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REVIEW

Practical Applications of Manipulating Plant Architecture by Regulating Gibberellin Metabolism

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Abstract The international trade in floriculture is estimated to be worth about US$150 billion, with the global demand for ornamentals steadily increasing. Consumer choice is influenced by factors such as plant architecture and flower colour. Conventional breeding has been responsible for the introduction of novel traits into ornamental plants and has played an important role in the development of new cultivars. However, a restricted gene pool and failure of distant crosses have led to the exploitation of somatic cell techniques, particularly genetic transformation, to generate plants with desirable traits. Gibberellins (GAs) are endogenous plant hormones that control key aspects of growth and development. Chemical growth regulators that modify GA biosynthesis are used extensively in horticulture to control plant stature, increasing production costs, manpower, and environmental risks. An alternative strategy involves genetic manipulation of GA metabolism to induce phenotypic changes, particularly alteration of stature. Because ornamentals are not used for human consumption, genetic manipulation approaches with these plants may be more acceptable in the immediate future to the general public, in certain parts of the world, than genetically manipulated food crops.

Keywords Gibberellins (GA) · GA oxidase genes · *Agrobacterium*-mediated transformation

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Economic Importance of Horticultural Plants

The ornamental industry comprises mainly foliage and flowering plants suitable for both protected (indoor and glasshouse) and outdoor cultivation. The commercial production of ornamental plants is increasing worldwide. According to Chandler (2003), the world trade in floriculture was estimated to be more than US$27 billion (equivalent to approximately 21 billion euros), with cut-flowers making up about one third of the value. More recent estimations by the Flower Council of Holland (http://www.flowercouncil.org/int/holland/facts_figures/, 2007) show a world production value of approximately 50 billion euros and a global consumption value by consumers of 100-150 billion euros.

The US and Europe are the main areas of production and consumption of floricultural products. In addition, areas with equatorial and subequatorial climates and low-wage labour forces are ideal for the production and export of cut flowers at affordable prices. Countries such as Colombia and Ecuador are the largest suppliers to the US market, while Ethiopia, Kenya, Morocco, and Turkey supply most EU markets. Recently, the Chinese flower industry has entered the export trade, with Japan and the west coast of the US being its first target markets (Chandler and Tanaka 2007).

Roses (*Rosa* x *hybrida*) are the most important flower crop and, with chrysanthemum (*Dendranthema grandiflora*), lily (*Lilium* sp.), gerbera (*Gerbera* x *hybrida*), tulip (*Tulipa* sp.), and carnation (*Dianthus caryophyllus*), they dominate the floricultural market, being available in many forms and colours (Chandler and Tanaka 2007). Flowering pot plants of considerable importance include many orchid species such as *Phalaenopsis* and *Dendrobium*, cyclamen (*Cyclamen persicum*), chrysanthemum, azalea (*Rhododendron* spp.),

petunia (*Petunia* x *hybrida*), and begonia (*Begonia* sp.), whereas indoor foliage plants such as ficus (*Ficus benjamina*), spathiphyllum (*Spathiphyllum* spp.), various cacti, and palm species also share a large proportion of the floricultural market (Chandler and Tanaka 2007). According to the US National Agricultural Statistics Service (http://www.nass.usda.gov/QuickStats/index2.jsp, 2008), bedding/garden plants and potted flowering plants account for more than half of the value of the floricultural industry in the US, with geranium (*Pelargonium* spp.), petunia, pansy (*Viola* spp.), impatiens (*Impatiens* spp.), begonia, and marigold (*Tagetes erecta*) being the most important; rose and azalea constitute the largest sale of shrubs.

In the UK, the retail value of cut flowers and indoor plants in 2008 was estimated to have reached £2.2 billion (http://www.flowers.org.uk/industry/UK_market.php). Due to low light intensity and temperature conditions, especially during the winter months, it is not possible economically to grow certain plants and flowers. Consequently, a considerable number are imported. The largest source of imports at the moment is the Netherlands, although many of the plants imported from the Netherlands originate from other countries via the Dutch auction house system. Significant amounts of flowers are also imported from Colombia, Israel, and Kenya. Pot plants are imported mainly from the Netherlands, Belgium, and Denmark (http://www.flowers.org.uk/industry/UK_market.php).

Future Requirements of the Horticultural Industry

The ornamental industry strives for novelty to generate new products (for example, plants with novel pigmentation and architecture) at competitive prices. Consumer purchase is governed largely by plant appearance, flower colour, and tolerance to insects and pests (Tanaka and others 2005).

Until recently, the introduction of novel traits into ornamental plants and the development of new cultivars have been based on conventional breeding and selection, including the domestication of wild species and the selection of novel "sports" from popular species already in cultivation. However, complex polygenic traits such as vegetative growth and flowering are difficult to manipulate using this approach and may take considerable time (Mishra and Srivastava 2004). The restricted gene pool and failure of distant sexual crosses during conventional breeding have generated interest in exploiting somatic cell technologies, including somatic hybridization/cybridization, exposure of somaclonal variation, and genetic transformation (Chandler and Lu 2005; Brand 2006), to produce plants to keep pace with the demand of the rapidly expanding floriculture industry. In nature, plants compete for light and space, resulting in dwarf phenotypes being eliminated during conventional selection. Consequently, dwarfed plants are difficult to obtain through natural breeding (Busov and others 2003). However, novelty may be achieved by regulating plant stature, that is, by creating compact (dwarf) plants or, conversely, by increasing plant height. To date, genetic manipulation programmes have been directed primarily at manipulating flower colour, as in the first report in petunia (Meyer and others 1987). However, the Australian company Florigene Pty Ltd. is the only one currently marketing genetically manipulated (GM) ornamental plants. Seventy-five million plants of its Moonshadow, Moonlite, Moondust, and Moonshade series of transgenic carnations, ranging from blue-violet to deep blue, have been sold in Australia, Japan, and the US in the last 11 years (Mol and others 1999; Chandler 2003; Fukui and others 2003).

Chemical Growth Regulators and Their Limitations

Chemical growth regulators are used extensively to modify plant stature (Rademacher 2000). Unfortunately, their use has escalated the cost of crop production, including increased manpower to deliver the chemicals to the crops, and contributed to environmental risks. Repeated applications of these chemicals may be essential to achieve the desired results but their effects may still be variable (Radi 2005). Chemical growth-regulating substances are classified as pesticides, and rigorous plant protection regulations, which apply to hazardous chemicals, are also relevant to their use. Chemical forms of GAs, such as prohexadione, interfere with anthocyanin synthesis and, hence, floral pigmentation (Rademacher 2000). Growth retardants are used routinely on many field crops to prevent lodging (for example, use of chlormequat on wheat), but in many cases they can cause undesirable effects.

The effects of chemical growth regulators are similar to those found in GA-deficient mutants. The GA biosynthetic pathway has been well established and most of the genes that are involved in the pathway have been characterized (Hedden and Phillips 2000). Therefore, it can be argued that exploitation of genetic manipulation techniques to modify growth could help to preserve the environment and benefit human health. Currently, an important limitation is that the public is reluctant to accept genetic manipulation technology, especially in Europe, because of its perceived risks, particularly the risk of transferring genes to wild species (Uzogara 2000). Importantly, terminator gene technology (Kuvshinov and others 2001) may prevent the flow of transgenes to wild species or other crops, thus reducing any of the anticipated risks.

Gibberellins and Their Control of Plant Development

Gibberellins are an extensive group of tetracyclic diterpenoid carboxylic acids, with structures based on the *ent*-gibberellane carbon skeleton (Yamaguchi 2006; Fig. 1). They are naturally occurring growth regulators and control many aspects of plant development, including seed germination, shoot growth, flowering, and fruit expansion.

GAs play a major role in seed germination. In monocotelydonous plants, they mobilise usable energy (secreting hydrolytic enzymes into the starchy endosperm, for example, in wheat), whereas in dicotyledons, they induce the production of hydrolytic enzymes, which weaken the seed coat (Peng and Harberd 2002; Singh and others 2002). They are present in greatest concentrations in developing organs and decrease with maturity. GAs also promote stem elongation (Little and MacDonald 2003) by initiating cell division in apical and subapical meristems. They have been implicated in determining cell identity in shoot apical meristems in which high cytokinin and low GA concentrations promote cell maintenance in stems. Other developmental processes that are stimulated by GAs include leaf expansion, trichome formation and flower development, the initiation of male flowers in the Cucurbitaceae, and female flowers in maize (*Zea mays*) and castor bean (*Ricinus communis*) (Sawhney and Shukla 1994). GAs are also found to stimulate transition from the vegetative to the flowering state (Hedden and Phillips 2000). Their production often increases in rosette plants after exposure to long days and/or low temperature, resulting in the induction of rapid stem extension and flowering. Red light promotes seed germination by increasing GA biosynthesis, which enhances tissue differentiation and development (Kamiya and Garcia-Martinez 1999; Yamaguchi and Kamiya 2000).

Significant progress has been achieved in the last decade in understanding the biochemical pathway of GA metabolism and the regulation of GA biosynthesis in plants. To date, 136 different GAs have been identified from 130 species of vascular plants and 7 species of bacteria and fungi. Of these GAs, GA_1, GA_3, GA_4, GA_5, GA_6, and GA_7 are some of the most bioactive forms. GA_1 is the most bioactive GA in the majority of plants, whereas GA_4 is the predominant form in *Arabidopsis* and members of the Cucurbitaceae (Sponsel and Hedden 2004). Talon and others (1990) found that shoots of *Arabidopsis* contained 15 times more GA_4 than GA_1, and that GA_4 is more effective in promoting stem elongation. Other GAs are thought to be precursors of bioactive GAs or catabolic products, which may lack physiological roles. GAs can also occur as conjugates. Several factors, including tissue type, developmental stage, and environmental responses, influence GA metabolism.

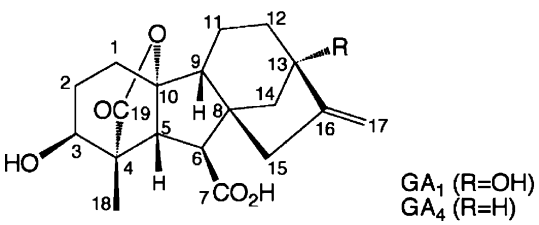

Fig. 1 Chemical structures of bioactive GAs

GA Biosynthesis in Higher Plants

GA biosynthesis can be divided into three stages (Yamaguchi 2008). The first occurs in plastids, where geranylgeranyl diphosphate (GGDP) is converted to *ent*-kaurene in a two-stage reaction, the intermediate compound being *ent*-copalyl diphosphate (CPP; Sponsel and Hedden 2004) (Fig. 2). The second phase is believed to occur in the endoplasmic reticulum and involves a series of oxidation reactions through which *ent*-kaurene is converted to GA_{12} and its 13 hydroxylated analogue, GA_{53} (Sponsel and Hedden 2004; Yamaguchi 2008). However, there is some evidence that *ent*-kaurene oxidase is also present in the plastid envelope. The final stage of GA biosynthesis takes place in the cytoplasm, where the bioactive gibberellins GA_1 and GA_4 are formed from GA_{53} and GA_{12}, respectively, by 2-oxoglutarate-dependent dioxygenases (GA 20- and GA 3-oxidases). Another group of dioxygenases, GA 2-oxidases, are responsible for the deactivation, by 2β-hydroxylation, of GA_1 and GA_4 and their precursors into the inactive molecules, maintaining GA homeostasis. The final concentration of GAs in the plant, and in individual tissues, is determined by both the rate of synthesis of GAs and their rate of conversion to inactive forms (Olezewski and others 2002).

Plants maintain GA homeostasis by depressing GA biosynthesis and stimulating catabolism. This occurs by downregulating GA 20-oxidase and GA 3-oxidase gene expression but upregulating GA 2-oxidase expression, the relative importance of which varies with species and tissues (Sponsel and Hedden 2004).

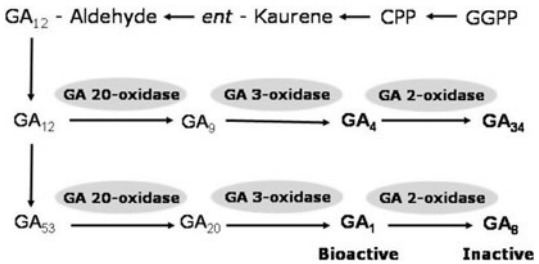

Fig. 2 Principal pathways of GA biosynthesis

Practical Application and Benefits of Manipulating GAs in Plants

Endogenous plant hormones, including GAs, have been modified naturally since the evolution of land plants commenced several million years ago (Yasumura and others 2007), and through the selection of desirable phenotypes in crop improvement in the last 12,000 years. More sophisticated methods that exploit genetic manipulation through somatic cell technologies involving somatic hybridization and transformation are also available to generate modern-day transgenic crops (Phillips 2004).

The GA signalling pathway is a major target for conventional breeding and genetic modification to alter plant stature. In view of increasing public concern about potential environmental damage and health hazards through the use of chemicals that modify GA metabolism and the limited availability of genes to modify stature through classical breeding, there is a requirement to consider the use of somatic cell techniques, particularly transformation, to modify GA biosynthesis. Similarly, it is possible that morphological and physiological traits in both horticultural and floricultural crops can be modified to increase productivity by manipulating GA metabolism and signalling pathways through molecular approaches (Mino and others 2006).

Overexpression of GA 2-oxidase to Induce Dwarfism

Many ornamental plants such as poinsettia and chrysanthemum are naturally tall and lack uniformity of growth. Consequently, chemicals such as cycocel (Cyclocel, BASF, Arnhem, the Netherlands; Citadel, Fine Americas, Walnut Creek, CA, USA), daminozide (Dazine, Fine Agrochemicals Ltd., Worcester, UK; B-9, Chemtura Corporation, Middlebury, CT, USA), and paclobutrazol (Bonzi, Syngenta, Wilmington, DE, USA; Piccolo, Pirouette, Fine Agrochemicals Ltd.) are used by producers to obtain uniformity by disrupting GA biosynthesis. However, frequent applications are needed to effect the desired changes in plant height. Consequently, modification of genes involved in the synthesis and catabolism of bioactive GAs has provided a new perspective for manipulating plant stature. Experiments conducted using *PcGA2ox1*, a gene encoding a GA 2-oxidase from *Phaseolus coccineus* (runner bean; Thomas and others 1999), introduced into *Solanum melanocerasum*, *Solanum nigrum* (Dijkstra and others 2008), *Petunia* spp., and *Nicotiana sylvestris* (Kourmpetli and others, unpublished data) as the target plants, resulted in dwarf phenotypes comparable to those induced following treatment with chemical growth retardants. A similar strategy was used to dwarf wheat (Hedden and Phillips 2000; Appleford and others 2008) and rice (Sakamoto and others 2003).

GA 2-oxidases are designated depending on whether they act on C_{19} or C_{20} GA precursors. Multifunctional activity of GA 2-oxidase was detected in *AtGA2ox2* and *AtGA2ox3* from *Arabidopsis thaliana, PcGA2ox1* from runner bean (Thomas and others 1999), *PsGA2ox1* from pea (Lester and others 1999; Martin and others 1999), *OsGA2ox3* from rice (Sakamoto and others 2001), *SoGA2ox1* from spinach (Lee and Zeevaart 2002), and *NoGA2ox3* from oleander (Ubeda-Thomas and others 2007). In contrast, a multifunctional role was not found for *PsGA2ox2* from pea (Lester and others 1999), *OsGA2ox1* from rice (Sakamoto and others 2001), and *SoGA2ox2* from spinach (Lee and Zeevaart 2002), together with *NoGA2ox1* and *NoGA2ox2* from oleander (Ubeda-Thomas and others 2007). Ectopic expression of all the above-mentioned GA *2ox* genes resulted in dwarfism. Because *PcGA2ox1* converts bioactive GA_4 and GA_1, formed during the last stages of GA biosynthesis, to inactive GA_{34} and GA_8, respectively, this provided the rationale for genetically manipulating plants for dwarfism with *PcGA2ox1*.

Any complications resulting from constitutive gene expression driven by, for example, the CaMV 35S constitutive promoter may be circumvented by the use of tissue-specific promoters. For example, in a study conducted to generate dwarf plants of *N. sylvestris* by expression of the *PcGA2ox1* gene, a stem tissue-specific promoter from *A. thaliana* was used which resulted in transgenic plants with normal flowering and seed set (Kourmpetli and others, unpublished data). This approach has potential not only for foliage plants and those cultivated for their flowers, but also for general amenity plants such as turf grasses, reducing the requirement for mowing. Tissue-specific promoters can be identified from the publicly funded freely available microarray databases such as AtGenExpress for *Arabidopsis*, isolated from suitable plant material, linked to *PcGA2ox1*, and expressed in ornamentals such as *N. sylvestris.* Importantly, in studies with *N. sylvestris*, plants transformed with a stem-specific promoter were of uniform height, unlike the range of phenotypes exhibited by plants transformed with the same gene but driven by the constitutive CaMV 35S promoter. These results are consistent with previous studies reported by Sakamoto and others (2003) in rice.

Expression of *PcGA2ox1* in ornamental and fruit trees could restrict pruning and maintenance costs (Mino and others 2006) and permit increased planting densities. Dwarf plants are also more drought tolerant than their nontransformed counterparts because they have less surface area, thus decreasing transpiration. Such genetically manipulated plants could easily fit the model of xeriscaping (http://en.wikipedia.org/wiki/Xeriscaping), a form of landscaping in

which plants thrive on reduced water availability, especially in those parts of the world where water is scarce.

Other approaches may be adopted to induce dwarfism. These include the use of antisense GA 20-oxidase (Coles and others 1999; Bulley and others 2005), interference or micro-RNA (RNAi), double-stranded RNA against specific GA biosynthetic genes (Fire 1999; Sharp 2001), and the introduction of a GA Insensitive gene (GAI; Yasumura and others 2007). The use of RNAi or gene silencing can be a robust technique for downregulating specific genes encoding GA biosynthetic enzymes or those genes acting directly on GA metabolism.

Overexpression of GA 3- and GA 20-oxidases to Increase Plant Stature

While the chemical dwarfing of plants is important in ornamentals such as "pot-mum" chrysanthemums, increase in stature may be desirable in other cases. In this context GA_3 (Progibb, Valent Biosciences Corporation, Libertyville, IL, USA; Falgro, Fine Agrochemicals Ltd.) is often used on ornamentals such as *Colocasia*, *Caladium*, *Dieffenbachia*, *Spathiphyllus*, *Synguinium*, and several other species (Brooking and Cohen 2001). Gibberellins are also used to prevent post-harvest leaf yellowing in cut flowers such as lily and alstromeria. In this respect, many ready-to-use GAs such as Perlan (Fine Agrochemicals Ltd.) are available commercially for use on horticultural crops. Again, genetic modification by manipulating GA biosynthesis may be an alternative strategy to spraying plants with GAs to increase plant stature. Thus, overexpression of GA 20-oxidase from various species increases plant growth, whereas transformation with GA 3-oxidase results in significant, but less dramatic, increase in growth. GA 3-oxidases have been cloned from several sources, including *Arabidopsis* (Chiang and others 1995), pumpkin (Lange 1997), pea (Martin and others 1997), lettuce (Toyomasu and others 1998), tomato (Robers and others 1999), tobacco (Itoh and others 1999), and wild cucumber (Ward and others, unpublished). Coles and others (1999) found that ectopic expression of *AtGA20ox1* resulted in a significant increase in plant height when introduced into *A. thaliana*, whereas Carrera and others (1999) reported that GA 20-oxidase was under feedback control, with a diurnal regulation in synthesis. Subsequently, they increased bioactive GA_1 in potato (*Solanum tuberosum*) by overexpressing *StGA20ox1*, with associated increase in growth and internode length (Carrera and others 2000). Similar results were reported in apple (Kusuba and others 2001). In the same year, Vidal and others (2001) expressed *NtGA20ox1* in tobacco to increase plant stature, this work being relevant to the genetic manipulation of ornamental tobacco species. Likewise, Biemelt and others (2004) investigated the impact of altered GA concentration on growth of tobacco plants transformed with the *AtGA20ox* gene from *A. thaliana* under the constitutive CaMV 35S promoter. Some of the plants generated were taller than their wild-type counterparts, indicating changes in the content of bioactive GAs. Similar results have been obtained in *S. nigrum* and the ornamental tobacco *N. sylvestris* using *MmGA3ox1* and *MmGA3ox2* genes from *Marah macrocarpus* and *AtGA20ox1* from *A. thaliana* (Bhattacharya 2008). Transformation of the woody ornamental aspen hybrid (*Populus tremuloides*) with 35S::*PtGA20ox1* resulted in an increase in internode length without an increase in internode number. Citrus trees are not only important fruit trees but also have ornamental value in formal garden settings. Thus, Fagoaga and others (2007) observed that sense and antisense overexpression of citrus 20-oxidase (*CcGA20ox1*) in the citrus hybrid carrizo citranage, commonly used as a rootstock, resulted in a change in plant architecture. Taller (sense) and shorter (antisense) phenotypes correlated with increased and reduced concentrations, respectively, of bioactive GA_1 in growing shoots. It is believed that GA 20-oxidase is the rate-limiting step in GA biosynthesis. Consequently, changes in its activity alter plant architecture.

Future Prospects for Genetic Manipulation Technology in Horticulture

In 2006, the purchase of ornamental plants in the US alone was US$20.8 billion (Potera 2007), emphasising the major opportunities for development and sales of existing and new ornamental plants. Tissue culture approaches, from simple micropropagation of elite germplasms to high-technology transformation of target plants, can be combined with traditional breeding to broaden the gene pool available for improvement of ornamentals and to introduce new, desirable traits. The development of floriculture-based technologies such as the petunia DNA microarray chip (Koltai and others 2008) now makes it possible to identify novel genes and, in the immediate future, to generate plants with new traits that appeal to the consumer. Plant hormones control key aspects of growth and development; chemical growth regulators act by modifying or substituting the action of natural hormones. The global use of plant growth regulators exceeds US$1 billion and increases annually, although there has been a recent decline in the number of chemicals available because of more stringent regulations (Phillips 2004). A genetic manipulation approach could reduce the requirement for synthetic growth regulators. Unfortunately, there has been considerable resistance to genetically manipulated products in Europe,

although it is likely that the status of ornamental plants may be reviewed alongside that of food crops. This is important, as the flower consumption per capita in Europe is the greatest in the world. However, outside Europe there has been little criticism of genetically modified plants (Potera 2007).

Considerable financial investment is needed to counteract the high costs of developing new cultivars (Robinson and Firoozabady 1993) and obtaining intellectual property rights to protect new varieties from exploitation by competitors. Tanaka and others (2005) indicated that the floriculture industry would benefit from the introduction of genetically modified novel traits. Undoubtedly, there is considerable potential for manipulating GA signalling in plants, and proof-of-concept has already been demonstrated. Because plant development is also affected by other growth hormones, including auxins, cytokinins, ethylene, brassinosteroids, jasmonic acid, salicylic acid, and polyamines (Appleford and others 2008), it is likely that biosynthetic pathways for these compounds will become targets for genetic manipulation in ornamentals. Indeed, modification of plant stature may necessitate manipulation of multiple hormonal pathways. Future research must be directed toward identifying tissue-specific or species-specific inducible promoters that could, for example, drive gene expression in vegetative tissues such as those of stem internodes without affecting flowering and seed production.

The possibility of using constructs for plant transformation that carry GA oxidase genes but which lack a gene for selection of transgenic plants, such as the neomycin phosphotransferase (*npt*II) gene for kanamycin resistance (Holn and others 2001), should be explored to facilitate the acceptance of transformation technology to regulate plant stature. In this respect, transgenic, regenerated plants can be selected in some species by their phenotype without the need for expression of a selectable marker gene. For example, plants of *S. melanocerasum* and *S. nigrum* transformed with the *PcGA2ox1* gene had characteristic dark green leaves associated with their compact growth (Dijkstra and others 2008). In addition to the use of transformation vectors based on the T-DNA and its border sequences of the Ti plasmid of *Agrobacterium tumefaciens*, it is possible to use DNA sequences similar to those of the T-DNA but which have originated from plant genomes. Plants transformed with such constructs are "cisgenic plants," as their transformation vectors, the promoters and terminators, are derived from the same plant species (Chandler and Tanaka 2007). In the longer term, such vectors may be more acceptable than those based on the DNA of the plant pathogen *A. tumefaciens.*

Although genetic modification provides the means to generate new cultivars by the incorporation of one or more genes, the expression of genes across plant species is often unpredictable, necessitating an empirical approach (Tanaka and others 2005). In addition, the application of genetic modification to ornamentals is still limited by the lack of efficient transformation and regeneration systems (Newell 2000) and a restricted market for individual ornamental species compared to major food crops. Indeed, the development of efficient, reproducible, and cultivar-independent transformation techniques remains vital to the growth of the floriculture industry.

Genetic modification necessitates transformed cells developing into viable plants. In some cases, labour-intensive tissue culture can be bypassed using approaches such as the "floral dip procedure," reducing time and cost. However, this simple technology, developed with *A. thaliana* (Clough and Bent 1998), remains limited to a few species and is not, at present, generally applicable to ornamental plants. Antagonism to genetic manipulation, in general, has restricted the application of the technology to ornamental plants (Azevedo and Araujo 2003; Phillips 2004). Unfortunately, there is no uniform system for international regulation of genetically modified organisms with significant differences between countries (Halsberger 2006). The Cartagena protocol (http://www.cbd.int/biosafety/protocol.shtml) is the first attempt to bring uniformity in laws governing genetic modification and many countries are adapting these laws to an agreed consensus on genetically manipulated plants, including ornamentals.

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References

Appleford NEJ, Wilkinson MD, Ma Q, Evans DJ, Stone MC, Pearce SP, Powers SJ, Thomas SG, Jones HD, Phillips AL, Hedden P, Lenton JR (2008) Decreased shoot stature and grain alpha-amylase activity following ectopic expression of a gibberellin 2-oxidase gene in transgenic wheat. J Exp Bot 56:112–120

Azevedo JL, Araujo WL (2003) Genetically modified crops: environmental and human health concerns. Mutat Res 544: 223–233

Bhattacharya A (2008) Genetic manipulation of plant growth and development by regulating gibberellin biosynthesis. PhD thesis, University of Nottingham, UK

Biemelt S, Tschiersch H, Sonnawald U (2004) Impact of altered gibberellin metabolism on biomass accumulation, lignin biosynthesis and photosynthesis in transgenic tobacco plants. Plant Physiol 135:254–265

Brand MH (2006) Ornamental plant transformation. J Crop Improv 17:27–50

Brooking M, Cohen H (2001) The influence of gibberellic acid on growth and flowering of some Zantedeschia cultivars grown outdoors. Acta Hort 673:15–22

Bulley SM, Wilson FM, Hedden P, Phillips AL, Croker SJ, James DJ (2005) Modification of gibberellin biosynthesis in the grafted apple scion allows control of tree height independent of the rootstock. Plant Biotechnol J 3:215–223

Busov VB, Meilan R, Pearce DW, Ma C, Rood SB, Strauss SH (2003) Activation tagging of a dominant gibberellin catabolism gene (GA 2-oxidase) from poplar that regulates tree stature. Plant Physiol 132:1283–1291

Carrera E, Jackson SD, Prat S (1999) Feedback control and diurnal regulation of gibberellin 20-oxidase transcript levels in potato. Plant Physiol 119:765–773

Carrera E, Bou J, Garcia-Martinez JL, Prat S (2000) Changes in GA 20-oxidase gene expression strongly affects stem length, tuber induction and tuber yield of potato plants. Plant J 22:247–256

Chandler S (2003) Commercialization of genetically modified ornamental plants. J Plant Biotechnol 5:69–77

Chandler SF, Lu C (2005) Biotechnology in ornamental horticulture. In Vitro Cell Dev Biol Plant 41:591–601

Chandler S, Tanaka Y (2007) Genetic modification in floriculture. Crit Rev Plant Sci 26:169–197

Chiang HH, Hwang I, Goodman HM (1995) Isolation of the *Arabidopsis* GA_4 locus. Plant Cell 7:195–201

Clough SJ, Bent AF (1998) Floral dip: a simplified method for *Agrobacterium*-mediated transformation of *Arabidopsis thaliana*. Plant J 16:735–743

Coles JP, Phillips AL, Croker SJ, Garcia-Lepe R, Lewis MJ, Hedden P (1999) Modification of gibberellin production and plant development in *Arabidopsis* by sense and antisense expression of gibberellin 20-oxidase genes. Plant J 17:547–556

Dijkstra C, Adams E, Bhattacharya A, Page AF, Anthony P, Kourmpetli S, Power JB, Lowe C, Thomas SG, Hedden P, Phillips AL, Davey MR (2008) Over-expression of a gibberellin 2-oxidase gene from *Phaseolous coccineus* L. enhances gibberellin inactivation and induces dwarfism in Solanum species. Plant Cell Rep 27:463–470

Fagoaga C, Tadeo FR, Iglesias DJ, Huerta L, Lliso I, Vidal AD, Talon M, Navarro L, García-Martínez JL, Peña L (2007) Engineering of gibberellin levels in citrus by sense and antisense overexpression of a *GA* 20-oxidase gene modifies plant architecture. J Exp Bot 58:1407–1420

Fire A (1999) RNA-triggered gene silencing. Trends Genet 15:358–363

Fukui Y, Tanaka N, Kusumi T, Iwashita T, Nomoto K (2003) A rationale for the shift in colour towards blue in transgenic carnation flowers expressing the flavonoid 3′,5′-hydroxylase gene. Phytochemistry 63:15–23

Halsberger AG (2006) Need for an "Integrated Safety Assessment" of GMOs linking food safety and environmental consideration. J Agr Food Chem 54:3173–3180

Hedden P, Phillips AL (2000) Gibberellin metabolism: new insights revealed by the genes. Trends Plant Sci 5:523–530

Holn B, Levy AA, Puchta H (2001) Elimination of selection markers from transgenic plants. Curr Opin Biotechnol 12:139–143

Itoh H, Ueguchi MT, Kawaide H, Chen X, Kamiya Y, Matsuoka M (1999) The gene encoding tobacco gibberellin 3β-hydroxylase is expressed at the site of GA action during stem elongation and flower organ development. Plant J 20:15–24

Kamiya Y, Garcia-Martinez JL (1999) Regulation of gibberellin biosynthesis by light. Plant Biol 2:398–403

Koltai H, Bar-Or C, Bar-Akiva A, Oren-Shamir M (2008) Characterization of the process of anthocyanine degradation in *Brunfelsia* flowers: a cross-species hybridization to DNA microarray approach. In: plant and animal genome XVI conference, W 340, San Diego, CA, 12–16 January 2008

Kusuba S, Honda C, Kano-Murakami Y (2001) Isolation and expression analysis of gibberellin 20-oxidase homologous gene in apple. J Exp Bot 52:375–376

Kuvshinov V, Koivu K, Kanerva A, Pehu T (2001) Molecular control of transgene escape from genetically modified plants. Plant Sci 160:517–522

Lange T (1997) Cloning gibberellin dioxygenase genes from pumpkin endosperm by heterologous expression of enzyme activities in *Escherichia coli*. Proc Natl Acad Sci USA 94:6553–6558

Lee JD, Zeevaart JAD (2002) Differential regulation of RNA levels of gibberellin dioxygenases by photoperiod in spinach. Plant Physiol 130:2085–2094

Lester DR, Ross JJ, Smith JJ, Elliott RC, Reid JB (1999) Gibberellin 2-oxidation and the SLN gene of *Pisum sativum*. Plant J 19:65–73

Little CHA, Macdonald JE (2003) Effects of exogenous gibberellin and auxin on shoot elongation and vegetative bud development in seedlings of *Pinus sylvestris* and *Picea glauca*. Tree Physiol 23:73–83

Martin DN, Proebsting WM, Hedden P (1997) Mendel's dwarfing gene: cDNAs from the Le alleles and function of the expressed proteins. Proc Natl Acad Sci USA 94:8907–8911

Martin DN, Proebsting WM, Hedden P (1999) The *SLENDER* gene of pea encodes a gibberellin 2-oxidase. Plant Physiol 121:775–781

Meyer P, Heidemann I, Forkmann G, Saedler H (1987) A new petunia flower color generated by transformation of a mutant with a maize gene. Nature 330:677–678

Mino M, Oka M, Tasaka Y, Iwabuchi M (2006) Molecular biology of the metabolism and signal transduction of gibberellins, and possible application to crop improvement. J Crop Improv 18:365–390

Mishra P, Srivastava AK (2004) Molecular investigations in ornamental floricultural plants. J Plant Biotechnol 6:131–143

Mol J, Cornish E, Mason J, Koes R (1999) Novel coloured flowers. Curr Opin Biotechnol 10:198–201

Newell CA (2000) Plant transformation technology. Mol Biotechnol 16:53–65

Olezewski N, Sun TP, Gubler F (2002) Gibberellin signalling: biosynthesis, catabolism and response pathways. Plant Cell S61-S80

Peng JR, Harberd NP (2002) The role of GA-mediated signaling in the control of seed germination. Curr Opin Plant Biol 5:376–381

Phillips AL (2004) Genetic and transgenic approaches to improving crop performance. In: Davies PJ (ed) Plant hormones: biosynthesis, signal transduction, action! Kluwer Academic Publishers, Dordrecht, the Netherlands, pp 582–609

Potera C (2007) Blooming biotechnology. Nature 25:963–965

Rademacher R (2000) Growth retardants: effects on gibberellin biosynthesis and other metabolic pathways. Annu Rev Plant Phys 51:501–531

Radi A (2005) Over-expression of pumpkin GA-oxidases in *Arabidopsis thaliana*. PhD thesis, University of Braunschweig, Germany

Robers M, Kaneta T, Kawaide H, Yamaguchi S, Yang YY, Imai R, Sekimoto H, Kamiya Y (1999) Regulation of gibberellin biosynthesis genes during flower and early fruit development of tomato. Plant J 17:241–250

Robinson KEP, Firoozabady E (1993) Transformation of floriculture crops. Sci Hort 55:83–89

Sakamoto T, Kobayashi M, Itoh H, Tagiri A, Kayano T, Tanaka H, Iwahori S, Matsuoka M (2001) Expression of a gibberellin 2-oxidase gene around the shoot apex is related to phase transition in rice. Plant Physiol 125:1508–1516

Sakamoto T, Morinaka Y, Ishiyama K, Kobayashi M, Itoh H, Kayano T, Iwahori S, Matsuoka M, Tanaka H (2003) Genetic manipulation of gibberellin metabolism in transgenic rice. Nat Biotechnol 21:909–913

Sawhney VK, Shukla A (1994) Male sterility in flowering plants–are plant growth substances involved? Am J Bot 81:1640–1647

Sharp PA (2001) RNA interference. Genes Dev 15:485–490

Singh DP, Jermakow AM, Swain SM (2002) Gibberellins are required for seed development and pollen tube growth in *Arabidopsis*. Plant Cell 14:133–147

Sponsel S, Hedden P (2004) Gibberellin biosynthesis and inactivation. In: Davies PJ (ed) Plant hormones: biosynthesis, signal transduction, action! Kluwer Academic Publishers, Dordrecht, the Netherlands, pp 356–380

Talon M, Koornneef M, Zeevaart JAD (1990) Accumulation of C_{19}-gibberellins in the gibberellin-insensitive dwarf mutant *gai* of *Arabidopsis thaliana* (L.) Heynh. Planta 182:501–505

Tanaka Y, Katsumoto Y, Brugliera F, Mason J (2005) Genetic engineering in floriculture. Plant Cell Tissue Organ Cult 80:1–24

Thomas SG, Phillips AL, Hedden P (1999) Molecular cloning and functional expression of gibberellin 2-oxidases, multifunctional enzymes involved in gibberellin deactivation. Proc Natl Acad Sci USA 96:4698–4703

Toyomasu T, Kawaide W, Mitsuhashi Y, Inoue Y, Kamiya Y (1998) Phytochrome regulates gibberellin biosynthesis during germination of photoblastic lettuce seeds. Plant Physiol 118:1517–1523

Ubeda-Tomás S, García-Martinez JL, López-Diaz I (2007) Molecular, biochemical and physiological characterization of gibberellin biosynthesis and catabolism genes from *Nerium oleander*. J Plant Growth Regul 25:52–68

Uzogara SG (2000) The impact of genetic modification of human foods in the 21st century. Biotechnol Adv 18:179–206

Vidal AM, Gisbert C, Talon M, Primo-Millo E, López-Diaz I, Garcia-Martinez JL (2001) The ectopic overexpression of a citrus gibberellin 20-oxidase enhances the non 13-hydroxylation pathway of gibberellin biosynthesis and induces an extremely elongated phenotype in tobacco. Physiol Plant 112:251–260

Yamaguchi S (2006) Gibberellin biosynthesis in *Arabidopsis*. Phytochem Rev 5:39–47

Yamaguchi S (2008) Gibberellin metabolism and its regulation. Annu Rev Plant Biol 59:225–251

Yamaguchi S, Kamiya Y (2000) Gibberellin biosynthesis: its regulation by endogenous and environmental signals. Plant Cell Physiol 41:251–257

Yasumura Y, Crumpton-Taylor M, Fuentes S, Harberd NP (2007) Step-by-step acquisition of the gibberellin-DELLA growth-regulatory mechanism during land-plant evolution. Curr Biol 17:1225–1230

Web References

Flower Council of Holland—Facts and Figures: http://www.flowercouncil.org/int/holland/facts_figures/

Flowers and Plants Association—The UK Market: http://www.flowers.org.uk/industry/UK_market.php

The Cartagena Protocol on Biosafety: http://www.cbd.int/biosafety/protocol.shtml

US National Agricultural Service (USDA)—Floriculture Crops: http://www.nass.usda.gov/QuickStats/index2.jsp

Wikipedia: http://en.wikipedia.org/wiki/Xeriscaping