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Influence of the *roIC* gene on phenotypic alterations in horticultural plants

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Abstract
The *roIC* gene, derived from *Agrobacterium rhizogenes*, has emerged as a powerful molecular tool for modifying phenotypic traits in horticultural crops. This article reviews the current understanding of *RoIC* -mediated phenotypic alterations across diverse ornamental and horticultural species. Research demonstrates that *RoIC* transformation consistently produces compact plant architectures characterized by reduced height, altered branching patterns, modified leaf and flower morphology, and changes in flowering time. These effects are mediated through alterations in plant hormone homeostasis, particularly involving cytokinin and auxin pathways. The severity of phenotypic changes correlates with *RoIC* expression levels and varies depending on the promoter used. Applications span major ornamental crops including petunia, carnation, rose, chrysanthemum, and various fruit crops, with significant implications for developing compact cultivars with improved horticultural characteristics. This review synthesizes findings from 30 key studies to provide a comprehensive understanding of *RoIC* gene function and its practical applications in ornamental plant breeding.

Keywords: *roIC* gene, plant transformation, compact growth habit, horticultural crops, morphological alterations

Introduction

Genetic transformation has revolutionized plant breeding by enabling the introduction of specific traits that would be difficult or impossible to achieve through conventional methods. Among the various genetic tools available, the *rol* (root loci) genes from *Agrobacterium rhizogenes* have attracted considerable attention for their ability to induce dramatic morphological changes in transformed plants. The *RoIC* gene, in particular, has emerged as a valuable tool for modifying plant architecture and other horticultural traits in ornamental and crop species.

The *RoIC* gene is part of the T-DNA (transfer DNA) of the Ri (root-inducing) plasmid of *Agrobacterium rhizogenes*, a soil bacterium that naturally infects plants and causes hairy root disease. When individual *rol* genes are transferred to plants through genetic transformation, they produce distinct phenotypic effects that can be harnessed for crop improvement. The *RoIC* gene specifically has been shown to induce a suite of morphological changes including dwarfism, altered branching patterns, modified leaf and flower characteristics, and changes in flowering time (Winefield *et al*., 1999), (Gardner et.al 2006), (Zuker *et al*., 2001) [9, 26, 27].

The potential of *RoIC* for horticultural applications lies in its ability to produce compact plant forms with enhanced ornamental value. Compact cultivars are highly desirable in the ornamental industry as they require less space, reduced chemical growth regulators, and often exhibit improved aesthetic qualities. Furthermore, *RoIC* transformation can modify multiple traits simultaneously, offering an efficient approach to cultivar development (Takahashi *et al*., 2006), (Scorza *et al*., 1994) [22, 25].

This article provides a comprehensive review of the influence of *RoIC* genes on phenotypic alterations in horticultural plants, examining the molecular mechanisms underlying these changes and their practical applications across diverse crop species.

Background and Theoretical Foundations

1. The *rol* Gene Family and *Agrobacterium rhizogenes*

Agrobacterium rhizogenes is a gram-negative soil bacterium that causes hairy root disease in susceptible plants through the transfer of T-DNA from its Ri plasmid into the plant genome. The Ri T-DNA contains four *rol* genes (*rolA*, *rolB*, *RoIC*, and *rolD*), each contributing to different aspects of the characteristic Ri phenotype (Boase *et al*., 2004) [3]. The typical Ri phenotype includes compact growth, altered leaf morphology, enhanced rooting ability, and various other morphological modifications (Christensen *et al*., 2009) [6].

While natural transformation by *A. rhizogenes* transfers all four *rol* genes simultaneously, modern genetic engineering techniques allow for the introduction of individual *rol* genes or specific combinations. This approach enables researchers to dissect the specific contribution of each gene and to tailor phenotypic modifications for particular horticultural applications (Casanova *et al*., 2005) [4], (Christensen *et al*., 2009) [6]. The *RoIC* gene has been particularly well-studied due to its strong effects on plant architecture and its potential for ornamental crop improvement (Smith *et al*., 2006) [9].

2. Molecular Function of *RoIC*

The molecular function of *RoIC* has been linked to alterations in plant hormone homeostasis, particularly affecting cytokinin metabolism. The *RoIC* gene product has been proposed to possess cytokinin-β-glucosidase activity, which could increase the levels of active cytokinins by releasing them from inactive glucoside conjugates (Gardner *et.al*, 2006) [9]. This enzymatic activity would explain many of the observed phenotypic effects, as cytokinins play crucial roles in regulating shoot branching, leaf development, and other growth processes.

Research has demonstrated that *RoIC* expression affects endogenous hormone levels and sensitivity. Studies on transgenic tobacco and potato plants expressing single *rol* genes revealed alterations in both hormonal content and plant sensitivity to exogenous hormones (Schmülling *et al*.,

1993) [21]. The *RoIC* gene has also been shown to influence auxin and abscisic acid levels, suggesting a complex interplay between multiple hormone pathways (Bettini *et al*., 2010) [2].

The severity of phenotypic alterations induced by *RoIC* is closely correlated with gene expression levels. Plants with higher *RoIC* transcript abundance typically exhibit more pronounced morphological changes (Winefield *et al*., 1999), (Gardner et.al 2006) [9, 26]. This dose-dependent relationship provides opportunities for fine-tuning phenotypic modifications by controlling expression levels through promoter selection and other regulatory mechanisms.

Phenotypic Alterations Induced by *RoIC* Transformation

1. Plant Architecture and Growth Habit

One of the most consistent and commercially valuable effects of *RoIC* transformation is the reduction in plant height, producing compact or dwarf phenotypes. This dwarfing effect has been documented across numerous horticultural species and is often accompanied by reduced internode length (Winefield *et al*., 1999), (Gardner et.al 2006), (Zuker *et al*., 2001), (Scorza *et al*., 1994) [9, 22, 26, 27].

In petunia, *RoIC* transformation resulted in significant reductions in plant height, with the severity of dwarfing correlating with *RoIC* transcript levels (Winefield *et al*., 1999) [26]. Similarly, transgenic carnation plants expressing *RoIC* exhibited reduced plant height while maintaining desirable flower characteristics (Zuker *et al*., 2001) [27]. The dwarfing effect was also observed in tobacco, where height reductions of up to 42% were recorded in plants expressing *RoIC* under the strong 35S promoter (Gardner et.al., 2006) [9]

Beyond height reduction, *RoIC* transformation frequently causes a break in apical dominance, leading to increased lateral branching. This effect produces bushier plants with more compact growth habits (Winefield *et al*., 1999), (Boase *et al*., 2004) [3, 26]. In Regal pelargoniums, *RoIC* expression resulted in a dwarf phenotype affecting both vegetative and floral characteristics (Boase *et al*., 2004) [3]. The increased branching pattern is particularly valuable for ornamental applications, as it can enhance the visual appeal and flower production of potted plants.

The compact growth habit induced by *RoIC* has been successfully demonstrated in diverse species including roses (Salm *et al*., 1997) [20], chrysanthemums (Takahashi *et al*., 2006) [25], Kalanchoe (Christensen *et al*., 2009) [5], and Osteospermum (Giovannini *et al*., 1999) [11]. In each case, the transformation produced plants with reduced stature and altered branching patterns suitable for commercial ornamental production (Smith *et al*., 2006) [9].

2. Leaf and Flower Morphology

RoIC transformation induces significant changes in leaf morphology across multiple species. Common alterations include reductions in leaf size, changes in leaf shape, and modifications to leaf color. In tobacco plants expressing *RoIC* , leaf width decreased by up to 50%, and leaves appeared lighter and slightly more yellow compared to non-transformed controls (Gardner et.al., 2006) [9] Similar reductions in leaf size were observed in petunia, where both leaf and flower dimensions were reduced in *RoIC* transgenic lines (Winefield *et al*., 1999) [26].

The characteristic leaf morphology associated with *RoIC* expression is part of the broader Ri phenotype and contributes to the compact appearance of transformed plants (Christensen *et al*., 2009) [6]. In some species, the altered leaf morphology may affect photosynthetic capacity or other physiological processes, though these effects vary depending on the severity of the transformation and the specific crop species.

Flower morphology is also significantly affected by *RoIC* transformation. Reductions in flower size have been reported in multiple ornamental species, including petunia (Winefield *et al*., 1999), carnation (Zuker *et al*., 2001) [26, 27], and various other flowers [30]. In tobacco, corolla length and diameter were significantly reduced in *RoIC* -expressing plants (Gardner *et.al*, 2006) [9] However, the impact on flower quality varies among species and transformation events. In carnation, *RoIC* transformation produced plants with improved horticultural traits, including better flower quality in some lines (Zuker *et al*., 2001) [27].

The effects on flower morphology must be carefully evaluated for each species, as excessive reductions in flower size may be undesirable for certain ornamental applications. However, in many cases, the compact flowers complement the overall dwarf phenotype and are commercially acceptable or even preferred (Zuker *et al*., 2001), (Smith *et al*., 2006) [9, 27].

3. Flowering Time and Reproductive Characteristics

RoIC transformation frequently affects flowering time, with many studies reporting earlier flowering in transgenic plants. In petunia, time to flowering was reduced in *RoIC* transgenic lines (Winefield *et al*., 1999) [26]. Similarly, *RoIC* expression promoted early flowering in Atropa belladonna when the gene was expressed under the CaMV 35S promoter (Kurioka et.al., 1992) [14]. This acceleration of flowering can be advantageous for ornamental production, reducing the time from propagation to marketable plants.

The promotion of flowering by *RoIC* has been linked to its effects on hormone homeostasis, particularly the cytokinin-like effects of the gene product Gardner et.al (2006[9]}, [30]. In some cases, such as in sweet potato RolB/*RoIC* homologs expressed in Arabidopsis, the genes triggered early flowering along with premature leaf senescence (Shkryl et.al., 1992).

However, *RoIC* transformation can also negatively impact reproductive characteristics. Reduced male and female fertility has been reported in several species, with the severity of fertility reduction correlating with *RoIC* expression levels Winefield *et al*., (1999) [26]. In tobacco, some *RoIC* -expressing plants showed no detectable pollen on anthers, indicating severe male sterility (Gardner et.al., 2006) [9] These fertility effects must be considered when developing *RoIC* -transformed cultivars, particularly for species where seed production is important.

4. Root Development

As part of the *rol* gene family originally identified for their root-inducing properties, *RoIC* affects root development in transformed plants. The Ri phenotype typically includes improved rooting ability, which can be advantageous for vegetatively propagated ornamental crops (Christensen *et al*., 2009) [5]. Enhanced rooting facilitates propagation and can improve plant establishment after transplanting.

In rose, *RoIC* transformation was specifically investigated for its potential to improve rootstock performance, with the goal of enhancing rooting characteristics (Salm *et al*., 1997) [20], (Salm. 1992). The improved rooting ability associated

with *RoIC* expression is particularly valuable for ornamental species that are difficult to propagate or that benefit from vigorous root systems.

Studies on potato plants harboring the *RoIC* gene examined effects on tuber formation and overall plant morphology, demonstrating that *RoIC* can influence underground organ development in addition to shoot characteristics (Romanov *et al*., 1998) [18]. In strawberry, *RoIC* transformation affected plant adaptability, productivity, and interactions with soil-borne organisms, suggesting complex effects on root function and plant-environment interactions (Landi *et al*., 2010).

Molecular and Hormonal Mechanisms

1. Hormone Homeostasis

The phenotypic effects of *RoIC* are primarily mediated through alterations in plant hormone homeostasis. The proposed cytokinin-β-glucosidase activity of the *RoIC* gene product would increase active cytokinin levels, explaining many of the observed morphological changes (Gardner et.al., 2006) [9] Cytokinins regulate numerous developmental processes including shoot branching, leaf expansion, and flowering time, all of which are affected by *RoIC* transformation.

Research on transgenic tobacco and potato plants expressing single *rol* genes demonstrated that *RoIC* affects both hormonal content and plant sensitivity to hormones (Schmülling *et al*., 1993) [21]. The gene influences not only cytokinin levels but also auxin and abscisic acid homeostasis (Bettini *et al*., 2010) [2]. This multi-hormone effect suggests that *RoIC* acts at a central point in hormone signaling networks, with cascading effects on multiple developmental pathways.

The balance between auxin and cytokinin is particularly important for regulating apical dominance and branching patterns. The break in apical dominance and increased lateral branching observed in *RoIC* -transformed plants is consistent with elevated cytokinin levels or enhanced cytokinin sensitivity Winefield *et al*., (1999), (Boase *et al*., 2004) [3, 26]. Similarly, the dwarfing effect may result from altered auxin-cytokinin ratios affecting cell division and elongation in stems.

Small changes in growth regulator levels, distribution, or perception can produce dramatic phenotypic effects, as demonstrated by the wide range of phenotypes observed even with relatively modest differences in *RoIC* expression levels (Gardner et.al., 2006) [9] This sensitivity to hormone balance explains why *RoIC* transformation produces pleiotropic effects affecting multiple aspects of plant development simultaneously.

2. Gene Expression and Promoter Effects

The severity and specificity of *RoIC* -induced phenotypic changes depend critically on gene expression levels and patterns, which are controlled by the promoter used to drive *RoIC* expression. Studies comparing different promoters have revealed that expression level is a key determinant of phenotype severity (Gardner et.al., 2006) [9]

The constitutive CaMV 35S promoter, which drives high-level expression in most plant tissues, typically produces the most dramatic phenotypic alterations Winefield *et al*., (1999), Gardner et.al (2006}, (Kurioka et.al., 1992) [9, 14, 26]. Plants expressing *RoIC* under the 35S promoter show the highest *RoIC* mRNA levels and the most severe dwarfing, branching, and other morphological changes. This strong promoter is useful when pronounced phenotypic modifications are desired.

Alternative promoters can produce more subtle or tissue-specific effects. The light-inducible *rbcS* promoter and the native *RoIC* promoter both produced significant phenotypic changes in tobacco despite *RoIC* mRNA levels that were not significantly different from non-transformed controls (Gardner et.al., 2006) [9] This suggests that even low levels of *RoIC* expression, or expression in specific tissues or developmental stages, can be sufficient to alter plant phenotype.

The relationship between *RoIC* expression level and phenotype is generally dose-dependent, with higher expression producing more severe alterations Winefield *et al*., (1999), (Gardner et.al., 2006) [9, 26] However, some plants exhibit unique combinations of traits that do not follow this simple relationship, suggesting that factors beyond overall expression level—such as tissue-specific expression patterns, developmental timing, or genetic background—also influence the phenotypic outcome (Gardner et.al., 2006) [9]

Applications across Horticultural Crops

1. Ornamental Flowers

RoIC transformation has been extensively applied to ornamental flower crops, where compact growth habits and modified floral characteristics are highly valued. The gene has been successfully used to develop improved cultivars in several major ornamental species.

Petunia: Petunia was among the first ornamental crops to be transformed with *RoIC* , demonstrating the gene's potential for altering multiple commercially important traits Winefield *et al*., (1999) [26]. The resulting plants exhibited reduced height, increased branching, and earlier flowering—all desirable characteristics for potted plant production. The success with petunia established *RoIC* as a valuable tool for ornamental crop improvement.

Carnation: *RoIC* -transgenic carnation plants showed improved horticultural traits including better plant architecture and, in some lines, enhanced flower quality (Zuker *et al*., 2001) [27]. Quantitative and qualitative analyses of greenhouse-grown plants confirmed that *RoIC* transformation could produce commercially viable carnation cultivars with compact growth habits suitable for pot production.

Rose: Rose transformation with *RoIC* has been investigated both for direct modification of ornamental characteristics and for improving rootstock performance (Salm *et al*., 1997) [20], (Salm., 1992). The goal of using *RoIC* in rose rootstocks is to enhance rooting ability and potentially influence scion growth through rootstock-mediated effects. This approach offers a novel strategy for rose improvement that avoids some of the pleiotropic effects associated with direct transformation of the scion.

Chrysanthemum: Chrysanthemum cultivars transformed with *RoIC* exhibited altered morphology consistent with the Ri phenotype Takahashi *et al*., (2006) [25]. The compact growth habit and modified leaf characteristics produced by *RoIC* transformation are particularly suitable for potted chrysanthemum production, where plant height control is a major concern.

Pelargonium: Transgenic Regal pelargoniums expressing *RoIC* exhibited dwarf floral and vegetative phenotypes (Boase *et al*., 2004) [3]. The transformation produced compact plants with reduced height and altered flower characteristics, demonstrating the applicability of *RoIC* technology to this important ornamental genus.

Other ornamentals: *RoIC* transformation has also been successfully applied to Kalanchoe (Christensen *et al*., 2009) [5], Osteospermum (Giovannini *et al*., 1999) [11], and various other ornamental species (Casanova *et al*., 2005) [4], (Christensen *et al*.,., 2009) [6]. In each case, the transformation produced compact plants with altered morphological characteristics suitable for ornamental applications.

2. Fruit Crops

While *RoIC* has been most extensively studied in ornamental species, it has also been applied to fruit crops with varying objectives and outcomes.

Citrus: Trifoliate orange (*Poncirus trifoliata*) plants transformed with *RoIC* were characterized for morphological and physiological changes (Kaneyoshi *et al*., 1999) [12]. The transformation of citrus with *RoIC* and other *rol* genes has been investigated for potential effects on tree architecture and fruit production (Gentile *et al*.,, 2004) [10]. Compact tree forms could facilitate orchard management and harvesting operations.

Pear: 'Beurre Bosc' pear was transformed with the *RoIC* gene to investigate potential applications in fruit tree improvement (Bell *et al*., 1999) [1]. As with citrus, the goal was to explore whether *RoIC* could be used to develop more compact tree forms suitable for high-density planting systems.

Strawberry: *RoIC* strawberry plants were evaluated for adaptability, productivity, and tolerance to soil-borne diseases, as well as mycorrhizal interactions (Landi *et al*., 2010). This research demonstrated that *RoIC* transformation affects not only plant morphology but also plant-environment interactions that are important for crop performance.

3. Vegetable and Other Horticultural Species

RoIC has been investigated in various vegetable and other horticultural crops, though applications in these species are less developed than in ornamentals.

Tomato: The insertion of *RoIC* in tomato affected plant architecture and endogenous auxin and abscisic acid levels (Bettini *et al*., 2010) [2]. This research provided insights into the hormonal mechanisms underlying *RoIC* effects and demonstrated the gene's potential for modifying vegetable crop architecture.

Potato: Potato plants harboring the *RoIC* gene were studied for effects on morphology and tuber formation (Romanov *et al*., 1998) [18]. The research examined how *RoIC* affects both above-ground plant architecture and underground tuber development, providing insights into the gene's effects on different organ systems.

Tobacco: While tobacco is not a major horticultural crop, extensive research on *RoIC* transformation in tobacco has provided fundamental insights into gene function and phenotypic effects Gardner et.al (2006}, Scorza *et al*., (1994), (Schmülling *et al*., 1993) [9, 21, 22]. These studies established many of the principles that guide *RoIC* applications in other species.

Other species: *RoIC* transformation has been investigated in Kentucky bluegrass (Mcclellan and Knauff, 1996) [13], Belgian endive and carrot (Limami *et al*., 1998) [16], radish (Dodueva *et al*., 1999), and various other species. These studies have expanded our understanding of *RoIC* function across diverse plant families and growth habits.

Horticultural Implications and Commercial Applications

The phenotypic alterations induced by *RoIC* transformation have significant implications for horticultural production and commercial applications. The most immediate and valuable application is the development of compact cultivars for the ornamental industry. Compact plants require less growing space, reducing production costs and allowing more efficient use of greenhouse facilities. They also require less or no application of chemical growth regulators, which reduces input costs and addresses environmental and regulatory concerns (Smith *et al*., 2006) [9].

The earlier flowering induced by *RoIC* transformation can shorten production cycles, allowing growers to bring plants to market more quickly and potentially produce more crop cycles per year Winefield *et al*., (1999), (Kurioka et.al., 1992) [14, 26]. This acceleration of flowering time represents a significant economic advantage for ornamental producers.

The increased branching and bushier growth habit produced by *RoIC* transformation can enhance the aesthetic appeal of potted plants, potentially commanding premium prices in the marketplace Winefield *et al*., (1999), (Boase *et al*., 2004) [3, 26]. For many ornamental species, a compact, well-branched plant form is highly desirable and can differentiate products in competitive markets.

The improved rooting ability associated with *RoIC* expression facilitates vegetative propagation, which is the primary propagation method for many ornamental species (Christensen *et al*., 2009) [6]. Enhanced rooting can reduce propagation time and costs while improving the success rate of cutting propagation.

For fruit crops, the potential to develop compact tree forms through *RoIC* transformation could enable high-density planting systems that increase yield per unit area and facilitate mechanized harvesting (Kaneyoshi *et al*., 1999), (Bell *et al*., 1999), (Gentile *et al*.,, 2004) [1, 10, 12]. However, applications in fruit crops must carefully consider effects on fruit quality, yield, and other production characteristics.

The use of *RoIC* in rootstocks represents an innovative approach that can influence scion characteristics while avoiding some of the pleiotropic effects of direct transformation (Salm, 1992). This strategy may be particularly valuable for crops where certain *RoIC* effects are desirable while others are problematic.

Challenges and Limitations

Despite the promising applications of *RoIC* transformation, several challenges and limitations must be addressed for successful commercial implementation.

Pleiotropic effects: *RoIC* transformation produces multiple phenotypic changes simultaneously, some of which may be undesirable Winefield *et al*., (1999), (Gardner *et.al*, 2006) [9,

[26] For example, reduced fertility can be problematic for species where seed production is important. The challenge is to harness beneficial effects while minimizing or eliminating unwanted traits. This may require careful selection of transformation events, optimization of expression levels, or use of tissue-specific promoters.

Expression level control: The severity of phenotypic alterations is closely linked to *RoIC* expression levels, but achieving optimal expression can be challenging (Gardner et.al., 2006) [9] Too little expression may produce insufficient phenotypic modification, while excessive expression can result in severely stunted plants with poor vigor. Fine-tuning expression through promoter selection and other regulatory mechanisms is essential for commercial applications.

Species and genotype variation: The effects of *RoIC* transformation vary among species and even among genotypes within species Gardner et.al (2006}, (Casanova *et al*., 2005) [4, 9]. This variation necessitates empirical testing for each target crop and cultivar. What works well in one species may not be directly transferable to another.

Regulatory and public acceptance: As with all genetically modified organisms, *RoIC* -transformed plants face regulatory hurdles and potential public acceptance issues in many markets [30]. The regulatory pathway for commercialization varies among countries and can be lengthy and expensive. Public perception of genetic modification in ornamental and food crops remains a concern in some regions.

Stability of transformation: The stability of *RoIC* expression and phenotype across generations and in different environmental conditions must be ensured for commercial applications (Fladung, 1996) [8]. Reversions, chimeras, and environmental effects on gene expression can all affect phenotype stability.

Fertility issues: The reduced fertility observed in many *RoIC* -transformed plants can complicate breeding programs and seed production Winefield *et al*., (1999), (Gardner et.al., 2006) [9, 26] For vegetatively propagated ornamentals, this may not be a major concern, but it limits applications in seed-propagated crops.

Future Directions

Future research and development of *RoIC* technology for horticultural applications should focus on several key areas:

Precision control of expression: Developing more sophisticated regulatory systems to control *RoIC* expression levels, timing, and tissue specificity will enable fine-tuning of phenotypic modifications. Inducible promoters, tissue-specific promoters, and other regulatory tools could provide greater control over the transformation phenotype (Gardner *et.al,* 2006) [9]

Combination with other genes: Combining *RoIC* with other genes affecting plant architecture, flowering, or other traits may produce synergistic effects or allow compensation for undesirable pleiotropic effects. Stacking multiple beneficial genes could create cultivars with optimized trait combinations (Casanova *et al*., 2005) [4].

Understanding molecular mechanisms: Further research into the molecular and biochemical mechanisms of *RoIC* action will enable more rational design of transformation strategies. Understanding how *RoIC* affects hormone homeostasis, gene expression networks, and developmental pathways will guide optimization efforts (Bettini *et al*., 2010), (Schmülling *et al*., 1993) [2, 21].

Genome editing approaches: CRISPR and other genome editing technologies could potentially be used to modify endogenous genes in the *RoIC* pathway, achieving similar phenotypic effects without introducing foreign DNA. This approach might address some regulatory and public acceptance concerns.

Rootstock applications: Expanding the use of *RoIC* in rootstocks to influence scion characteristics represents a promising strategy that deserves further investigation (Salm., 1992). This approach may allow beneficial effects on plant architecture while avoiding some pleiotropic effects.

Evaluation in diverse species: Systematic evaluation of *RoIC* effects across a broader range of horticultural species will identify new applications and reveal general principles of gene function. Particular attention should be paid to underutilized ornamental species and specialty crops.

Field and production trials: More extensive field and production trials are needed to evaluate the performance of *RoIC* -transformed plants under commercial growing conditions. These trials should assess not only morphological characteristics but also crop yield, quality, pest and disease resistance, and economic performance (Landi *et al*., 2010).

Marker-free transformation: Developing marker-free transformation systems for *RoIC* introduction could address regulatory concerns and improve public acceptance. Clean gene technologies that avoid antibiotic resistance markers and other selectable markers are increasingly important for commercial applications.

Table 1: *RoIC* -modified horticultural plants.

Plant species	Type of crop	Major phenotypic alterations induced by *RoIC*	Primary horticultural significance	Reference
Petunia (*Petunia hybrida*)	Ornamental	Reduced plant height, increased branching, smaller leaves and flowers, early flowering, reduced fertility	Compact pot plants with improved ornamental value	Winefield *et al*., (1999) [26]
Carnation (*Dianthus caryophyllus*)	Ornamental	Compact growth, reduced height, improved flower quality in some lines	Improved greenhouse and pot cultivation	(Zuker *et al*., 2001) [27]
Chrysanthemum (*Chrysanthemum* spp.)	Ornamental	Compact plant habit, altered leaf morphology, reduced stature	Height control for potted chrysanthemums	Takahashi *et al*., (2006) [25]

Regal Pelargonium (*Pelargonium* × domesticum)	Ornamental	Dwarf vegetative and floral phenotype	Compact ornamental cultivars	(Boase *et al*., 2004) [3]
Rose (*Rosa hybrida*)	Ornamental	Improved rooting ability, compact growth (mainly in rootstocks)	Enhanced rootstock performance and propagation	(Salm *et al*., 1997) [20], (Salm., 1992)
Kalanchoe (*Kalanchoe blossfeldiana*)	Ornamental	Altered biomass distribution, compact growth	Improved potted plant quality	(Christensen *et al*., 2009) [5]
Osteospermum (*Osteospermum ecklonis*)	Ornamental	Compact growth, modified ornamental traits	Enhanced ornamental characteristics	(Giovannini *et al*., 1999) [11]
Tobacco (*Nicotiana tabacum*)	Model plant	Reduced height (up to 42%), shortened internodes, increased branching, smaller leaves and flowers, altered leaf colour, male sterility	Model system for studying *RoIC* function	Gardner et.al (2006}, Scorza *et al*., (1994), (Schmülling *et al*., 1993) [9, 21, 22]
Potato (*Solanum tuberosum*)	Vegetable	Altered plant morphology, modified tuber formation, hormone imbalance	Understanding tuber development and hormone regulation	(Romanov *et al*., 1998), (Schmülling *et al*., 1993), (Fladung, 1996) [8, 18, 21]
Tomato (*Solanum lycopersicum*)	Vegetable	Modified plant architecture, altered auxin and ABA levels	Improved understanding of hormone-mediated architecture	(Bettini *et al*., 2010) [2]
Strawberry (Fragaria × ananassa)	Fruit	Altered adaptability, productivity, disease tolerance, mycorrhizal interaction	Enhanced stress tolerance and field performance	(Landi *et al*., 2010)
Pear ('Beurre Bosc')	Fruit	Compact tree architecture	High-density orchard systems	(Bell *et al*., 1999) [1]
Trifoliate orange (*Poncirus trifoliata*)	Fruit rootstock	Morphological and physiological alterations, compact growth	Citrus rootstock improvement	(Kaneyoshi *et al*., 1999) [12]
Citrus spp.	Fruit	Modified tree architecture and growth habit	Easier orchard management and harvesting	(Gentile *et al*.,, 2004) [10]
Kentucky bluegrass (*Poa pratensis*)	Turf grass	Altered growth habit following transformation	Turf improvement research	(Mcclellan and Knauff, 1996) [13]
Belgian endive (*Cichorium intybus*)	Vegetable	Annual flowering and morphological alterations	Modified flowering behaviour	(Limami *et al*., 1998) [16]
Carrot (*Daucus carota*)	Vegetable	Annual flowering and altered morphology	Flowering control studies	(Limami *et al*., 1998) [16]
Radish (*Raphanus sativus*)	Vegetable	Altered cytokinin content and spontaneous tumour formation	Hormonal studies	(Dodueva *et al*., 1999)
Atropa belladonna	Medicinal plant	Early flowering and altered morphology	Reduced generation time	(Kurioka et.al., 1992) [14]
Arabidopsis thaliana *(expressing sweet potato RolB/RoIC homolog)*	Model plant	Early flowering and premature leaf senescence	Functional characterization of Rol homologs	(Shkryl et.al., 1992)

Table 2: Common phenotypic effects of *RoIC* across horticultural plants

Trait	**General effect of *RoIC***
Plant height	Reduced (dwarf/compact plants)
Internode length	Shortened
Branching	Increased lateral branching; loss of apical dominance
Plant architecture	Compact, bushy habit
Leaf size	Reduced
Leaf colour	Often lighter green or yellowish
Flower size	Usually reduced
Flowering	Earlier flowering in many species
Rooting	Enhanced rooting ability
Hormone regulation	Altered cytokinin, auxin and ABA homeostasis
Fertility	Frequently reduced, especially pollen fertility
Commercial value	Improved suitability for potted ornamentals and high-density cultivation

Conclusion

The *RoIC* gene from *Agrobacterium rhizogenes* has proven to be a powerful tool for modifying phenotypic traits in horticultural plants. Across diverse ornamental and crop species, *RoIC* transformation consistently produces compact plant architectures characterized by reduced height, altered branching patterns, modified leaf and flower morphology, and changes in flowering time. These effects are mediated through alterations in plant hormone homeostasis, particularly involving cytokinin and auxin pathways, with the severity of phenotypic changes correlating with gene expression levels.

The applications of *RoIC* technology are most advanced in ornamental crops, where compact growth habits and modified floral characteristics are highly valued. Successful transformations have been demonstrated in petunia, carnation, rose, chrysanthemum, pelargonium, and numerous other ornamental species. The technology offers

significant commercial advantages including reduced production costs, shorter production cycles, and enhanced aesthetic appeal of finished plants.

While challenges remain - including pleiotropic effects, expression level control, and regulatory considerations - ongoing research continues to refine *RoIC* applications and expand our understanding of gene function. Future developments in precision expression control, combination with other beneficial genes, and novel application strategies such as rootstock transformation promise to further enhance the utility of *RoIC* for horticultural crop improvement.

As the ornamental and horticultural industries continue to seek sustainable and efficient production methods, *RoIC* transformation represents a valuable biotechnological tool that can contribute to the development of improved cultivars with enhanced commercial and aesthetic characteristics. The extensive body of research reviewed here demonstrates both the potential and the practical applications of this technology, providing a foundation for continued innovation in horticultural plant breeding.

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