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Cytokinin Phytohormonal Effects on Crown Structure

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Abstract. This literature review explores the relevance of cytokinins to tree canopy form, integrating scientific research with current and potential applications to tree care methods. Current and most popular tree care methods call for growers to physically alter the shape of a tree by staking, pruning, and pinching, which can be time-consuming and expensive. Application of phytohormones (also known as plant growth regulators, PGRs) can provide ornamental growers and arborists with alternative methods to manipulate tree crown characteristics. Following a digest of the science of cytokinin activity, the review investigates the current and potential uses of phytohormones as a cost-effective, alternative method of manipulating tree shape. It discusses how the different forms of cytokinin PGRs, acting alone and in concert with other PGRs, can be used, what they can be used for, methods of application, and timing of applications within the phenological cycles of trees. By integrating current basic and applied literature, the review seeks to summarize understanding of cytokinin regulation of crown structure, while exploring potential applications in the tree care industry.

Key Words. Branching; Bud Formation; Crown Alteration; Cytokinin; Plant Growth Hormones; Plant Growth Regulators; Tree Physiology.

A BRIEF DESCRIPTION OF CYTOKININS AND THEIR ROLES IN PLANT DEVELOPMENT

Cytokinins are one of the most important phytohormones in regulating development and growth in plants. Numerous endogenous cytokinins have been identified, and synthetic cytokinins are available on the market for exogenous application (Buban 2000; Wertheim 2000; NeSmith 2004; Carey 2008). Cytokinins play an essential role in plant development throughout the life cycle, ranging from the germination of seeds to fruit set (Sakakibara et al. 2006; Kyozuka 2007). Various cytokinins are synthesized in the plastids of plant tissues (including stems, leaf primordia, meristems, seeds, and especially roots), regulate development in neighboring tissues, and, after transport in xylem and phloem, regulate whole-plant developmental patterns. Root-produced cytokinins coordinate shoot:root resource allocation and are important for communicating plant nitrogen status (Pons et al. 2001). Naturally occurring cytokinins are nitrogen-rich molecules that contain either aliphatic isoprenoid or aromatic side chains (Sakakibara 2006). When cytokinins trigger receptors in the cell membranes of target cells, they activate kinases cascades (molecular chains of phosphate transferring molecules) that regulate gene transcription in nuclei. Cytokinin-activated kinase cascades may interact with signals from other phytohormones or photoreceptors, such as phytochrome (Boonman et al. 2007; Taiz and Zeiger 2010). Cytokinins may be present in both active forms and as potential regulatory molecules in inactive conjugates with sugars, sugar phosphates, and other molecules (Sakakibara 2006).

At tissue and organ levels, cytokinin concentrations change throughout the year due to phenology and maturation state of plant tissues (Andres et al. 2002; Juvany et al. 2013). Activity is generally associated with regulating cell division. In reproduction and embryo development, they regulate sex determination and pollination, seed dormancy, and germination (Schmulling 2002; Bishopp et al. 2006). After germination, they enhance cell division in root/shoot meristems, regulate the formation of vascular elements, and regulate leaf development (Moore 1998; Carey 2008). In mature tissues, they regulate genes associated with chlorophyll

biosynthesis and nutrient partitioning, they open stomata, and they delay senescence. Important to plant crown formation, branch and meristem development are controlled by cytokinins (Roitsch and Ehneß 2000; Rasmussen et al. 2009).

Cytokinin and other phytohormones are controlled by a system of checks and balances within the plant. Cytokinin synthesis is autonomously down-regulated as total concentrations of cytokinin increase in plant organs, and as inactivation by enzymes are stimulated by other phytohormones, particularly auxin. Developing plant shoot organs compete with one another for water and nutrients by producing negative-effect hormones, which either down-regulate production of phytohormones required by competing organs or inactivate available phytohormones. For example, the influence of apical bud dominance over lateral buds led to the discovery of auxin as the first identified phytohormone (Thimann and Skoog 1933), where the removal of apical bud and a primary leaf of bean plants (*Phaseolus vulgaris*) induced rapid expansion of secondary leaves by interruption of auxin produced in the shoot apex, leading to increased gibberellin content (Humphries and Wheeler 1963). Unbeknownst to Thimann and Skoog, auxin and gibberellins phytohormonal checks and balances were at play.

Basic research into plant physiological processes is usually conducted on "model plants," such as *Arabidopsis* and *Nicotiana*, where the accumulation of vast data bases permit connecting the dots between genomic and biochemical activity and whole-plant physiology. As most physiological processes are highly conserved, models derived from basic research can be applied to other species with the caveat that physiognomy and environment may require their modification. While definitive understanding of the action of phytohormones in particular situations may require species-specific studies, the diverse body of literature on phytohormones permits valuable generalization of phytohormone effects and activity.

CYTOKININ IN BRANCHING AND CROWN DEVELOPMENT

Crown architecture is due to a complex interaction of phytohormones, most commonly auxin, gibberellins, and ethylene, working in combination with cytokinins. Phytohormones are responsible for regulating branch angle, the amount of branching, shoot growth, and the activation of lateral buds (Cline and Dong 2002; Oates et al. 2004; Sansberro et al. 2006; Müller and Leyser 2011).

In the shoot apical meristem, cytokinin is a major regulator of meristem characteristics and branch initiation. Arabidopsis mutants that lacked cytokinin showed a severe reduction in shoot apical meristem size, indicating the importance of cytokinins in shoot development (Kyozuka 2007). Cytokinin controls the outcome of undifferentiated cells in shoot apical meristems (Kurakawa et al. 2007). In a developing shoot, there is a cell elongation zone of approximately 10 to 15 cm in length subtending the meristem. The elongation zone is an area of undifferentiated cells that begin to form into determined organs, as phytohormone balances shift in nearby tissues. In the apical meristems of tobacco plants (*Nicotiana tabacum* L.), cytokinins induce the biosynthesis of auxin, which regulates the formation of bud primordia in the expanding shoot (Nakagawa et al. 2005; Cortleven and Valcke 2012). Bud distance from an active growing meristem determines the amount of cytokinin, which is correlated with triggering lateral bud burst and further branch development. Therefore, the development of a new shoot meristem depends on whether the activated bud (and its associated undifferentiated cells) is associated with the internode that has not begun to elongate or one that has already partially completed the elongation process (Elfving and Visser 2006). The two principal regulatory pathways are apical dominance (when the terminal bud of a shoot or branch prevents activity of dormant lateral buds) and apical control (when the terminal bud inhibits the growth of branches from activated lateral buds).

It has been long known that the apical meristems on dominant shoots inhibit bursting of lateral buds. The power of control of lateral bud bursting by shoot apices is the primary mechanism by which woody plants assume their typical crown form. Strong apical dominance leads to monopodial crowns, typical of many conifers, while weaker dominance results in highly branched sympodial-shaped crowns, typical of angiosperm trees and shrubs. The process of apical dominance is maintained by down-regulating cytokinin supply to lateral buds by the phytohormones auxin and abscisic acid (ABA) (Ward and Leyser 2004) from shoot apical meristems and develop-

ing foliage, and by strigolactones, a form of steroid produced in roots (Hayward et al. 2009). Auxin produced in the shoot apex travels basipetally through xylem parenchyma and stimulates the production of cytokinin dehydrogenase, which inactivates cytokinins diffusing toward lateral buds. ABA appears to have a role in suppressing lateral bud development in woody plants that acts independently of auxin (Frewen et al. 2000). The mechanism associated with strigolactones, is less well understood, but their presence also down-regulates cytokinin activity. Both auxin and ABA may also down-regulate cytokinin synthesis in root plastids (Frewen et al. 2000; Tanaka et al. 2006). These phytohormonal mechanisms maintain dominant shoot status by sustaining its larger sink for water, nutrients, and carbohydrates.

Branch buds are initiated in the shoot apex (apical meristem and developing foliage), and their flushing activity requires activation by cytokinin. The effect of the shoot apex on lateral bud activity diminishes as distance between apical and lateral buds lengthen. As the influence of negative-effect phytohormones decreases and cytokinin and resource availability to lateral buds increase with distance from the apical meristem, lateral buds are released from suppression (Rasmussen et al. 2009). When lateral buds are released from suppression, their endogenous cytokinin levels increase, high nutrient levels are associated with high rates of cell division, and new branches form (Humphries and Wheeler 1963).

Auxin synthesized in the shoot apex has also been identified as the principle regulator of apical control (Cline 1991; Wilson 2000). Both apical dominance and apical control are regulated by phytohormones through their effects on vascular tissue development and by altering sink strength for carbohydrates and nutrients. In apical dominance, connections between the vascular system and dormant buds are prevented. In apical control, cambial stimulation by phytohormones from the shoot apex results in selective enhancement of vascular tissue supplying the shoot apex (Cline and Harrington 2006). What both developmental mechanisms have in common is the reduction or elimination of cytokinin availability to lateral buds and branches. In apical dominance, cytokinins are actively deactivated. While in apical control, the transpiration streams (with its root-produced cytokinins) are diverted to the shoot apex. Selective loading mechanisms for cytokinins are believed to be active in both xylem (i.e., transpiration streams) and phloem, regulating transport to sinks for cytokinin in other plant tissues (Sakakibara et al. 2006). In turn, cytokinins affect growth metabolism, enzyme activity, and the biosynthesis of other phytohormones through regulation of gene activity (Sakakibara et al. 2006). Cytokinin effects are largely limited to aboveground via manipulation of sink strength.

Branch density and angle are affected by both exogenous and endogenous cytokinin and its interaction with auxin. When the terminal bud is clipped (auxin supply is interrupted), many of these dormant buds develop, and the branch density increases as apical control is lost, resulting in a 'full' tree. Once the apical meristem is excised, auxin levels in the stem decrease, repression of cytokinin biosynthesis is released, and cytokinins levels increase to promote lateral bud growth. After a lateral bud is activated, it assumes control as the apical meristem of its subtending shoot. An endogenous supply of auxin is synthesized in the new apical meristem and represses cytokinin availability to lateral buds on its branch (Tanaka et al. 2006).

Cytokinins generally induce branching, but the concentrations and effects vary widely among species and by interactions with other phytohormones (Carey 2008). In addition to interactions with auxin, gibberellins and cytokinins are mutually antagonistic. Cytokinins inhibit gibberellin formation, and gibberellin inhibits cytokinins responses (Weiss and Ori 2007). Abscisic acid inhibits seed germination, stimulates ethylene production, and causes stomata to close (Kong et al. 2009). Cytokinin inhibits the activity of ABA on all of these processes (Carey 2008; Kong et al. 2009), maintaining more rapid growth and, in many cases, preventing phase change of vegetative meristems to floral meristems and prolonging juvenile maturation states.

Additional factors that affect cytokinin activity in branching are the level of the particular cytokinin (Carey 2008), the sensitivity/responsiveness of the tissue to cytokinin, and for exogenous applications, the location of cytokinin application (Bangerth et al. 2000). High levels of cytokinins in branch shoots stimulate bud growth and lateral stem formation (Bangerth et al. 2000; Carey 2008). A particular tissue may or may not be competent to recognize the presence of cytokinins

(Carey 2008). The intensities of these factors may vary due to tissue age, stress, environment, life-stage of plant development or other conditions. For example, younger *Picea rubens* trees show a higher reaction to exogenous cytokinin application with the increase of needles within a given area on the branch, increase in stem mass, and an increase in stem length (Figure 1). The concentration of cytokinin had the same effect across the three variables. In apples, certain cultivars, such as 'Gala' and 'Delicious,' show greater response to exogenous cytokinin application than others.

Exogenous auxin application inhibits growth of lateral branches (Cline 2002), but the inhibition can be canceled by endogenous cytokinin (Durbak et al. 2012). Exogenously applied cytokinin stimulates the cell of elongation zone in plants (Cortleven and Valcke 2012), and can delay maturation and competency to flower (Taiz and Zeiger 2010). Rasmussen et al. (2009) found exogenous cytokinin application increased leader length, bud width, bud count, and needle number when applied to the leading shoot of a branch in *Abies Nordmanniana*. While exogenous application of cytokinins can produce dramatic effects in the short-term, cytokinins do not affect apical meristems in the long-term. Once suppressed lateral buds begin to grow, plants return to prior balances of auxin and cytokinins (Carey 2008).

ENVIRONMENTAL EFFECTS

Little is known about the interactions of cytokinin activity with environmental stress factors (i.e., moisture, temperature stress, and pathogen infections). Many environmental variables have yet to be tested and reported. However, scientists do know that genes regulating endogenous cytokinin production are directly coordinated with macronutrient content, particularly nitrate content. Cytokinin has a negative effect on root growth and on stem growth. As cytokinins are widely reported to prevent or delay reproductive maturation and seasonal dormancy, potential interactions and/or feedbacks may occur between environmental factors, such as photoperiod, temperature, and drought as exogenous signals for reproduction or dormancy.

Both cytokinin synthesis and water movement through roots are up-regulated by soil nitrate availability. Cytokinin is translocated through the transpiration stream in xylem conduits, and up-regulates nitrate responsive genes in the phloem of roots and shoots. The rate of nitrogen uptake increases cytokinin synthesis, the rate of water transport, and the rate of cytokinin transport (Sakakibara et al. 2006).

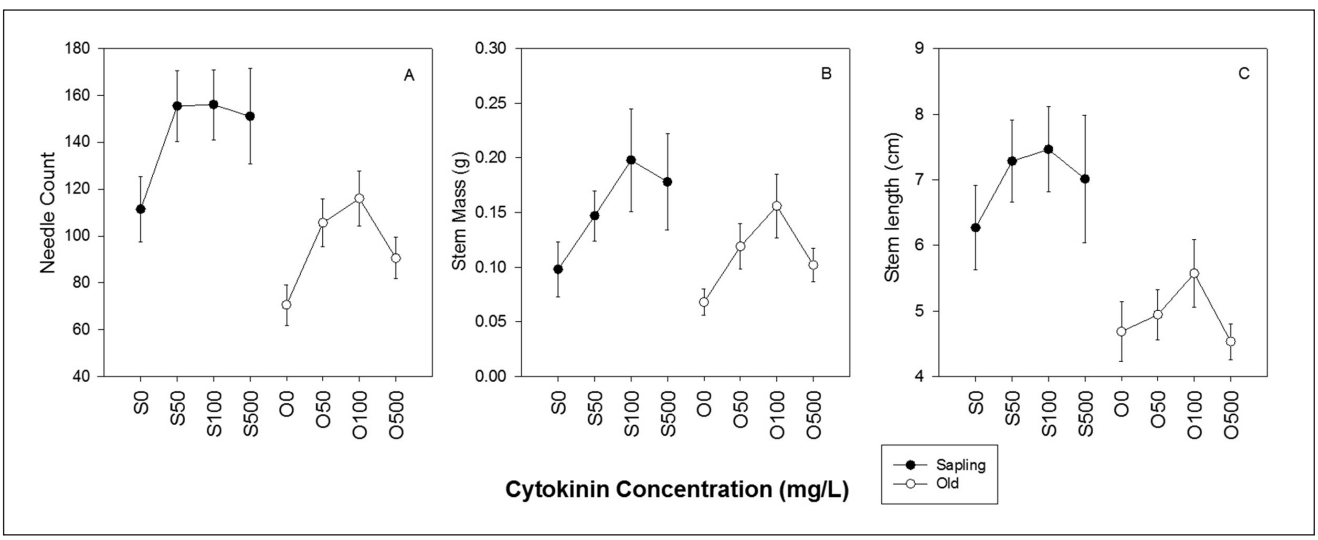

Figure 1. Differential effects on foliage and shoot growth of cytokinin application related to tree age in red spruce (*Picea rubens* Sarg.). The x-axis gives tree age as (S) sapling mean 25 years and old-growth (O) mean 160 years and 0 to 500 mg L^{-1} exogenous B-6-P application. Both species exhibit maximum treatment effects at 50–100 mg L^{-1} (Autio 2013), and age differentials consistent with those previously reported for red spruce (Greenwood et al. 2008). Bars indicate standard errors.

Sun/Shade Foliar Adaptation and Chlorophyll Synthesis

Boonman et al. (2007; 2009) linked sun-shade attributes with cytokinin activity, transpiration rates and chlorophyll b concentrations. Low transpiration rates are found in shade environments, areas with high humidity, and in the tops of crowns of old trees (presumably, due to xylem length and complexity). Low transpiration rates correlate with low cytokinin levels because of the lowered delivery of cytokinin through translocation. Boonman et al. concluded that pigment content is influenced by the interaction of light environment throughout its effect on the transpiration stream and cytokinin concentrations. Therefore, the addition of cytokinin can enhance shade effects in canopies as it down-regulates chlorophyll synthesis. Cytokinins have been linked to sun-shade foliar responses in herbaceous species. Carabelli et al. (2007) reported that cytokinins are associated with suppression of leaf bud development in *Arabidopsis*. Decreased concentrations of cytokinin in shade foliage resulted from lower transpiration rates and decreased water flow.

CYTOKININS AS TOOLS IN ARBORICULTURE AND HORTICULTURE

Industries that could benefit from hormonal technology include the tree care industry, woody plant horticulture, and fruit care industries. Synthetic plant growth regulators (PGRs) are usually structural analogues of hormones (Moore 1998). Cytokinins are based on nitrogen-carbon rings and naturally occur in both isoprenoid and aromatic forms. Forms vary in their side chains, which impart receptor specificity in target cells (Sakakibara 2006). Analogous manufactured chemicals that mimic the structures and functions of natural phytohormones can also have significant effects on plant growth and development.

The best-known hormonal cytokinin found in plants is zeatin, and the most common forms of synthetic cytokinin are its analogs based on benzyladenine, or BA (Moore 1998). One cytokinin product registered for use on ornamental plants is Configure®; a benzyladenine-based PGR. It can be applied as a foliar spray or a substrate drench at concentrations from 1 to 3000 $mg \cdot L^{-1}$ (Carey 2008; Table 1; Table 2). A few others, such as Topolin® (Buban 2000), 9-Benzyladenine (Canal et al. 2000), Triacanthine, 6-Chloroprine, and 4PU (Zhang and Hasenstein 1999) have resulted in larger fruit sizes and increased return bloom the following year, a movement from inactive to active forms of BA, an increase in lateral budbreak, and a decrease in terminal budbreak as seen in experimental studies (Table 1; Table 2). In addition, many other chemicals are known to have partial cytokinin activity (Carey 2008).

Table 1. Cytokinin formulations and trade names. See text for further information on group components.

Cytokinin group	Common names
BA	2iP, BA, BA 0.1%, BAP, BA 0.2, BA 0.5, Verdan, BA + TIBA®, BA + Alar®, BA + TIBA® + Alar, 6-CP, Cytex®, BA + IBA®, GA + BA + IBA, ProShear®, and other BA/GA mixes
BA + Kinetin	BA + Kinetin®—also contains GA and auxin or IBA
BPA	BPA, Accel, SD8339®
Kinetin	Kinetin® 2–500 ppm, Kinetin (270 ppm) with or without GA3 90, GA + Kinetin 100 ppm + 100 ppm
BA + GA	BA or BA + GA, Promalin®, PBA, Thidiazuron®, Fascination®, Lanolin®

Many attempts have been made over the years to experimentally integrate cytokinin products into horticultural practices focused on lateral branch stimulation in young nursery trees (Elfving and Visser 2005). Benzyladenine+GA4,7 was first registered in the late 1970s for agricultural crops, and pyranylbenzyladenine PBA was registered in the late 1970s for use on ornamentals. From the 1970s until the 1990s, a product called Pro-shear® (2% BA) was used on white pine trees (*Pinus strobus* L. in Christmas tree plantations) to increase branch development by increasing lateral bud set in the year of application. However, it is no longer produced (Baker 2001). Some products are not labeled for use in every state or country due to variations in state regulation laws and often by marketing decisions by manufacturers. In many cases, cost–benefit analysis may discourage efforts at registration compliance in multiple jurisdictions. Cytokinins-based PGRs are commonly used in a 1:1 ratio with Gibberellin 4,7 in a product called Promalin® (Carey 2008).

Exogenous cytokinins are usually applied to plants via foliar sprays or drenches and are

Table 2. Cytokinin PGR mixtures, application procedures, results, and commonly treated woody plants. Results of individual application trials are listed in the Appendix.

Woody plant group	Applications	Effects on growth
Cytokinin formulation BA		
Conifer	• BA 0.01 to 225 ppm/scions dipped prior to grafting or single foliar spray • 400 ppm/1 foliar spray; BA 400 ppm reduced height but trees were deformed with poor root growth • BA 450 ppm/six foliar sprays at five-day intervals in May and again when weather warmed • BA 500 to 1000 ppm/foliar spray applied four times at two-week intervals or whole tree foliar spray application 6 weeks after budbreak • BA 2000 ppm/Lanolin paste applied in late summer and autumn • 0.1% 9-BA Vasoline paste applied to cut roots (worked best)	• Growth inhibition • Phytotoxicity • Branching agent • Propagation
Deciduous	• BA 11 to 34 ppm/solution applied to the base of a stem via an absorbent wick in mid-summer • BA 10 ppm/soak of four-year-old dormant seedlings • 50–200 ppm ± Promalin 1000 ppm/foliar sprays • BA 100 ppm/stem dip • BA 225 ppm/droplet applied daily to a lateral bud	• Branching agent • Propagation
Fruit Trees	• BA 200 ppm/drops placed onto buds of cut branches in January • BA 300 ppm/single foliar spray in summer at various times • BA 150 to 600 ppm/single foliar sprays in autumn	• Dormancy release • Flower enhancer • Branching agent
Shrub	• BA 1 to 100 ppm/continuous dip of dormant cut stems • BA 1 to 100 ppm, Thidiazuron 1 to 50 ppm/continuous dip of cut stems or BA added at various times • 10 to 100 ppm/foliar spray every three days 2–32 times • BA 200 ppm and 2iP 100 ppm most effective/single foliar sprays onto unpinched plants • BA 100 to 1000 ppm/1–2 foliar sprays in summer • BA 2500–5000 ppm/1–5 foliar sprays one week apart in April	• Dormancy release • Flower enhancer • Branching agent
Cytokinin formulation BA + GA		
Deciduous	• BA + GA (Promalin) 1500 ppm/foliar spray applied 10 weeks after the end of spring • BA + GA (BAP-10) 1250 ppm/two to four weekly foliar spray applications • BA + GA 400 ppm of BA & 2iP and 450 ppm of Promalin/single foliar sprays • BA + GA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays onto rooted cuttings	• Branching agent • Dormancy release
Fruit Tree	• BA + GA 500 ppm each/three applications at one week intervals to one-year-old plants; very effective when followed by injection and Lanolin • BA + GA (Promalin) 1500 ppm/single foliar spray in June to one-year-old plants • BA 1 to 900 ppm, BA + GA (Promalin) 1000 ppm/one to two applications worked best	• Branching agent
Shrub	• BA + GA (Fascination) 125 to 500 ppm/two foliar spray applications at day 0 and day 21 • BA + GA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays • 450 ppm of Promalin/single foliar sprays • BA + GA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays onto rooted cuttings • BA+ GA, PBA, Thidiazuron all at 200 ppm/single foliar spray • BA + GA (BAP-10) 1250 ppm/two to four weekly foliar spray applications • Promalin 5000 ppm in April was better than pruning	• Branching agent
Cytokinin formulation Kinetin		
Conifer	• Kinetin 100 to 500 ppm	• Growth inhibitor
Deciduous	• Kinetin 50 ppm/applied to seeds • Kinetin 100 to 500 ppm; Kinetin 500 ppm worked best	• Growth inhibitor • Dormancy release
Fruit Tree	• Kinetin 2 ppm/apply in late autumn for best results • Kinetin 65 to 130 ppm/monthly foliar spray applications • Kinetin 100 to 500 ppm	• Branching agent • Dormancy release
Shrub	• Kinetin 80 ppm/released shoots from dormancy when applied to them • Kinetin 100 to 500 ppm • Growth inhibitor • GA + Kinetin 100 ppm + 100 ppm/applied every four days to the flower bud • Kinetin 270 ppm with GA 90 ppm/increased branching more than either chemical alone	• Dormancy release • Branching agent • Bud break and formation
Cytokinin formulation BA + Kinetin		
Conifer	• BA + Kinetin 1.17 ppm + 1.17 ppm Kinetin in 1125 ml water/apply in early harvest • Kinetin 1.17 ppm + BA 1.17 ppm/45 ml soil drenches every two weeks from June to September	• Branching agent–no effect • Stress tolerant
Shrub	• 1.17 ppm BA + 1.17 ppm Kinetin/45 ml soil drenches every two weeks from June to September; the low 1.5 ml rate increased plant quality; the 3.0 ml rate increased growth • BA 100 ppm/foliar spray 2 to 32 times with no effect on growth	• Stress tolerant • Branching agent • Dormancy release

absorbed through the cuticle (Canal et al. 2000). Plants can absorb cytokinins through leaf or root epidermis and transport them to growing points. It is likely that younger tissues with thinner cuticle and epidermal layers absorb more cytokinins than older tissues (Carey 2008). Activity level depends on the form of synthetic cytokinin (Hartmann et al. 2001; Davies 2004b) and the amount applied to a particular site (Carey 2008).

Currently, arborists use a mixture of chemicals and synthetic hormones to manipulate tree growth, shape, and increase branching, while avoiding unwanted damage to other plants, animals, and humans. Extrinsic regulation of development and form can be accomplished at any growth stage. Tree shape alteration can begin in embryos. Both Lyyra et al. (2006) and San-Jose (2001) found that a liquid BAP cytokinin pulse induced adventitious shoot formation in cotyledons of black willow (*Salix nigra* Marsh.) and sweet chestnut (*Castanea sativa* Mill.). At the seedling stage, spray treatments of cytokinin have been used to alter tree shape by hindering stem elongation and promoting adventitious bud formation in Douglas-fir seedlings (Lisheng, et al. 2009). Cline et al. (2006) found that whole-tree (but not terminal leader) foliar BA applications promoted both bud formation and second flushing in six-year-old Douglas-fir seedlings. During release from quiescence in mature trees, cytokinin levels increase, and branching is controlled by relative levels of cytokinin and auxin as the crown develops (Mazri 2013).

Generally, cytokinin in stem tissue is required for activation of dormant lateral buds, and auxin transported basipetally from shoot apices interferes with this process through apical dominance. Branching agents work by interrupting apical dominance, which triggers lateral bud growth, which 'fills in' the plant. Apical dominance can be interrupted in several ways, including by pruning of apical meristems, to reduce auxin, or by applying exogenous cytokinins (Carey 2008). Christmas tree growers have also experimented with applying artificial cytokinins and increasing cytokinin to auxin ratios.

The complexity of the branching pattern depends on the temporal and spatial development of branches. These characteristics, although they are plastic in their response to environmental cues and human intervention, are in large part genetically determined. Therefore, regulation of crown structure is determined by an interaction between the developmental program that specifies branching patterns in different plant species generating species-specific plant forms and natural and/or artificial influences.

Terminal bud dominance and control can be manually manipulated by pruning. Growers and horticulturists commonly use pruning to shape the crown of commercial and urban trees, interrupting the basipetal flow of auxin. Arborists use a multitude of pruning techniques to achieve their goals of aesthetics, safety, and tree health. However, pruning is time-consuming and requires substantial skill and training to avoid unintended consequences.

Pruning lateral branches will change stem taper and therefore affect wood quality and strength. Pruning and lopping of trees in ways that remove large amounts of foliage disrupts both auxins and cytokinins levels. As a consequence of poor pruning practice, large numbers of dormant buds, epicormic buds may develop rapidly. They are often poorly attached but grow quickly under proper environmental conditions. Because of their weak attachment, the branches are easily shed and present a significant hazard in urban settings (Moore 1998). Furthermore, overpruning of a tree will result in lower photosynthetic and hormonal transport levels, which may directly decrease fruiting (Carey 2008).

Plant growth regulators have outstanding potential for arboricultural manipulation of urban trees and avoiding some of the negative aspects of manual pruning. They are currently used in some contexts but, like pruning, require competent and professional workers to avoid situations where direct application of hormones and PGRs result in unacceptable environmental risks. Cytokinins have impressive effects on plant growth and development, but there is an inherent danger in their use (Moore 1998). Many PGRs can be harmful or toxic, and should be used with extreme care (Harrison et al. 2014). Documented and established protocols are available for best PGR practices, and as in any chemical released into the environment users must be thoroughly trained in best practices (as outlined in Table 2).

Although cytokinins contribute to many plant processes, they are not yet widely used in horticulture outside of a few specialized areas, such as tissue culture, apple/cherry production, and Christmas tree farms. In the apple industry, when applied to flowering trees, they promote bloom thinning, which results in higher fruit production in future years (Buban 2000; Baker 2001). When sprayed onto young fruit, cytokinins improve the shape of fruit and increase size. They are used on young apple trees to promote lateral bud break and increase radial growth on branches (Wilson 2000). They are also used on pear trees and nut trees for similar reasons (Andres et al 2002). Cytokinin PGRs are also used on table grapes to increase the size of fruits (Cruz-Castillo et al. 1999).

The bioregulators Cyclanilide® (CYC) and Promalin (PR) show species specific differences in their effects of induced branch height in apple and sweet cherry trees in nurseries (Elfving and Visser 2005; Elfving and Visser 2006). Application of the cytokinin 6-benzyladenine (BA) with or without gibberellic acid isomers GA4 and GA7 (GA4 and GA7) also improves branch formation in apple and sweet cherry trees (Elfving and Visser 2006). Cytokinins generally increase branch size and the number of branches of apple trees, which in turn increases fruit yield. Cytokinins are promising as fruit thinners because they are not harmful to beneficial insects (as carbaryl thinners are) and also promote branching and flowering the following year (Elfving and Visser 2006; Mickelbart 2011).

Both CYC and PR act by altering auxin to cytokinin ratios. CYC is an auxin transport and action inhibitor (Pederson et al. 1997), and PR contains the cytokinin growth promoter 6-benzyladenine (Sachs and Thimann 1967). When Elfving and Visser (2006) applied both to separate tree plots of nursery sweet cherry trees, they found that although the mode of action of CYC and PR products are different, their effects on branching and tree structure seem to be dictated more by tree species than product. CYC induced new lateral shoots starting above the bud union, and lower than spontaneously formed branches that developed on untreated trees. PR did not affect the final height of the lowest induced branch. CYC produced branches starting at a progressively lower height above the bud union on the central leader as the product concentration increased. In contrast, PR did not affect the final height of the lowest induced branch.

In another study, a cytokinin treatment of 0.5 mM BA was applied five to six weeks following two weeks of cytokinin foliar spray treatments of the terminal spring-flushing leader shoots, which resulted in a small increase in the total number of lateral buds and a large increase in current bud outgrowth (Cline et al. 2006). A second terminal bud flushing occurred in only 28.4% of the control seedlings in the five experiments compared with 81.5% of the BA-treated seedlings, indicating that BA substantially enhanced second flushing of the terminal buds. After testing BA applications in different concentrations, both as drops and sprays, 0.5mM BA foliar spray was found to be optimal under greenhouse conditions.

Cytokinins are currently registered for use on apples (Accel®, Promalin) and sweet cherries (Promalin) as fruit thinners, to improve 'typiness', and to induce lateral branching and budbreak (Buban 2000; Western Plant Growth Regulator Society 2000; Baker 2001; Yu et al. 2008).

Application Considerations

The most commonly applied cytokinin, BA, is only slightly soluble in water (Hrotkó et al. 1999; Magyar and Hrotkó 2005). However, other highly active cytokinins, such as 6-{N-[2-(N-Methoxy-N-methylamino) ethyl]amino} purine are water soluble (Maruyama et al. 1993; Pons et al. 2001; Oates et al. 2004; Sugiura 2004), but are not readily available as commercial preparations. Benzyladenine mixtures therefore require an organic solvent, such as isopropanol (BA soluble up to 3960 $mg \cdot L^{-1}$), chloroform (soluble up to 288 $mg \cdot L^{-1}$), HCL, KOH, DMSO, propylene glycol, ethoxylated tallowamines, ammonium hydrazide, sodium hydrazide, methanol or ethanol, and topical applications usually employ a surfactant, such as Tween®. Once in solution, further dilutions can be accomplished with water or a water-alcohol solvent. Mirdehghan and Rahemi (2004) reported that BA can also be dissolved in hot water and then cooled to a supersaturated solution. Common application concentrations range from 0.1 to 10 $mg \cdot L^{-1}$ (BA), which correspond to typical concentrations used in tissue culture media (Table 2). Researchers who

specialize in commercial production usually apply concentrations from 50 mg·L^{-1} to 5000 mg·L^{-1}, once or twice at one to two week intervals (Carey 2008).

THE FUTURE OF CYTOKININS IN ARBORICULTURE AND HORTICULTURE

Potential uses for cytokinin phytohormones include: to decelerate senescence and to promote growth and bud formation, to improve grafting results, to be used as branching agents, and to improve branching angles (Mok 1994).

Regulating Reproductive Phase Change, Senescence, and Dormancy

The phytohormone gibberellic acid (GA) is associated with phase change to reproductive competency, and ethylene is associated with various forms of plant tissue senescence. Cytokinins mixed with anti-GAs may have synergistic effects on branching (Werbrouk et al. 1996), and cytokinin combined with anti-ethylene products may have synergistic effects on preventing senescence and promoting continued growth.

Not only are the degradation processes that accompany senescence delayed by exogenous application of cytokinin, but in some instances there is a genuine reversal in phase change that marks rejuvenation (Moore 1998). Several researchers have successively used exogenous cytokinins to induce rejuvenation in plants with success in pines (Zhang et al. 2003; Carey 2008) and spruce (Day and Greenwood 2011).

Cytokinins in conjunction with a reduction in nutrient levels may control height, as cytokinins can help prevent leaf yellowing or senescence that occur with nutrient deficiency (Funnell and Heins 1998; Banko and Stefani 2008). Cytokinin applications may be useful for high-chill crops grown in low-chill areas. Cytokinins applied during the early stages of winter dormancy or in the late stages of dormancy can induce plants to be released from dormancy earlier (Cline et al. 2006). This is currently done for fruit crops, such as apple, plum, and peach (Alvarado-Raya et al. 2000).

The influence of cytokinins on bud number and activation offers promise as a means of regulating flowering. BA increases the number of buds that form, and when managed properly with subsequent application of the flowering promoting phytohormone gibberellic acid, growers may increase the number of flower buds. BA + GA mixes have also been used to thin the flowers on apples to avoid uneven fruit yield. In the latter case, the phytohormone mixture is sprayed on flowering trees in heavy flower years to cause flowers to drop off (Western Plant Growth Regulator Society 2000). The effect of cytokinins on flowering have been studied in numerous other plants; however, the results are inconsistent (Carey 2008).

Improving Grafting Results

Since cytokinins are involved in cellular differentiation and xylem formation, grafts treated with cytokinins potentially survive at a higher percentage or close more quickly (Valdés and Fernández 2004). Exogenous cytokinins induce phloem regeneration and callus formation in coleus wounds, cause grafts to close faster, and cause root stocks to move more nutrients to scions (Valdé and Fernández 2004). Cytokinins have also improved graft success in spruce (*Picea* spp.), improved scion bud sprouting in some citrus, and improved graft success in *in vitro* graft experiments (Meier et al. 2012). However, Hartmann et al. (2001) and Werner et al. (2003) caution that cytokinins do not provide uniform results in promoting successful grafts because phytohormone levels vary for each plant species as well as the type of cytokinins used and their timing. For example, rose grafts tended to sucker below the graft union more when treated with cytokinins.

In plant propagation, the best-known and most far-reaching use of cytokinins at the moment is as a component of tissue culture media. While these techniques are not directly associated with regulating crown development, this application has widespread implications for tree breeding and production programs (Moore 1998).

Branching Agent

Plants that normally produce few branches during production can be encouraged to branch with cytokinins. Many plants have to be manually pinched, pruned, sheared, or disbudded during production in order to stimulate branching. This is a time-consuming and therefore expensive procedure. In woody plants, cytokinins have been studied as a

replacement for pinching in many crops with mixed results, depending on species and PGR product. Cytokinins have been shown to be somewhat effective in replacing the need for shearing in Christmas trees, such as *Buxus sempervirens* L. 'Suffruticosa', *B. sempervirens* 'Vardar Valley', and *B. sinica* var. *insularis* (Musselwhite et al. 2004), for pinching in *Clematis* spp. (Puglisi 2002), and holly (Oates et al. 2004), but not in *Caladium* spp. (Whipker et al. 2005). The value of cytokinins to promote branching in juvenile trees may be highly life-stage specific. The seedlings of many woody plants do not form lateral buds or branches in the earliest stages of development. As developmental states change rapidly during the early growth of tree seedlings (Day and Greenwood 2011), the effects of cytokinins may be highly life-stage and species specific and should be evaluated for individual species/developmental-state combinations.

Cytokinins have been used to increase branch production on sweet cherry trees (Hrotkó et al. 1999; Neri et al. 2004; Magyar and Hrotkó 2005) and there is potential to use this effect on ornamental plants and in urban landscapes (Carey 2008). Cytokinins could be co-applied with dikegulac sodium (Atrimmec®), or ethephon (Florel®) for synergistic effects on branching. Dikegulac sodium or ethephon would inhibit the apical meristems and thus reduce apical dominance. In this procedure, cytokinins would stimulate adventitious bud and shoot formation and release dormant buds from quiescence. Cytokinins could also be used in conjunction with ethylene compounds to stimulate branching. The applications should not be made simultaneously, as cytokinin reduces sensitivity to ethylene, requiring that ethylene be applied first and followed by cytokinins a week later (Carey 2008). In addition, ethephon requires a low pH carrier solution and cytokinins are absorbed best at neutral pH, suggesting they should not be mixed (Carey 2008). Nursery tree height can be regulated by timing bioregulator applications to obtain branches starting within a specific range of height above the bud union, as long as species-specific bud formation characteristics are taken into account. Producers interested in establishing branch meristems at a particular height on trees can adjust application programs based on the desired height of branching and the characteristics of the bud formation responses (Elfving and Visser 2006).

Improving Branching Angles

As cytokinins stimulate branching, exogenous application may potentially limit upward growth by promoting competition for plant resources between branches. Cytokinins have been observed to improve branch angles in some narrow-angled woody crops, such as Bradford pear (*Pyrus calleryana* Decne.) (Wertheim 2000; Stern and Flaishman 2003; Costa et al. 2004). This effect could apply to other ornamental woody plants to improve branch angles during production and thus enhance retail quality and landscape aesthetics (Wilson 2000).

In regulating branch angle, cytokinins may be used in mixes with other growth inhibitors, but no working combinations have yet been established. Products containing a mixture of cytokinins and gibberellins (Fascination®, Fresco®, Promalin) that are used to prevent leaf yellowing and bud burst in Easter lilies and tulips may prove useful in this respect. There may be a potential for growers to save money by substituting cytokinin PGRs for manual pinching (Mickelbart 2011).

Photoreceptors, such as phytochrome and cryptochrome, and cytokinins interact through multiple signaling pathways to regulate photosynthetic acclimation to light gradients. In this role, cytokinins regulate both anatomy and photosynthetic pigments to control the photosynthetic capacity of plant crowns, including regulating branching (Boonman 2007). Exogenously applied cytokinin or localized overproduction of cytokinin has been demonstrated to rescue the effects of partial shade treatments (Pons et al. 2001; Boonman et al. 2007).

SUMMARY AND CONCLUSION

Current research demonstrates roles for phytohormones, particularly cytokinins, for regulating branching, bud formation, and foliage patterns that affect crown shape in trees. Auxin and cytokinin work in conjunction to control bud formation. Many PGRs are made from synthetic phytohormones, with benzylaminopurine being the largest and most well-studied group of cytokinin-based PGRs.

Newly developed information and technology in phytohormonal actions have great potential to improve techniques for regulating tree crown development and advancing the tree care and horticulture industries. The goal of this study is to use

this literature review to understand the mechanics and physiological processes of branching, and to aid in distinguishing where more research is necessary.

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Résumé. Cette revue de littérature évalue la pertinence des cytokinines en lien avec la forme du houppier de l'arbre, intégrant les résultats de recherches et leurs applications actuelles et potentielles aux méthodes d'entretien arboricoles. Les méthodes actuelles les plus populaires de culture des arbres en pépinière amènent les producteurs à modifier physiquement la forme d'un arbre par le tuteurage, la taille ou le pincement, ce qui peut nécessiter beaucoup de temps et s'avérer onéreux. L'application des phytohormones (appelés également régulateurs de croissance) peut fournir aux producteurs de plantes ornementales et aux arboriculteurs des méthodes alternatives pour orienter le développement du houppier des arbres. Après une étude abrégée de la science sur l'activité des cytokinines, cette revue analyse l'utilisation actuelle et potentielle des phytohormones comme méthode alternative rentable afin d'orienter la forme de l'arbre. Elle expose comment les différentes formes de cytokinines, agissant seules ou en combinaison avec d'autres régulateurs de croissance, peuvent être utilisées, ce à quoi elles peuvent être utilisées, les méthodes d'application et le moment optimal pour les applications dans les cycles phénologiques des arbres. En intégrant les études appliquées et fondamentales en cours, la revue vise à résumer notre compréhension sur la régulation de la cytokinine sur la structure des houppiers, tout en explorant des applications potentielles pour le milieu arboricole.

Zusammenfassung. Dieser Literaturüberblick untersucht die Relevanz von Zytokininen bei der Baumkronenform, unter Berücksichtigung von wissenschaftlicher Forschung mit gegenwärtigem und potentiellem Einsatz bei Baumpflegemethoden. Gegenwärtige und äußerst populäre Baumpflegemethoden erwarten von den Züchtern eine Veränderung der Baumform durch Verformen, Rückschnitt und Ausdünnen, was sehr teuer und arbeitsintensiv sein kann. Die Applikation von Phytohormonen (auch bekannt als Pflanzenwachstumsregulatoren, PGRs) kann Baumschulen und Arboristen eine alternative Methode zur Manipulation von Baumkronencharakteristika liefern. Einem Auszug aus der Erforschung der Phytohormonaktivität zufolge, untersucht dieser Überblick die gegenwärtigen und potentiellen Verwendungen von Phytohormonen als eine kosten-effektive, alternative Methode zur Manipulation von Baumformen. Es diskutiert, wie die verschiedenen Formen von Zytokinin PGRs, die allein und im Verbund mit anderen PGRs agieren, verwendet werden können, wofür sie verwendet werden können, die Methoden der Applikation und die Zeiten der Applikation innerhalb des phänologischen Kreislaufs der Bäume. Durch eine Integration der gegenwärtigen Grundlagen- und Anwender-spezifischen Literatur versucht diese Übersicht ein Verständnis für die Regulation von Zytokinin in der Kronenstruktur zusammen zu fassen, während potentielle Applikationen in der Baumindustrie erforscht werden.

Resumen. Esta revisión de la literatura explora la relevancia de las citoquininas que se forman en las copas de los árboles, integrando la investigación científica con las aplicaciones actuales y potenciales a los métodos para el cuidado de los árboles. Los métodos de cuidado de los árboles actuales y más populares piden a los productores alterar físicamente la forma de un árbol con el tutoreo, la poda y despunte, que puede llevar mucho tiempo y es costoso. La aplicación de fitohormonas (también conocidos como reguladores del crecimiento de plantas, PGRs) puede proporcionar a los productores ornamentales y arboristas métodos alternativos para manipular las características de la copa del árbol. Siguiendo la actividad de la citoquinina, la revisión investiga los usos actuales y potenciales de las fitohormonas como un método alternativo rentable de la manipulación de la forma del árbol. Se discute cómo, actuando solo y en concierto con otros reguladores de crecimiento, se pueden utilizar las diferentes formas de citoquinina, PGRs, para encontrar métodos y ritmo de las aplicaciones dentro de los ciclos fenológicos de los árboles. Mediante la integración de la literatura básica y aplicada actual, la revisión busca resumir la comprensión de la regulación de la estructura de citoquinina de la copa, mientras que explora el potencial de las aplicaciones en la industria del cuidado de los árboles.

APPENDIX

Species- and cultivar-specific exogenous applications of cytokinin formulations to affect growth characteristics (more citations can be located in the literature cited of Carey 2008).

TREE	CYTOKININ: BA	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Acanthopanax sieboldianus (5-leaf *Aralia*)	1–100 ppm/continuous dip of dormant cut stems	1–100	BA	Propagation–delayed budbreak but increased the % of breaks	(Yang and Read 1997)
Aralia elata (Japanese angelica tree)	50–200 ppm/one spray onto trees; 50 ppm was best	50	BA	Branching agent/ propagation	(Sugiura and Azuma 2005)
Camellia × *williamsii*	10–100 ppm/foliar spray every three days, 2–32 times	10–100	BA	Branching agent–no effect on branching	(Richards and Wilkinson 1984)
Castanea dentate (chestnut)	BA (1–100 ppm)/stem dip; BA 100 ppm	100	BA	Propagation–delayed budbreak but increased the % of buds that broke	(Yang and Read 1997)
Chamaecyparis lawsoniana (Port Orford cedar Christmas trees)	500–1000 ppm/foliar spray applied four times at two-week intervals	500–1000	BA	Growth inhibitor/ Branching agent–caused severe phytotoxicity and did not increase bud formation	(Duck et al. 2004)
Chrysobalanus icaco (coco plum)	400 ppm of BA and 2iP and 450 ppm of Promalin/ single foliar sprays	400 and 450	BA	Branching agent	(Rudniki and Rejman 1982)
Forsythia × *intermedia*	BA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays onto rooted cuttings	200	BA	Branching agent	(Grzesik and Rudnicki 1985)
Hydrangea	BA 1750–3500 ppm/ three foliar sprays one week apart; BA 100–600 ppm/ two foliar sprays in summer	1750–3500 and 100–600	BA	Senescence inhibitor–no effect on senescence but flowering was delayed	(Shanks and Link 1964)
Ilex crenata (Japanese holly)	BA 100–600 ppm/two foliar sprays in summer; BA 125–1000 ppm/one spray; best results from 450 ppm and 1000 ppm	100–600	BA	Branching agent–increased branching, increased the number of shoots, reduced shoot length and leaf size	(Wright 1975; Wright 1976; Gilliam and Wright 1977; Keever and Foster 1990)
Ilex glabra (inkberry holly)	BA 1750–3500 ppm/ three foliar sprays one week apart; the best time to apply BA is when the leaves start to harden off	1750–3500	BA	Branching agent	(Oates et al. 2005b)
Ilex opaca (American holly)	BA 10–1000 ppm	10–100	BA	Flower enhancer–inconsistent effects on sex of flowers	(Milbocker 1967)
Ilex paraguariensis (Yerba mate)	BA 495–2973 ppm/single foliar spray early summer; 1980 ppm was most effective	495–2973	BA	Branching agent–stimulated lateral branching	(Sansberro et. al. 2006)

TREE	CYTOKININ: BA	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Ilex vomitoria (yaupon holly)	BA 125–1000 ppm/single foliar spray; BA 1000 was most effective	1000	BA	Branching agent–increased budbreak	(Keever and Foster 1990)
Nandina domestica (heavenly bamboo)	BA 1000–5000 ppm/1–5 foliar sprays one week apart; BA 2500–5000 in April was most effective	2500–5000	BA	Branching agent–induced lateral branching	(Keever and Foster 1990; Keever and Morrison 2003; Oates et al. 2005b)
Photinia × *fraseri* (Fraser's Photinia)	BA 500–2500 ppm/single foliar spray; BA 1000 ppm in March greatly increased budbreak overpruning	1000	BA	Branching agent	(Keever and Foster 1990; Owings and Newman 1993)
Picea glauca (black spruce)	BA 500–1000 ppm/foliar spray applied four times at two-week intervals	500–1000	BA	Growth inhibitor/branching agent–increased lateral bud formation and caused phytotoxicity and deformities	(Duck et al. 2004)
Picea glehnii (Sakhalin spruce)	BA 0.01–10 ppm	0.01–10	BA	Growth inhibitor	(Shibakus 1980)
Picea omorika, (Serbian spruce Christmas trees)	BA 500 to 1000 ppm/foliar spray applied four times at two-week intervals	500–1000	BA	Growth inhibitor/branching agent	(Duck et al. 2004)
Picea pungens (Colorado blue spruce Christmas trees)	BA 500–1000 ppm/foliar spray applied four times at two-week intervals or whole tree single foliar spray application six weeks after budbreak; BA 2.25–225 ppm/scions dipped prior to grafting or single foliar spray	2.25–225 ppm and 500–100	BA	Branching agent/growth inhibitor/propagation–BA at 22.5 ppm increased graft success, BA at 225 ppm is best applied at budbreak to stimulate new bud formation	(Mulgrew and Williams 1985; Mazzola and Costante 1987; Beeson and Proebsting 1989; Duck et al. 2004)
Pinus banksiana (Jack pine)	BA 50–400 ppm/one foliar spray; BA 400 ppm reduced height but trees were deformed with poor root growth	400	BA	Growth inhibitor–BA was rejected as appropriate for this use	(Schnurr et al. 1996)
Pinus densiflora (Japanese red pine)	BA 2000 ppm/Lanolin paste applied in late summer and autumn	2000	BA	Flower enhancer/yield enhancer–seed yield was decreased and the seed had a slightly lower germination rate than controls	(Wakushima 2004)
Pinus mugo var. *mughus* (Mugo pine)	BA 225–900 ppm/six foliar sprays at five-day intervals in May and again when weather warmed; 450 ppm is best	450	BA	Branching agent	(Stiff and Boe 1985)
Pinus nigra (Austrian pine)	BA 2000–6000 ppm/1–2 foliar sprays 30–90 days after sowing seed	2000–6000	BA	Branching agent/growth enhancer–reduced height and branching	(Boe 1990)

TREE	CYTOKININ: BA	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Pinus palustris (long leaf pine)	BA 2000–5000 ppm, PBA, Kinetin, 6-CP, Cytex (5% solutions)/applied to the terminal bud biweekly in May three times	2000–5000	BA	Growth enhancer–BA, PBA, Kinetin and 6-CP caused too many buds to form, all promoted height growth	(Hare 1984)
Pinus ponderosa (Ponderosa pine)	BA 10–1000 ppm	10–1000	BA	Branching agent/plant propagation	(Cohen and Shanks 1975)
Pinus strobes (white pine)	BA 300 ppm/single foliar spray on the terminal leader in June	300	BA	Branching agent	(Hinesley and Wright 1988)
Pinus sylvestris (Scots pine)	BA 2000 to 6000 ppm/1–2 foliar sprays 30 to 90 days after sowing seed; BA 2000 ppm increased branching but plants were slightly shorter	2000	BA	Branching agent/growth enhancer/propagation–BA mixed with other PGRs greatly increased fascicular branch development	(Whitehill and Schwab 1975; Boe 1990)
Pinus thunbergii (Japanese black pine)	0.1% 9-BA Vasoline paste applied to cut roots (worked best) or BA 2000 ppm/Lanolin paste applied to the bud	2000	BA	Branching agent	(Yamaji and Tomioka 1980; Wakushima 2004)
Pittosporum tobira (Japanese pittosporum)	2iP, BA/single foliar spray onto unpinched plants; BA 200 ppm and 2iP 100 ppm most effective	300	BA	Branching agent	(Rudniki and Rejman 1982)
Populus hybrids (poplar)	BA 225 ppm/droplet applied daily to a lateral bud	225	BA	Branching agent	(Cline and Dong-Il 2002)
Prunus persica (peach)	BA 100 to 200 ppm/drops placed onto dormant buds of cut branches; applications of 200 ppm were best in January	200	BA	Dormancy release	(Weinberger 1969)
Prunus × *keio-zakura* (flowering cherry)	BA 300 ppm/single foliar spray in summer at various times	300	BA	Flower enhancer	(Yamasaki 2003)
Pseudotsuga menziesii (Douglas-fir)	BA 112 ppm and 1000 ppm/whole-tree single foliar spray application in spring	112 and 1000	BA	Branching agent	(Mazzola and Costante 1987; Cline et al. 2006)
Pyrus calleryana (Callery pear)	BA 150–600 ppm, Promalin 300–1200 ppm/single foliar spray in autumn	150–600	BA	Branching agent–Promalin 1200 ppm was slightly better than BA 600 ppm at increasing shoots and crotch angles significantly	(Keever et al. 1993)
Quercus alba (white oak)	BA 1–100 ppm/continuous dip of dormant cut stems; 100 ppm worked best	100	BA	Propagation	(Yang and Read 1997)
Quercus robur (English oak)	BA 10 ppm/24 soak of four-year-old dormant seedlings	10	BA	Stress tolerance/branching agent–increased branches and leaves	(Smith and Schwab 1980)

TREE	CYTOKININ: BA	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Rhapheolepis indica (Indian hawthorn)	BA 1750–5000 ppm/three foliar sprays in spring at 1- to 3-week intervals; BA(BAP-10) 1250–5000 ppm/2–4 weekly foliar spray applications; 1250 ppm is most effective and rates above 2500 ppm caused phytotoxicity	1250	BA	Branching agent	(Oates et al. 2004; Oates et al. 2005a; Oates et al. 2005b)
Rhododendron (Azalea, florist)	BA 2000 ppm in April increased branching but not as much as pruning; Promalin 5000 ppm in April was better than pruning	2000	BA	Branching agent	(Keever and Foster 1990; Bell et al. 1997)
Salix alba (white willow)	BA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays	200	BA	Branching agent	(Grzesik and Rudnicki 1985)
Sophora microphylla (Kowhai)	BA 11–34 ppm/solution applied to the base of a stem via an absorbent wick in mid-summer	11–34	BA	Branching agent	(Carswell et al. 1996)
Spiraea japonica (Japanese spiraea)	BA 200 ppm, Promalin 1000 ppm/single foliar spray or three foliar sprays; BA applied three times increased branching but was not as good as Ethrel; Promalin reduced branching at all application methods as did BA applied only once	200	BA	Branching agent	(Grzesik and Rudnicki 1985)
Spiraea × *vanhoutteii* (Van Houtte's spiraea)	BA 1–100 ppm, Thidiazuron 1–50 ppm/continuous dip of cut stems or BA added at various times	1–100	BA	Propagation/budbreak	(Yang and and Read 1991)
Viburnum odoratissimum (sweet Viburnum)	BA 1–900 ppm, BA + GA (Promalin) 250–1000 ppm/ 1–2 applications worked best; Promalin 1000 ppm was effective in greatly increasing branching	1–300	BA	Branching agent–BA 300 ppm and above caused severe phytotoxicity	(Schoene and and Yeager 2005)
Weigela florida (Weigela)	BA (200 ppm), Promalin (1000 ppm)/single foliar spray or three foliar sprays onto rooted cuttings	200	BA	Branching agent	(Grzesik and 1985)
TREE	**CYTOKININ: BA + GA**	**RATE (PPM)**	**CYTOKININ**	**PURPOSE OF EXPERIMENT**	**CITATION**
Astilbe taquetii	BA + GA (Fascination) 125–500 ppm/two foliar spray applications at day 0 and day 21	125–500	BA + GA	Branching agent–significant phytotoxicity	(Lieth and Dodge 2004)
Buxus sempervirens, *B. sinica* (boxwood)	BA + GA (Promalin) 1500 ppm/foliar spray applied 10 weeks after the end of spring growth was best at increasing lateral shoots	1500	BA + GA	Branching agent/remove Dormancy	(Musselwhite et al. 2004)

TREE	CYTOKININ: BA + GA	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Carica papaya (papaya)	BA + GA 500 ppm each/three applications at one week intervals to one-year-old plants; foliar sprays were most effective followed by injection, then Lanolin	1000	BA + GA	Branching agent	(Giampan et al. 2005)
Hibiscus moscheutos (rose mallow)	BA + GA (Fascination) 125–500 ppm/two foliar spray applications at day 0 and day 21; but wasn't very effective	125–500	BA + GA	Branching agent	(Lieth and and Dodge 2004)
Pyrus calleryana (Callery pear)	BA + GA (Promalin) 1500 ppm/single foliar spray in June to one-year-old plants	1500	BA + GA	Branching agent	(Jacyna et al. and Dodge 2004)
Rhaphiolepis indica (Indian hawthorn)	BA or BA + GA (Promalin)/ single foliar spray application	—	BA + GA	Branching agent	(Keever and Foster 1990)
Rhododendron (Azalea, Vireya)	BA, PBA, Thidiazuron all at 200 ppm/single foliar spray; PBA was most effective, Thidiazuron was a close second	200	BA + GA	Branching agent	(Criley 2000)
Ternstroemia gymnanthera (Japanese cleyera)	BA or BA + GA (Promalin)/ single foliar spray application	—	BA + GA	Branching agent	(Keever and Foster 1990)

TREE	CYTOKININ: KINETIN	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Berberis thunbergii (Japanese barberry)	Kinetin 100–500 ppm	100–500	Kinetin	Growth inhibitor	(McCarthy and Bünemann 1981b)
Camellia sinensis (tea)	Kinetin 80 ppm released shoots from dormancy when applied to them	80	Kinetin	Dormancy release	(Kulasegaram 1969)
Carica papaya (papaya)	Kinetin 65–130 ppm, BA 250–500 ppm/monthly foliar spray applications	65–130, 250–500	Kinetin	Branching agent	(Morales-Payan and Stall 2003)
Cornus alba (Siberian dogwood)	Kinetin 270 ppm; Kinetin + GA increased branching more than either chemical alone	270	Kinetin	Branching agent	(Loach and Whalley 1975)
Elaeagnus angustifolia (tea olive)	Kinetin 50 ppm/applied to seeds	50	Kinetin	Germination promoter	(Hamilton and Carpenter 1976)
Lonicera xylosteum (dwarf honeysuckle)	Kinetin 100–500 ppm; applications had no effect	—	Kinetin	Growth inhibitor	(McCarthy and Bünemann 1981b)
Picea abies (Norway spruce)	Kinetin 100–500 ppm	100–500	Kinetin	Growth inhibitor	(McCarthy and Bünemann 1981a)
Rhododendron (Azalea)	GA + Kinetin 100 ppm +100 ppm/applied every four days to the flower bud	100	Kinetin	Budbreak and formation	(Furuta and Straiton 1965)

TREE	CYTOKININ: KINETIN	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Ribes (black currant)	Kinetin 2 ppm/apply in late autumn for best results	2	Kinetin	Dormancy release	(Lenz and Karnatz 1969)
Salix purpurea (purple willow)	Kinetin 100–500 ppm; Kinetin 500 ppm worked best	500	Kinetin	Growth inhibitor	(McCarthy and Bünemann 1981b)
Syringa spp. (lilac)	Kinetin and BA rates and application method not listed	—	Kinetin	Dormancy release–BA inhibited germination of seeds that were not dormant	(Junttila 1970)
Tsuga canadensis (Canadian hemlock)	Kinetin 100–500 ppm	100–500	Kinetin	Growth inhibitor	(McCarthy and Bünemann 1981a)
Viburnum opulus (American cranberrybush)	Kinetin 100–500 ppm	100–500	Kinetin	Branching agent	(McCarthy and Bünemann 1981b)
Weigela florida (Weigela)	Kinetin 270 ppm with GA 90 ppm	270	Kinetin	Branching agent	(Loach and Whalley 1975)
TREE	**CYTOKININ: BA+ KINETIN**	**RATE (PPM)**	**CYTOKININ**	**PURPOSE OF EXPERIMENT**	**CITATION**
Cotoneaster dammeri (bearberry cotoneaster)	BA + Kinetin (Early Harvest PGR–also contains GA and auxin) 1.5–3.0 ml in 1125 ml water; (1.17 ppm BA + 1.17 ppm Kinetin)/45 ml soil drenches every two weeks from June to September	2.34	BA + Kinetin	Stress tolerance/branching agent–no effect on growth	(Ruter 2000)
Cotoneaster salicifolius (willowleaf cotoneaster)	BA + Kinetin (Early Harvest PGR–also contains GA and auxin) 1.5–3.0 ml in 1125 ml water; (1.17 ppm BA + 1.17 ppm Kinetin)/45 ml soil drenches every two weeks from June to September	2.34	BA + Kinetin	Stress tolerance/branching agent–no effect on growth	(Ruter 2000)
Rhododendron	BA 100 ppm/foliar spray 2–32 times with no effect on growth	100	BA + Kinetin	Branching agent	(Richards and Wilkinson 1984)
Spiraea japonica (Japanese spiraea)	BA + Kinetin (Early Harvest PGR–also contains GA and auxin) 1.5–3.0 ml in 1125 ml water (1.17 ppm BA + 1.17 ppm Kinetin)/ 45 ml soil drenches every two weeks from June to September; the low 1.5 ml rate increased plant quality; the 3.0 ml rate increased growth	2.34	BA + Kinetin	Stress tolerance/branching agent	(Ruter 2000)
Thuja occidentalis (Arborvitae)	BA + Kinetin (Early Harvest PGR–also contains GA and auxin) 1.5–3.0 ml in 1125 ml water; (1.17 ppm BA + 1.17 ppm Kinetin)/ 45 ml soil drenches every two weeks from June to September	2.34	BA + Kinetin	Stress tolerance/branching agent–no effect on growth	(Ruter 2000)

TREE	CYTOKININ: BA+ KINETIN	RATE (PPM)	CYTOKININ	PURPOSE OF EXPERIMENT	CITATION
Weigela florida (Weigela)	BA + Kinetin (Early Harvest PGR–also contains GA and auxin) 1.5–3.0 ml in 1125 ml water (1.17 ppm BA + 1.17 ppm Kinetin)/45 ml soil drenches every two weeks from June to September	2.34	BA + Kinetin	Stress tolerance/branching agent–no effect on growth	(Ruter 2000)
Rhododendron (Azalea)	PBA (200 ppm) + GA (200 to 100 ppm)/six foliar sprays during the winter	200, 300, 400	BA + Kinetin	Budbreak dormancy	(Nell and Larson 1974)