УДК 577.21: 57.05

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BIOTECHNOLOGY IN FLORICULTURE

Genetic modification techniques are now well established in agriculture (Brooks and Barfoot, 2009; James, 2010). The same extensive commercial application of genetic modification has not been seen in horticulture and floriculture, with the exception of the development of cut flower crops modified for novel flower colour.

In this paper a review is provided of the potential applications of genetic modification in floriculture, illustrated with the example of the production of delphinidin-related anthocyanins in flowers of transgenic carnation and rose. Possible reasons for the lack of commercialisation of transgenic floricultural species are discussed.

Introduction

Europeans are the largest consumers of cut flowers in the world. Though North America, Japan and, increasingly, China are major markets, Europe is by far the biggest. Europe has an excellent logistics system for the distribution of cut flowers, allowing flowers that are imported on a daily basis from Africa, Colombia, Ecuador, India and many other countries to be shipped throughout Europe. To the East, the major cities of Russia, Ukraine and Belarus are also destinations for flowers from Europe, trucked from the auctions of the Netherlands, or flown in directly from producers around the world, but particularly from Colombia and Ecuador.

In the floriculture industry, novelty is of critical importance to breeders. In rose, for example, there are hundreds of different varieties available to growers, in a whole range of flower colours and types. For breeders, the ability to bring out new distinct varieties provides both a marketing opportunity and a possibility to take an increased market share. For consumers, new varieties provide a wider choice. Until the development of genetic modification methods, breeders were constrained by the natural gene pool of a species and the extent to which mutation breeder and/or inter-specific hybridisation methods could be used to expand this natural gene pool. With the advent of genetic modification techniques much wider possibilities have now become available.

1. The potential applications of genetic modification in floriculture

1.1. Transformation

Many major floriculture crops can now be transformed, as summarised in Table 1 and reviewed by Shibata (2008). This includes the important cut flower crops rose and carnation and the pot plants begonia and cyclamen (table 1).

1.2. Potential target traits for genetic modification

It is still the case that in agricultural crops commercial varieties are largely insect resistance or tolerance and herbicide resistance. Varieties with modified secondary metabolism are now being developed also [59]. Herbicide resistance is of less value than insect resistance in floriculture where thrips, aphids and spider mites are the biggest problems, especially for exporters of cur flowers (most plant health inspection agencies require imports to be free of even dead insects). Control of these insect pests by genetic manipulation is not yet feasible.

At the consumer level, herbicide resistant bedding plants might be of some value in a landscaping situation, as might the development of herbicide resistant grasses for lawns [40].

In flowers the second most important trait to producers that could be modified, after insect resistance, is the control of fungal disease. There have been efforts to engineer pathogen resistance in some floricultural crops [19, 36, 43, 46, 55, 61] but as yet genetically modified commercial varieties are not available.

For growers, characteristics relating to quality and productivity, which are not yet amenable to genetic modification, are also very important, as these affect the cost of production and so revenue. However, genes which affect such traits are becoming available and a have been shown to produce potentially useful phenotypes [13, 54].

As outlined before, novelty is extremely important in floriculture and the most obvious form of novelty to the consumer will be in plant or flower shape, architecture and size, and the form and colour of the flowers and foliage. Modification of scent is now possible [24, 42] but it is modification of flower colour that is most advanced, in terms of generating commercially useful varieties.

Table 1. Transformation of floricultural crops

Species	Reference
Begonia semperflorens	Hoshi et al., 2003
Begonia tuberhybrida	Kiyokawa et al., 2001
Cyclamen persicum	Aida et al., 1999 Boase et al., 2002
Cymbidium	Yang et al., 1999
Petunia hybrida	Horsch et al., 1985
Pelargonium,geranium	Bi et.al., 1999 Boase et.al, 2004
Phalaenopsis	Belarmino and Mii, 2000
Saintpaulia ionantha	Mercuri et al., 2000 Kushikawa et al., 2001
Torenia hybrida	Suzuki et al., 2000
Verbena × hybrida	Tamura et al., 2002
Alstroemeria	Akutsu et al., 2004
Antirrhinum	Cui et al., 2004
Carnation	Lu et al., 1991 Firoozabady et al., 1995 van altvorst et al., 1996
Chrysanthemum	Lemieux et al., 1990 de Jong et al., 1995 Sherman et al.,1998a
Dendrobium	Kuehule and Sugii, 1992 Men et al., 2003
Gerbera hybrida	Orlikowska and Nowak, 1997 Nagaraju et al., 1998
Gladiolus	Kamo et al., 1995
Lisianthus	Deroles et al., 1995 Ledger et al., 1997
Lilium	Ahn et al., 2004 Hoshi et al., 2004
Rosa hybrida	Soug et al., 1996 van der Salm et al., 1997 Kim et al., 2004

2. Flower colour modification in rose and carnation

2.1. Anthocyanin biosynthesis pathway

Flower colour is primarily due to the presence of anthocyanins and carotenoids. Yellow and orange flowers normally contain carotenoids. The anthocyanins pelargonidin, cyanidin and delphinidin 3-glucosides are coloured pigments, responsible for pink, mauve, red and blue shades of flowers. Flowers that produce delphinidin-based pigments generally have a violet-blue shade. The anthocyanin biosynthesis pathway is an intermediate of the phenylpropanoid pathway and an early critical enzyme is chalcone synthase, which catalyses the biosynthesis of 4,2', 4', 6'-tetrahydroxychalcone. This compound is converted to naringenin by the enzyme chalcone isomerase and naringenin is subsequently converted to the dihydroflavonol dihydrokaempferol (DHK) by the enzyme flavanone 3-hydroxylase. DHK can then be hydroxylated at the 3' position by the enzyme flavonoid 3' hydroxylase (F3'H) to produce dihydroquercetin (DHQ), or at both the 3' and 5' positions by the enzyme flavonoid 3',5' hydroxylase (F3'5'H) to produce dihydromyricetin (DHM). In the general horticultural and scientific literature flavonoid 3' hydroxylase is sometimes called the "red gene" and flavonoid 3',5' hydroxylase the "blue gene".

Table 2. **Flower colour modification in flower crops using genetic modification**

Species	Modification	Reference
Chrysanthemum	Down regulation of chalcone synthase to produce non-pigmented flowers	Courtney-Gutterson et al., 1994
Petunia	Production of yellow flowers	Davies et al., 1998
Lisianthus	Down regulation of chalcone synthase to produce sectorial non-pigmented flowers	Deroles et al., 1995
Gerbera	Down regulation of chalcone synthase to produce non-pigmented flowers	Elomaa et al., 1993
Rose	Production of delphinidin-related anthocyanins to change flower colour	Katsumoto et al., 2007
Torenia	Down regulation of anthocyanin biosynthesis to produce non-pigmented flowers	Nakamura et al., 2006

The colourless dihydroflavonols (DHK, DHM or DHQ) are then subsequently converted to the coloured anthocyanins by the enzymes dihydroflavonol — 4-reductase (DFR), anthocyanidin synthase and flavonoid-3 glucosyltransferase, with DHK being converted to the brick-red pelargonidin-based pigments, DHQ being converted to the red cyanidin-based pigments and DHM being converted to the purple-blue delphinidin-based pigments. The activity of the "blue gene" (flavonoid 3'5') is therefore necessary for biosynthesis of the delphinidin-based anthocyanins responsible for mauve, violet or blue flowers. F3'5'H does not occur in many of the major cut-flowers normally, as the gene encoding the F3'5'H enzyme is not present. Examples are carnation, rose, chrysanthemum and gerbera.

Flower colour modification has been achieved experimentally in a number of flower crops, and has included phenotypic changes caused by down-regulation of the anthocyanins pathway. Papers describing flower colour modification are summarised in Table 2. Recent reviews covering the same subject include Gutterson (1995), Tsuda et al. (2004), Tanaka (2006), Tanaka et al. (2008), Tanaka and Chandler (2009) and Yoshida et al. (2009).

2.2. Flower colour modification in carnation

The colour-modified carnation varieties that have been developed by Florigene, in collaboration with Suntory Limited are the only genetically modified flowers sold commercially anywhere in the world. The genetically modified "Moon" series carnation varieties produce mauve, purple or violet flowers, and can be seen at the Florigene website (www.florigene.com). These varieties were developed by an *Agrobacterium*-based transformation method [44] from carnation varieties that produced white or cream flowers. The genetic modification has resulted in the expression of F3'5'H genes in specific, white cultivars of carnation. These white cultivars were selected on the basis of lack of activity of both flavonoid 3'-hydroxylase and dihydroflavonol reductase but with the rest of the anthocyanin pathway intact. Expression of the flavonoid 3'5' hydroxylase gene results in the production of the dihydroflavonol dihydromyricetin. Addition of a petunia DFR (which has a higher specificity for DHM over DHQ and cannot utilise DHK), ensures that only delphinidin-based pigments are produced in the petals. Because delphinidin-based pigments are not found in carnations naturally, the flowers from the genetically modified plants are a unique colour due to the novel production of delphinidin-based anthocyanins in the flowers of transgenic plants [26, 27, 49, 65].

Flowers are grown in Ecuador and Colombia for distribution to the USA, Canada, Japan and the EU [44]. So far, ten different commercial varieties of carnation have been developed using this strategy.

2.3. Flower colour modification in rose

The transgenic rose variety "Applause" was released in Japan, late in 2009 (http://www.suntory.co.jp/flower). This transgenic variety has lavender-shaded, novel coloured flowers. The variety is grown in Japan but it is expected that production will commence in Colombia in the near future, for the US market.

Expression of the pansy (*Viola spp*) F3'5'H (flavonoid 3'5'-dihydroxylase) gene in rose resulted in a significant amount of delphinidin-related anthocyanin accumulation in flowers of the transgenic plants [10]. Expression of the pansy F3'5'H genes in several transgenic lines produced flowers in which delphinidin accounted for up to 95 % of the total anthocyanidin [33].

3. Barriers to commercialisation

Even though genetic modification can be used to create novel varieties in floriculture, there have, with the exception of the carnation and rose cultivars mentioned above, been few practical applications of this new technology. The reason for this lack of exploitation is that the commercialization of a transgenic plant product is far more complex than that for a conventionally bred plant product [11, 12]. As a result there are considerable additional development and regulatory compliance costs. These additional costs are a barrier to commercialisation for the minor crops, where the market may be very small, and because of the need to apply for regulatory approval on a country by country basis it is sometimes not possible to consider a global marketing strategy for a product.

3.1. The costs of development

Many floricultural species are vegetatively propagated, which means that to produce a range of colours in a particular species — for example if one was to be targeting insect resistance- would require a large number of transformation experiments, unless a breeding line was transformed. In the latter case there would need to be consideration of the longer term requirement for introgression of the gene of interest into a range of commercial cultivars. The transformation process itself may be expensive to develop, because not all varieties have an equal susceptibility to infection with *Agrobacterium* and not all varieties are easy to regenerate.

Transgenic lines which have the desired phenotype must be trialled carefully to make sure the key commercially valuable characteristics of the parental variety, for example disease resistance and productivity, have been retained. It is also necessary to make sure phenotypic expression of the transgene is stable. The necessity for molecular analysis for regulatory compliance is a major additional cost, as will be discussed below.

Freedom to operate issues for transgenic plant products introduces costs that are not usually incurred by conventional breeders. Components of a transgenic plant that are protected could be the transformation method, promoter and terminator sequences, selectable marker genes, transformation vector components and the genes introduced for phenotype modification. The parental variety may be protected by plant breeders rights and if so the transgenic plants derived from the variety may be considered essentially derived [12]. In that case the original breeder may have to be consulted prior to commercialisation.

3.2. The costs of regulatory compliance

Regulation of genetically modified plants has been imposed by nearly all countries, and exists for all the key flower producing and consuming countries. These regulations typically impose strict confinement to GM plants during trial stages, restricting the ability to trial a genetically modified plant in multiple

environments. For a cut flower product this may be a redundant requirement, as the product is likely to be grown in greenhouse and/or covered conditions in most countries in which it is produced.

In other countries the product may not be grown at all, and only imported as a final product — the cut flower. Four major regulatory issues to consider are:

1. In some cases, the cost of regulation makes entry to market in small countries prohibitively expensive, even when there are customers that want the product. This is because of costs associated with the need for translation, multiple copies of written materials (including copies of all cited papers in some cases) local hearings, fees and travel.

2. In the case of cut flowers destined for import only not all countries require a field trial as part of the regulatory process. This is a very sensible approach, given the risk of gene flow is inherently higher at the places of production, where the products will have already been approved. However, in some countries there is a need to carry out country-specific field trials for products which have been grown and sold commercially for many years elsewhere. For a vegetatively propagated greenhouse grown crop it is not clear how the additional data improves the risk assessment process. The trade problems posed by asynchronous approval of globally traded GMOs have been recently reviewed by Stein and Rodriguez-Cerezo (2009).

3. Some legislation requires the generation of insert(s) and flanking genome sequence and molecular based unique identification protocols [20]. Generation of this data is a very difficult and expensive exercise, and cn not always be accomplished. In non-food crops particularly, is a relatively small component of the risk assessment.

4. Assessment on an event-by-event basis is required in most countries, even though those events may be very similar, and issues such as the probability of gene flow [21, 53] are generic to the species in question. For example, our transgenic carnation product pipeline develops new varieties of transgenic carnation using essentially the same genes (including the same selectable marker) generating essentially the same phenotype (production of delphinidin-related anthocyanins). What largely differs between transgenic events is the parent variety and the flower colour shade produced.

Table 3. **Typical datasets required for genetically modified plant products**

Dataset	Examples of data required
Quantitative comparison to parental variety used for transformation	Morphological characteristics, growth form and production characteristics, evaluation of potential for gene flow [71, 72]
Biology of the plant and history of safe use	Comprehensive literature review of reproductive biology, history of use, current use and geographic distribution
Characterization of the altered phenotype	Level of expression, quantifiable measurements of the novel phenotype
Evaluation of potential harmful effects	Bioassay of plant and soil extracts, toxicity evaluations, animal feeding test
Molecular characterization	Description of origin and function of all genetic elements, southern analysis with several probes, complete sequence of transformation vector, northern analysis, PCR based tools allowing identification of individual lines, comparison to nucleotide and amino acid sequence databases

The comparator trials routinely carried out on a small scale are used to identify lines which are as close to similar to the parent line as possible, aside from flower colour. However, under the current system it is necessary to produce data packages for every new variety which results in a large allocation of resources to generate applications that are largely identical to previous submissions.

Transgenic plants are subject to more regulatory oversight than non-transgenic plants and it is necessary to collect significant data sets for potential transgenic plants. The content of these datasets are summarized in Table 3. Further information, specific to the release of transgenic carnation, is provided in Terdich and Chandler (2009).

Conclusions

Genetic modification of an ornamental plant can be a successful venture, from both a scientific and a commercial perspective. The "Moon" series of colour modified carnations have been sold now for nearly a decade and tens of millions of flowers have entered the traditional growing, distribution and retail chains for cut-flowers. There is no reason to think transgenic rose flowers will not be equally as readily accepted in the marketplace. To date there has been no negative response from consumers to genetically modified flowers. The transgenic varieties have proven to be genetically very stable during mass scale vegetative propagation and there have been no unexpected effects on either the environment or on the health of those handling the flowers.

The major obstacle to dozens of other genetically modified ornamental products entering the marketplace is largely in the barriers that the regulatory systems in many parts of the world place on the freedom to trial and develop GM varieties of ornamentals (refer to commentary in [8]). As is the case for cut-flowers, ornamental products are often an internationally traded commodity and until there is an internationally agreed system for regulating genetically modified plant products it will continue to prove very difficult to release ornamental products, due to the costs and expertise required for commercial development. To ease this burden the regulatory requirements for non-food varieties, such as ornamentals, should be reduced.

Acknowledgements

The comments of this article are the personal views of the author and not those of International Flower Developments Inc., Suntory Holdings Limited or Florigene Limited.

Acknowledgement to Suntory Holdings Limited.

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Recommended to publication by B. O. Levenko

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БИОТЕХНОЛОГИЯ В ЦВЕТОВОДСТВЕ

Методы генетических модификаций в настоящее время широко используют в сельском хозяйстве. Такого экстенсивного коммерческого использования генетических модификаций не наблюдается в садоводстве и цветоводстве, за исключением получения цветочных растений для срезки с модифицированной окраской цветков. В обзоре представлены данные относительно возможного применения генетических модификаций в цветоводстве, проиллюстрированные примерами получения трансгенных растений гвоздики и розы с генами дельфинидина. Обсуждаются возможные причины отсутствия коммерциализации трансгенных видов цветочных растений.

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БІОТЕХНОЛОГІЯ У КВІТНИКАРСТВІ

Методи генетичних модифікацій у наш час широко використовують у сільському господарстві. Такого екстенсивного комерційного використання генетичних модифікацій не спостерігається в садівництві та квітникарстві, за винятком отримання квіткових рослин для зрізування з модифікованим забарвленням квіток. В огляді наведено дані щодо можливого застосування генетичних модифікацій у квітникарстві, проілюстровані прикладами отримання трансгенних рослин гвоздики та троянди з генами дельфінідину. Обговорюються можливі причини відсутності комерціалізації трансгенних видів квіткових рослин.