (GAs) and auxins, the plant hormones that are primarily responsible for shoot elongation. The first growth retardants, certain nicotinium derivatives, became known in 1949. Many other compounds have subsequently been detected, some of which have been introduced into agronomic or horticultural practice. Plant growth retardants represent the commercially most important group of plant bioregulators (PBRs) or plant growth regulators, although compared to herbicides, insecticides, and fungicides, they play a relatively minor role and represent only a few percent of the worldwide sales of crop-protecting chemicals, totaling approximately US $28 billion in 1999.

In addition to other agronomic tools, PBRs can be used relatively flexibly by the farmer to adjust his crop in a desired way to changes in growing conditions. Plant growth retardants have found a number of practical uses: In intensive small grain cultivation in Europe, they have become an integral part of the production system by reducing the risk of lodging due to intensive rainfall and/or wind; in cotton excessive vegetative growth may be controlled, thereby helping adjust a perennial plant species to an annual cycle of cultivation; fruit trees can be kept more compact, thereby reducing costs for pruning and obtaining a better ratio between vegetative growth and fruit production; the quality of ornamental and bedding plants is generally improved by keeping them compact, which also reduces the space in a greenhouse required for production; costs for trimming hedges and trees and for mowing turf grasses may also be reduced by applying plant growth retardants. For more details on applications of plant growth retardants the reader is referred to.

Reduction of shoot growth can also be achieved by compounds other than growth retardants. For instance, compounds with a low herbicidal activity or herbicides applied at lower rates may cause a stunted shoot without bringing about visible symptoms of phytotoxicity. Reductions in plant productivity have to be expected, however. Examples of such plant growth suppressants are mefluidide, amidochlor, maleic hydrazide, or chlorflurenol, which might be used, for example, to reduce shoot growth of turf grasses. In principle, breeding offers an alternative way to achieve desired alterations in plant development. However, a fixed genotype is less flexible towards changing growing conditions and does not allow an active steering of growth.

We can classify the existing growth retardants into two main groups: ethylene-releasing compounds, such as ethephon, and inhibitors of GA biosynthesis. Most growth retardants act by inhibiting gibberellin (GA) biosynthesis. To date, four different types of such inhibitors
are known: (a) Onium compounds, such as chlormequat chloride, mepiquat chloride, chlorphonium, and AMO-1618, which block the cyclases copalyldiphosphate synthase and ent-kaurene synthase involved in the early steps of GA metabolism. (b) Compounds with an N-containing heterocycle, e.g. ancymidol, flurprimidol, tetcyclacis, paclobutrazol, uniconazole-P, and inabenfide.

These retardants block cytochrome P450-dependent monooxygenases, thereby inhibiting oxidation of ent-kaurene into ent-kaurenoic acid. (c) Structural mimics of 2-oxoglutaric acid,
which is the co-substrate of dioxygenases that catalyze late steps of GA formation. Acylcyclohexanediones, e.g. prohexadione-Ca and trinexapac-ethyl and daminozide, block particularly 3ß-hydroxylation, thereby inhibiting the formation of highly active GAs from inactive precursors, and (d) 16,17-Dihydro-GA₅ and related structures act most likely by mimicking the GA precursor substrate of the same dioxygenases.

Enzymes, similar to the ones involved in GA biosynthesis, are also of importance in the formation of abscisic acid, ethylene, sterols, flavonoids, and other plant constituents.
**Controlling stem growth in greenhouse crops**

The application of growth retardants to potted plants results in shorter more rigid stems and darker green foliage, characteristics that increase the value of the crop. In chrysanthemums, daminozide is effective as a foliar spray and ancymidol may be used as both a foliar spray or a soil drench. Ancymidol treatment may, however, result in a delay in flowering.

In poinsettia, chlormequat chloride is used extensively for height control since it is less expensive than ancymidol. In lily, uniconazol is used because it is the most effective compound for reducing stem height in this plant (Fig. 3).

![Soil drench and Foliar spray](image_url)

**Fig. 3.** Effect of uniconazol on the growth and flowering of the potted *Lilium lancifolium*. Uniconazol (ppm) was applied as soil drenching or foliar spray.

Paclobutrazol (1-(4 chlorophenyl)4,4-imethyl-2-(1,2,4-triazol-1-yl)pentan-3-ol) and the
triazole fungicide triadimefon will also control stem height, but higher concentrations are required in comparison to ancymidol. Another triazole, uniconazole (Sumagic), is also registered for use on poinsettias. This compound is less persistent than paclobutrazol, but provides good height control in a variety of herbaceous and wood ornamental plants.

**Controlling rank growth in cotton**

Under certain conditions of high fertility and favorable environmental conditions excessive vegetative growth of cotton results. Mepiquat chloride(1,1,dimethylpiperidinium chloride) applied at the time of flowering can reduce growth by 20–30%. Early yield of cotton is often increased by this treatment presumably due to greater light penetration into the canopy, thus allowing fruit set to take place in flowers produced on the lower nodes of the plant. Reduced vegetative growth also allows greater coverage of insecticides, fungicides, and defoliants, the latter increasing the efficiency of mechanical harvesting.

**Lodging control in cereals**

Stem lodging is one of the most serious problems in wheat, when this crop is grown under the conditions of high fertility in Europe. The ability to use nitrogen to increase yield is limited by its adverse effect on stem growth. Chloromequat chloride and be used to reduce stem height and increase stem diameter. Yield is increased as a result of reduced stem lodging. In addition, in some years when lodging is not a problem, yield may still be increased because the growth retardant treatment results in a stimulation of tillering. Other cereals do not respond as well to chloromequat chloride as wheat. However, lodging control has been obtained in barley and rye with a combination of mepiquat chloride and ethephon.

**Reducing growth of turfgrass**

Chemical control of grass growth especially on sites such as highway dividers, near airfields, on steep slopes that are difficult or dangerous to mow, can be economically attractive alternative. Several compounds such as chlorflurenol (methyl-2-chloro-9-carboxylate), mefluidide(N-(2,4-dimethyl-5(trifluoromethyl)sulfonyl)amino)-phenylacetamide), and paclobutrazol have been registered for use as plant growth regulators for grass control. Chlorflurenol acts by inhibiting cell division in the shoot meristem, whereas mefluidide
inhibits cell elongation. Both compounds have been found to reduce the frequency of mowings required over the course of the growing season. Paclobutrazol reduces mowing frequency by to an even greater extent than the other compounds: however, it does not effectively suppress seedhead formation. Combinations of paclobutrazol with higher maleic hydrazide, chlorflurenol or mefluidide should provide adequate seedhead suppression and persistence throughout the growing season for almost complete control of grass growth.

**Increasing fruit set in grape**

Application of chlormequat chloride to vinifera grapes before bloom increases fruit set of seeded berries. Cluster fresh weight is increased as a result of treatment. Daminozide is more effective than chlomequat chloride in increasing fruit set of the labrusca varieties. In addition to increasing cluster yield, vine growth is reduced by growth retardant treatment. It is not clear whether the increase in fruit set by the growth retardant is due to a direct effect on this process by decreasing GA levels (GA is used for berry thinning) or an indirect effect resulting from decreased vegetative growth. Exceedingly vigorous shoot growth is often associated with poor fruit setting in the field. Moreover, if shoot tips are removed, fruit set in grape can be increased, and the growth retardants are not capable of further increasing fruit set in detopped plants.

**Advancing fruit color development**

Daminozide may be used to advance anthocyanin production in the fruit skin and flesh of sweet cherry. The rate of color development is increased as well as the total amount of pigment synthesized. Other processes associated with fruit ripening such as fruit softening are not affected by daminozide treatment. Daminozide will also increase anthocyanin synthesis in apple, as well as reduce fruit softening in cold storage and pre-harvest fruit drop. Physiological disorders that develop at harvest or in storage have also been reported to be less severe after a mid-summer application of daminozide. The mechanism by which daminozide enhances color development in fruit is not clear. In apple. daminozide will inhibit ethylene production by blocking the conversion of methionine to aminocyclopropane-l-carboxylic acid, and delay the appearance of the respiratory climacteric. This will permit a delay in the harvest date and perhaps allow anthocyanin production to continue for a longer
time before harvest. In some cases, however, daminozide will not only accelerate color production but also stimulate the production of greater amounts of anthocyanin in the apple skin or the flesh of cherry, therefore suggesting a more direct effect of the compound on pigment synthesis. It has shown that anthocyanin production in apple is associated with increasing activity of the pentose phosphate pathway in the catabolism of carbohydrate. Meanwhile daminozide inhibits succinate dehydrogenase activity in isolated mitochondria. Perhaps by inhibiting Krebs cycle activity, greater carbon flow occurs in the pentose pathway, which forms the essential precursors for anthocyanin. In isolated apple skin discs, however, it was not possible to demonstrate a anthocyanin production in the presence of daminozide.

**Induction of flower bud formation**

Both apple and pear trees do not generally cone into full production until the trees are at least 5 years of age. Flowering can be stimulated in young trees will also occur after daminozide application. Increasing return bloom of mature trees will also occur after daminozide application. in apple, or chlormequat chloride treatment of pear. The growth retardants decrease shoot elongation in fruit trees, and perhaps by inhibiting vegetative growth, flower bud initiation is promoted.

**Controlling tree size**

Acylcyclohexanediones, e.g. prohexadione-Ca and trinexapac-ethyl are probably the most effective compounds found to date for controlling shoot elongation in fruit trees. Controlling tree size with these compounds will be an effective way of maintaining tree height for maximum spraying and harvesting efficiency in conjunction with modern pruning practices such as summer mowing of the tree canopy. Growth of woody landscape plants may also be effectively controlled using the triazoles, paclobutrazol and uniconazole. This practice is particularly useful during nursery container production.
ETHYLENE-RELEASING AGENTS

While the biological effects of ethylene on plant growth have been documented for some time, little practical use of ethylene in agriculture was possible due to its gaseous nature. In the early 1970s experimental formulations of compounds became available that decompose on or within a plant to release ethylene. One of the first of these compounds, ethephon, (2-chloroethylphosphonic acid) is stable at pH values of 4 or less, but at higher pH values, the compound decomposes to produce ethylene, chloride and phosphate ions. Since the cytoplasmic pH is greater than 4, once ethephon is absorbed, cleavage to ethylene inside the cell begins. Two other compounds, etacelasil (2-chloroethyl-tris-ethoxyethoxy silane) and 2-chloroethyl-bis-phenylmethoxy silane, also decompose to ethylene, but much more rapidly.
than ethephon, and are less sensitive to changes in pH.

\[
\begin{align*}
\text{Cl} & \text{CH}_2 \text{CH}_2 \text{PO}_3^- \\
\rightarrow & \text{C}_2\text{H}_4 + \text{Cl}^- + \text{PO}_3^- \\
\end{align*}
\]

2-Chloroethyl-phosphonic acid

**Increasing latex flow in Hevea**

The amount of rubber produced in the form of coagulated latex is a function of the duration of latex flow from the tapping cut that is made in the tree bark. Ethephon is applied to a region near the tapping cut and causes latex flow to increase in duration, resulting in an increase in the volume of latex collected. Rubber yield increases of 50-100% are common. The mechanism for increased flow of latex by ethephon is not well understood. It is believed that lutoids, non-rubber containing bodies within the latex, are disrupted by tapping and cause coagulation or plugging of the latex vessels, as a result of changes in osmotic potential, or shear forces imposed by the high flow rate through the narrow pores of the vessel. Ethephon may stabilize the lutoids making them less susceptible to disruption. Alternatively, it has been proposed that ethephon treatment leads to an increase in cell wall thickening of the vessels making the walls less likely to contract during tapping, and therefore fewer lutoids would be disrupted, all of which will increase latex flow.

**Promoting abscission**

The use of mechanical harvesting devices in cherry production had been limited because the force required to remove the fruit at the time of fruit maturity resulted in damage to the trees. Ethephon may be applied approximately 10 days before anticipated harvest to reduce the fruit removal force to allow mechanical harvesting of the crop without tree injury.

Walnuts are also harvested mechanically after treatment with ethephon. The edible kernel of the walnut reaches maturity come 3-4 weeks before harvest, due to the time required for hull dehiscence. Ethephon treatment accelerates this process. The quality of the harvested
nuts is also increased because they do not remain on the tree for long periods of time after maturation and, therefore, avoid decomposition due to heat and disease.

Olive fruit also have a high fruit removal force at maturity. In addition, the fruit is attached to long willowy branches that do not lend themselves mechanical shaking. Ethephon causes fruit abscission, but also excessive leaf abscission reducing flowering the following spring. Etacelasil can be used, however, because it reduces the attachment force without defoliation, This compound releases ethylene at a much faster rate than does ethephon. There may be a requirement for elevated ethylene levels of longer duration to induce leaf abscission than for fruit abscission, making the silyl compounds more useful as fruit abscission agents than ethephon.

Ethylene-releasing agents are also being used to remove young fruit from apple and peach trees that have set a potentially excessive fruit crop. In peach, 2-chloroethylmethyl-bis-phenylmethoxy silane has provided acceptable fruit abscission without defoliation in many areas of the southeastern US.

Promoting fruit ripening

The ripening process in mature fruit can be accelerated by ethephon application. Presumably the fruit are sensitive to ethylene at this stage of development, but have not produced enough endogenous ethylene to stimulate the ripening process. In apple, ethephon can be used to accelerate fruit softening and advance fruit color production by several weeks, although an additional application of compounds that delay abscission be mad in conjunction with ethephon(Table 3).

In tomato, ethephon is used to accelerate ripening and concentrate maturity of the fruit for mechanical harvesting. Ethephon stimulates the production of lycopene by fruit and therefore can increase total yield of ripe fruit in the production of processing tomatoes, since this crop is harvested at one time only.

In grape, ethephon has been found to promote color development and decrease total fruit acidity. In some of the cooler grape growing regions acidity is often excessive for optimum win quality. Ethephon treatment may also be useful when natural fruit color development is poor.
Table 3. Effects of ethephon, daminozide and NAA on abscission, firmness, and color of ‘McIntosh’ apples.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Drop (%)</th>
<th>Firmness (%)</th>
<th>Red color (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>29</td>
<td>6.6</td>
<td>51</td>
</tr>
<tr>
<td>Daminozide</td>
<td>2</td>
<td>7.4</td>
<td>56</td>
</tr>
<tr>
<td>Daminozide + ethephon</td>
<td>77</td>
<td>7.0</td>
<td>67</td>
</tr>
<tr>
<td>Daminozide + ethephon + NAA</td>
<td>5</td>
<td>7.0</td>
<td>190</td>
</tr>
</tbody>
</table>

**Delaying flowering in fruit crops**

Application of ethephon in the fall of the year prior to the spring flowering period delays bud expansion and anthesis in cherry and peach. Ethephon appears to increase the length of the dormant period of flower bud, which results in a delay in bloom, reducing the potential for spring frost damage to flowers. In some cases, ethephon also increases mid-winter flower bud cold hardiness by maintaining high levels of the cryoprotectants sorbitol and sucrose in the flower pistil.

**Promoting leaf senescence in tobacco**

Ethephon is used to promote leaf yellowing in flue-cured tobacco. Ethephon increases the number of leaves that may be harvested at one time, and decreases the curing time for the leaf. This treatment is especially useful in the cooler tobacco growing regions where the uppermost leaves, which are the last to be harvested, may be damaged by frost.

**ABSCISIC ACID**

There are no practical uses of abscisic acid (ABA) because of the high cost of synthesis and its instability in UV light. However, given the effect of ABA on abscission, dormancy, and transpiration, synthetic ABA analogs might play a significant role in crop production. The ABA analogs LAB 173 711 and LAB 144 143 are acetyleneacetal-type compounds that have been found to reduce water use in crop plants, increase cold hardiness, and delay flowering in peach.
Recently, promotive effect of natural ABA was reported. Application of mixtures of natural type abscisic acid, (S)-(+)-abscisic acid (SABA), and gibberellic acid (GA₃) promoted floral-bud initiation and flowering in the long-day plants, spinach, pansy, primrose and petunia, even under short-day conditions. The effective concentrations for spray application of SABA/GA₃ were restricted within the limits of 10-1 respectively. Applications of SABA and/or GA₃ as high as 50 induced no flowering. However, flowering in short-day plants, dahlia, morning-glory and Christmas-cactus was not promoted by the mixtures.

**CYTOKININS**

Benzyladenine (Pro-Shear) is used on white pine to increase lateral bud formation and subsequent growth and branching, while tetrapyranylbenzyladenine (Accel) is registered for use on carnations and roses for increased lateral branching. Pomina, a mixture of benzyladenine and GA₄/7 is used to control fruit shape in 'Delicious' apple. High temperature during the bloom period will often reduce the length to diameter ratio resulting in rounder fruit, uncharacteristic of the more normally elongated fruit of this variety that consumers expect. Pomina applied at bloom will increase length to diameter ratio of the fruit (Fig. 6). Increased fruit size may also result from treatment.

Pomina is also being used to increase lateral branching in non-bearing apple trees. Young trees typically have a strong, vigorously growing central leader with a few upright growing
In-Jung Lee

branches. For fruit production, this is an undesirable tree shape and mechanical devices are used to force the lateral branches to grow more horizontally. Pomina will stimulate branching and increase the branch angle, as well as increase shoot elongation, all of which aid in the development of a scaffold branching system more suitable for fruit production.

Fig. 6. Effect of Pomina(upper) on fruit size of pear. Below; untreated check

MISCELLANEOUS COMPOUNDS

Maleic hydrazide

Maleic hydrazide has been used since the 1950s for tobacco sucker growth control, the prevention of bud sprouting in onions and potato, and for the control of turfgrass growth. At one time, maleic hydrazide accounted for almost 90% of the sales of plant growth regulators.

In tobacco production, the terminal bud is removed from the plant after a selected number of leaves has been produced. This practice, called topping, increases the size, weight, and quality of the cured leaf. Axillary buds, which develop as a result of topping, will reduce the effect of terminal bud removal on leaf yield and quality. Maleic hydrazide will provide excellent control of axillary bud growth when applied as a foliar spray to the upper two-thirds of the plant, after terminal bud removal.

Maleic hydrazide is also used to control storage sprouting of onions and potatoes. The compound is applied as a pre-harvest foliar spray, since it is rapidly translocated to storage organs. Maleic hydrazide inhibits cell division in a wide range of plants, and the ability of
the compound to be translocated to meristematic tissue probably accounts for the effect of the compound on axillary bud growth in tobacco and the sprouting of tubers and bulbs. Maleic hydrazide is an analog of uracil and may inhibit cell division by reducing nucleic acid biosynthesis in shoot and root meristems.

\textit{Citrus abscission agents}

Several abscission agents are being developed for the mechanical harvesting of oranges intended for processing use rather than fresh market. The products, Release (5-chloro-3-methyl-4-nitro-1-pyrazole) and Pik-Off (ethandiol dioxime), induce abscission by causing superficial injury to the rind of the fruit. Wound ethylene is synthesized and presumably is the cause of the reduction in fruit removal force. Application of ethephon to trees with mature fruit will also induce abscission, however, significant defoliation often will occur with this chemical.

\textit{Sugarcane ripeners}

One of the more useful compounds for increasing yield in sugarcane is glyphosine, which in Hawaii, has increased sucrose yield by 10-15%. The herbicide Glyphosate, an analog of glyphosine, is also effective, and lower rates of application can be used. Glyphosate will decrease terminal growth of the cane, and other workers have shown that removing the upper leaves of the stalk increases sucrose translocation from lower leaves into the stem and ripening joints. In addition, these compounds apparently alter the partitioning of carbohydrate in the sugarcane internode. More carbohydrate goes into sucrose storage at the expense of fiber production.

\textit{Cotton defoliants}

The organophosphate DEF and Folex are used as leaf abscission agents before mechanical harvesting of cotton. Two new compounds are being evaluated for this purpose. Dimethipin (2,3-dihydro-5,6-dimethyl-1,4-dithiin-1,1,4,4-tetraoxide) and thidiazuron (1-phenyl-3(1,2,3-thiadiazol-55-yl)urea) induce defoliation and provide control of regrowth vegetation other leaf abscission.