

Gibberellins and Cytokinins: a Review[©]

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INTRODUCTION

Gibberellins and cytokinins are considered to be part of the five major key hormones in plants. The others are auxins, ethylene and abscisic acid (Chen and Shepley, 1975). All five interact with each other to directly affect cell systems and indirectly by signaling pathways to maintain balanced ratios (Perilli et al., 2010; Perniosavá et al., 2011). Gibberellins (GAs) and cytokinins, are instrumental in many growth processes (Bernier 1988; Chen and Shepley, 1975; Heldt et al., 2011) such as initiation of floral parts, flowering itself, fruiting, leaf and stem morphology, and seed germination. Changes in the ratios of GAs and cytokinins to each other and to the other hormones often result in distinct and divergent morphological features such as dwarfism, contorted or twisted growth, weeping forms, fastigate, and columnar forms and unique leaf forms (Figs. 1 and 2).



Fig. 1. Pendulous form of *Picea abies*.



Fig. 2. *Picea abies* normal form.

With respect to GAs there are over 125 known forms, 100 are found in plants and the remaining others are found in fungi and bacteria (Crafts and Miller, 1974; Crozier et al., 2000). In general they are all derivations of a central chemical structure with varying side chains.

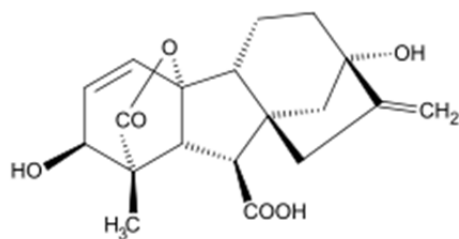


Fig. 3. Gibberellic acid 3.

Cytokinins occur in plants and fungi (Crozier et al., 2000; Heldt et al., 2011) and a rather unique form, kinetin (Barciszewski et al., 2000) which occurs in both humans and plants. All of the natural forms of cytokinins are derived from purine (isoprenoid structures) however, there is another class of chemicals known as phenyl ureas which are structurally different but on many occasions behave strongly as cytokinins (Barciszewski et al., 2000). The best known and most frequently encountered of the phenyl ureas is thidiazuron (Devlin et al., 1989), a totally synthetic cytokinin which has numerous applications in horticulture and agriculture. Another class of chemicals totally distinct from either isoprenoids and phenylureas is the nitroquanidines (Wang, 1996). To date the nitroquanidines are not available except for research use.

NATURALLY OCCURRING CYTOKININS IN PLANTS

- N6-(Δ 2-isopentenyl)adenine, 2iP (isoprenoid) (Fig. 4: isoprenoid structure)
- Trans-zeatin, zeatin (isoprenoid)
- Dihydrozeatin (isoprenoid)
- Cis-zeatin (isoprenoid)
- Methoxytopolin, meo T, plus 3 other topolin types (aromatic isoprenoids)
- Kinentin, 6-furfuryladenine (Bernier, 1988)

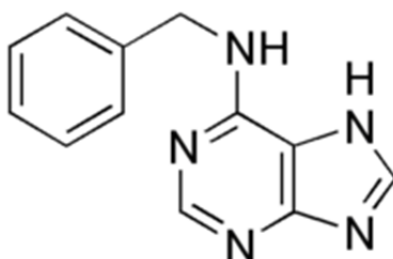


Fig. 4. Isoprenoid structure.

Phenylureas, general formula, side chains vary creating novel forms (Fig. 5).

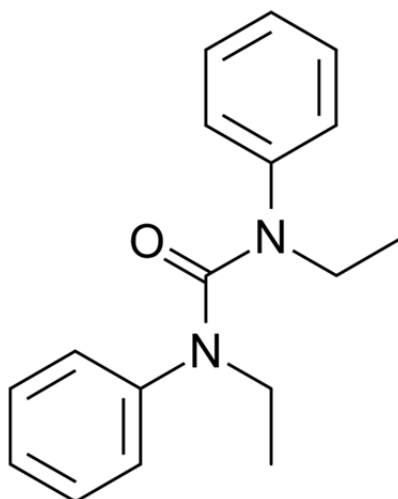


Fig. 5. Phenylurea structure.

Nitroquanidines, general formula (Fig. 6), side chains can vary considerably with significant changes in activity as synthetic cytokinins.

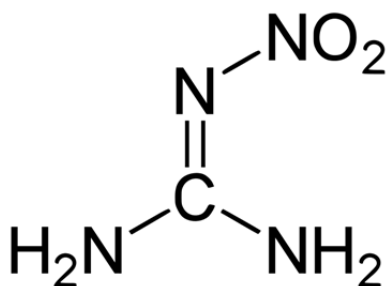


Fig. 6. Nitroquanidine general formula.

In general zeatin is considered to be a natural cytokinin with the highest biological activity followed by 6-benzyladenine (BAP), and 2iP (N6-(Δ 2-isopentenyl)adenine). But derivatives have been made with activities greatly exceeding the conventional natural forms. Research has shown that the formate, acetate, propionate, and indole acetate esters of 2-chlorozeatin have activity 2 \times that of zeatin. Also 8-methyl benzyl adenine, 8-methyl kinetin and 6-(3-methyl-2-butenylamino)-8-methyl purine are all more active than the naturally occurring forms (Varner and Ho, 1976).

ACTIVITY OF GIBBERELLINS

Of the natural plant forms of gibberellins GA₁, GA₃, GA₄, and GA₇ are the most common (Heldt et al., 2011). While there are other GAs to be found in plant tissues they are most commonly converted to one of the more prominent four types. While the four common GAs (Anonymous, 2013; Al-Juboory-Karim and William, 1990; Barciszewski et al., 2000; Bessler, 1997) are frequently encountered they almost always have different roles in plant tissues. Most important of the four is GA₁ and GA₄. When GA₄ and GA₇ are applied to pines flowering is the primary affect, where as when GA₃ is utilized there is no flowering response. Applied GA₃ in some other plants results in suppression of flowering (Waring and Philips, 1982), whereas GA₄ promotes flowering. In *Lolium* sp. (perennial rye grass) GA₃₂ is very active, GA₅ moderately active, GA₃ less so and GA₁, not at all (Bernier, 1988). In some cases the GAs responsible for flowering are essentially ineffective for promotion of stem elongation. Some GAs are known to cause normally female flowering plants to give rise to male flowers (Al-Juboory-Karim et al., 1990; Waring and Philips, 1982).

In some cases GAs are effective only when coupled with altered environmental stresses such as flooding or root pruning. The timing of GA applications is sometimes critical and in dwarf *Pharbitis*, GA₃ is promotive when applied just prior to short day conditions but it is inhibitory after that (Waring and Philips, 1982). In grapevines GA₃ is promotive for flowering at the early stage of floral development but becomes inhibitory once cytokinins take over the process (Bernier, 1988). Oddly the reverse sequence is found in *Fushia* and *Solanum lycopersicum*. Haissig (1972) concluded that GAs play an active role in regulating the actions of auxins in plants and can have an antagonism to auxins affecting the rooting of cuttings. Epicormic shoots are also a result of the interaction of GAs and cytokinins influencing the formation of buds in unusual places (Sachs and Thimann, 1967).

Insects, diseases and environmental damage can alter the GA/cytokinin ratios with each other and with the other hormones (Figs. 7 and 8) (Diener, 1981). When such conditions exist different growth forms are frequent. Some butterfly larvae excrete cytokinins with their saliva to prevent the senescence of the leaves that they are feeding on (Heldt et al., 2011).



Fig. 7. Rose rosette disease causing tissue malformation in *Rosa* ‘Radler’, Knock Out™ rose.



Fig. 8. *Solidago rugosa* adversely affected by boring insects laying eggs in the stem, cytokinin production and gibberellins balances disturbed resulting in witches broom of the stem.

The main function of GAs is to induce cell growth and stem elongation. They are also influential in perennials and biennials for the formation of rosettes in preparation for flowering the following spring (Heldt et al., 2011; Varner and Ho, 1976) (Fig. 9).



Fig. 9. Rosette formation in *Silphium laciniatum*, a gibberellin induced response brought on by short days.

Gibberellins are known to induce cone formation in conifers and can be used to initiate flowering in some plants regardless of photoperiodic signals or vernalization treatments (Barciszewski et al., 2000; Bernier, 1988). They also affect seed maturation, fruiting and seed germination (Chen and Shepley, 19757). They can also retard leaf senescence (Barciszewski et al., 2000).

Gibberellins and cytokinins interact with each other and the other major growth hormones to create specific morphological features (Schoene and Yeager, 2005). The weeping forms of *Picea* (Fig. 1) and *Pinus* are but two examples of these types of changes. Graft unions can alter or inhibit either basally or acropetally the transfer of these chemicals in plant systems resulting in the dominance of one type of tissue over another (Figs. 10 and 11).

Since graft unions can alter the flow of these chemicals within plants, suckering can be exacerbated by a flux of bud initiation below the graft union.



Fig. 10. Understock of *Cornus kousa* exhibiting dominance over a grafted portion of the weeping form.



Fig. 11. Graft union increasing the cytokinin balance beneath the union causing a proliferation of buds that can lead to extensive suckering.

Physical changes to plants such as severe browsing, mechanical cutting back, fire, or flooding can cause altered morphological features such as extra large leaves or elongated stems, extensive shoot proliferation (Figs. 12 and 13).



Fig. 12. Epicormic shoots on *Sequoia sempervirens* due to fire damage.



Fig. 13. Extra large leaves on *Paulownia tomentosa* due to gibberellin/cytokinin imbalance caused by stubbing back to the ground.

SEED GERMINATION

Gibberellins are naturally found in high concentrations in immature seeds. As seeds age the ratio of GAs to cytokinins and to abscisic acid change so that abscisic acid controls germination so that seeds do not germinate at inappropriate times. Cold moist stratification reverses this process and allows the GAs to resume control. However, cold

moist stratification is not the only mechanism for changing gibberellin levels in seed. Dry storage is common in grasses such as *Andropogon virginicus* which often will germinate much better after a prolonged dry storage than when sown fresh.

The use of applied GAs to offset the requirements for cold moist or dry storage is well documented (Schoene and Yeager, 2005; Deno, 1994; Chen and Shepley, 1975; Dunand, 1989; Waring and Philips, 1982; Yan and Dilday, 1993). Gibberellins often will circumvent the need for cold moist stratification but they will also offset dry storage in grasses, requirements for darkness (Dybing and Westgate, 1989) in *Delphinium* and light in Grand Rapids lettuce (Chen and Shepley, 1975). Dunand and others (Dunand, 1989; Yan and Dilday, 1993) found that applied GAs substantially improved the seedling germination and vigor in semi-dwarf rice cultivars.

Gibberellins terminate seed dormancy presumably by changing seed coat permeability (Varner and Ho, 1976) and also by turning on specific enzymes such as the amylases. Commercial brewing practices use the induction of amylases in barley by applied GAs to convert starches to sugars as part of the malting process (Heldt et al., 2011).

Cytokinins too have some role in seed germination (Srinivasan et al., 2006). Kinetin positively affects the germination of *Acer psuedoplatanus*, carpet grass (*Axonopus fissifolius*), clover (*Trifolium* sp.), and light sensitive lettuce (*Latuca* sp.) Kinetin and GA₃ and combinations can overcome abscisic acid retardation of the germination in *Latuca* sp. and excised embryos of *Fraxinus* (Chen and Shepley, 1975). Commercially, cytokinins are added to grains germinating for the malting process (Chen and Shepley, 1975) and are used to stimulate germination of rice to insure a more uniform stand in field planting (Heldt et al., 2011; Yan and Dilday, 1993).

Naturally occurring GAs and cytokinins interact on a number of levels. In brief, cytokinins initiate cell division and the creation of lateral bud formation as previously discussed. In concert with GAs new growth is promoted. Principally this is to induce flower formation and flowering structures (Bernier, 1988). In combination with auxins and GAs other types of tissues and plant structures are formed such as roots, fruits, and seeds. Both GAs and cytokinins will alter (Field et al., 1989) the number of flower buds on *Solanum lycopersicum* and *Nicotiana* spp. (Chen and Shepley, 1975). When *Nicotiana tabacum* was treated with a range of cytokinins, kinetin showed tremendous potential at promoting flower formation (Cousson and Tram, 1980). Cytokinins also regulate senescence of fruits, flowers, and leaves by being antagonistic to the effects of ethylene (Heldt et al., 2011). Cytokinins are responsible for the “cancerous” tumors caused by crown gall formation due to the infection from *Agrobacterium tumifaciens* (Heldt et al., 2011). It is interesting to note that cytokinins have an absolute requirement in plants and in spite of massive surveys no plant mutant has been found that is totally deficient in cytokinins, whereas there are examples of the other major hormones being absent (Varner and Ho, 1976).

ROLES FOR EXOGENOUSLY APPLIED GIBBERELLINS AND CYTOKININS

Tissue Culture

One of the most important and prevalent roles of applied cytokinins is in tissue cultures, i.e., without cytokinins there would be no tissue culture of plants (Heldt et al., 2011). In detail cytokinins are known to increase DNA synthesis in the tissue culture process. They also increase the formation of specific enzymes necessary for cellular metabolism (Wang, 1996). Research has shown that BA in tissue culture increases RNA and both soluble and insoluble proteins (Perilli et al., 2010). In general plant tissue culture makes use of the natural occurring cytokinins, benzyladenine, 2iP, kinetin, and zeatin (Heldt et al., 2011). Under some circumstances thidiazuron is used but it is totally synthetic and can alter internal chemical balances. Using cytokinins in plant tissue culture can lead to alteration in the resulting plantlets leading to mutations collectively known as somaclonal variation. Thidiazuron has been implicated as a causal agent in somaclonal variation (Varner and Ho, 1976). In plant tissue culture two plant hormones are of critical

importance, cytokinins and auxins. When the auxin/cytokinin levels are high, root formation is the immediate result. When the reverse is true and auxin/cytokinin levels are low, shoot formation is the probable result.

While GAs are not normally used in tissue culture as it is presumed that tissues will make sufficient amounts for necessary functions, however Varner (Varner and Ho, 1976), found that high cytokinin/gibberellin ratios in tissue cultures results in shortened dark green plants. Tissue culture plants with the reverse, high gibberellin/cytokinin levels result in slender plants with pale long narrow leaves.

Also, work by Geetha et al. (1998) an exception to the general rule found that GAs in tissue culture did have some positive aspect in shoot growth after multiplication.

Other Aspects of Cytokinin Applications

Cytokinins have uses other than tissue culture in a variety of plant production and post harvest systems. Regardless of the photoperiod applied cytokinins can alter flowering times and other morphological changes in plants (Bernier, 1988; Gonzales and Prokakis, 1989; Heldt et al., 2011; Wang, 1996). Benzyladenine (BA) and other isoprenoid cytokinins are used to reduce flower abortion in soybeans (*Glycine max*) (Dybing and Westgate, 1989).

Since cytokinins are known to be inhibitors or antagonistic to the actions of ethylene they are vastly important in the production of cut flowers, cut-flower storage, and potted plants by prolonging the shelf life during transit (Jiang et al., 2009).

Another important aspect of applied cytokinins is the propensity for cytokinins to release lateral buds from dormancy and to initiate new lateral buds (Bessler, 1997; Findley et al., 1994; Garner et al., 1997; Kever, 1994; Kever and Brass, 2013; Kuminek et al., 1987; Tamas, 1988; Varner and Ho, 1976; Yang and Reid, 1992). This technique can be used to create new tissue for cuttings and for clean shoots useful for tissue culture (Yang and Reid, 1992). Tran (Tran and Kiem, 1981) mentions that buds can be initiated in *Begonia* leaves by treatment with the cytokinin 6-(γ,γ -dimethylallylamino)purine (an isoprenoid) (DMAAP).

Sometimes the use of cytokinins is insufficient to create enough secondary shoots and research by Kever and others (Al-Juboory-Karim et al., 1990; Al-Juboory-Karim and Williams, 1990; Foley and Kever, 1993; Schoene and Yeager, 2005; Yang and Reid, 1992) found that combining cytokinins with GAs results in significant increases of secondary buds suitable for propagation.

It should be noted that different cytokinins have different responses in plant tissues (Heldt et al., 2011). Waring and Philips (1982) showed in mosses that benzyl adenine induced bud formation at 1 μ M, whereas 2iP caused changes at 100 nM and zeatin acted at 5 nM. The synthetic cytokinin, thidiazuron, is used to break bud in apples (*Malus*) and the natural cytokinins when applied to dormant roses releases buds from dormancy and increases flower numbers over the long haul (Halevy, 1986).

Thidiazuron, a synthetic cytokinin, is known to be especially active (Varner and Ho, 1976) when compared to the natural forms but this activity level makes it ideal for field conditions. Oddly it sometimes behaves in a completely different manner and it is used as a defoliant in cotton plants (*Gossypium* sp.) (Devlin et al., 1989). The synthetic phenyl ureas which have cytokinin activity are under scrutiny as herbicides (Srinivasan et al., 2006). The natural cytokinins, such as BA, 2iP, and kinetin do not initiate such changes in plants.

While cytokinins are generally considered to be antagonists of auxin (Haissig, 1972; Heldt et al., 2011) especially in the rooting of cuttings, Davis and Haissig (1990) suggest that improved rooting of cuttings can be achieved by the use of cytokinins as a foliar application after auxin has been applied to the cuttings. The reasons appear to be enhanced leaf retention and delayed senescence during the rooting process.

Cytokinin manipulation can be achieved by means other than applied chemicals. Transgenic tobacco plants have been developed to have natural excess cytokinins thereby

delaying the otherwise natural senescence of the fully mature leaves (Heldt et al., 2011). This is of great benefit in allocating harvesting sequences.

Exogenous Applications of Gibberellins

Previously mentioned has been the use of GAs for seed germination. In commercial usage GA₃ is ubiquitous (Heldt et al., 2011). However, the use of GAs in seed germination has some cautionary elements. Gibberellins are known all too well to influence the internodal distances in stems (Heldt et al., 2011). Work by this author showed that should GA use in seed germination exceed 1000-2000 ppm excessive stem elongation can occur which results in tall spindly seedlings that cannot support their own weight.

Aside from seed germination, GAs have many practical applications. When applied to adult forms of *Hedera helix* (English Ivy) the adult form can be reverted back to the juvenile form and cease flowering (Varner and Ho, 1976). Gibberellins are often utilized for the production of seedless fruits such as grapes (*Vitis* sp.) (Halbrooks and Croveti, 1989; Heldt et al., 2011) with substantial increases in fruit size. They can be used to offset the biennial bearing tendencies in apples (*Malus domestica*) and convert them to annual bearing. Golden delicious apples are prone to russetting and GA applications can be used to prevent that disorder. Citrus can be treated with GAs to retard rind -aging and as with grapes to increase fruit size They are also used in cherry (*Prunus avium*) fruit production and in increasing yield in sugar cane (*Saccharum officinarium*) (Sponsel, 2010). The use of GAs to promote flowering has been discussed previously in this paper.

Gibberellin Inhibitors

Because GAs are so ubiquitous in many aspects of plant growth some natural forms of plant growth do not always fit into prescribed production practices. Interference with the actions of auxins as Hassig (1972) mentioned is but one example. Other include excessive growth and flowering initiation that retards the rooting process in cutting production. Sometimes excessive plant growth stymies efforts to maintain control over specific crops and a disproportionate amount of plant growth can make handling and shipping difficult. Gibberellin inhibitors have been developed, such Paclobutrazol, Uniconazole, and CCC (Heldt et al., 2011). These anti-GA chemicals are used both in agriculture and horticulture to great effect to reduce stem growth, stem height, and the growth status of a range of plants. They are also used to increase the yield in crops such as soybeans (*Glycine max*). Inhibitors such as CCC and diaminozide increase flower set in some species by limiting GA expression whereas in other species GAs are utilized to promote flowering. This further implies that GA responses in plants are often on a species-to-species basis and generalities cannot necessarily be assumed (Field et al., 1989).

COMMERCIAL SOURCES OF GAS AND CYTOKININS

The agricultural and horticultural industries have closely followed the research considering the use of GAs and cytokinins (Table 1).

Table 1. Commercial preparations of gibberellins and cytokinins.

Valent:	Fascination, a BA/GA ₄₋₇ , combo, 1.8% each ProGibb T&O, GA ₃ , 4% ProGibb, 40% GA ₃
Fine Americas:	Fresco, BA/GA ₄₋₇ , 1.8% each Configure, 2% BA Florgib, 4% GA ₃
Norac Concepts Inc., Canada:	Falgro, 4% GA ₃ , 1.0 g tables

IN CONCLUSION

It should be generally understood that the subject of plant hormones and hormonal interactions is an on-going process and as research progresses new understanding and developments continue to add to the utilization of plant growth regulators for the production of nursery, greenhouse, and agricultural crops. This paper is by no means definitive and new information is all but continuous. It is hoped that this at least brings some attention to how these natural materials can be used for the plant production industry.

SPECIFIC QUESTIONS COME TO MIND

- 1) With the knowledge of thidiazuron as an agent to break dormancy in buds of *Malus* (Heldt et al., 2011) could that chemical be used to treat dormant bare-root *Crataegus* in order to break dormancy as *Crataegus* is notoriously difficult to resume growth from a dormant bare-root plant?
- 2) In light of the fact that GAs when used for seed germination an over dose can cause extensive stem elongation resulting in weak stemmed plants, could cytokinins be used instead so that the stem elongation problem is no longer present?
- 3) Could the suggestion presented by Davis and Haissig (1990) that applied cytokinins after the application of auxins have merit in delaying or eliminating the senescence affiliated with mist production of cuttings?

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