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Practical and Genetic Solutions for Quality *Sandersonia aurantiaca* Flowers

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ABSTRACT

This review introduces the reader to a cut flower that has been developed from a wild-grown South African native plant. New Zealand's growers, breeders, production and postharvest researchers have optimised cultivation, harvest and postharvest care of *Sandersonia aurantiaca* so that cut flowers can be exported to northern hemisphere destinations for maximum returns (in their out-of-season production window). Sandersonia is a lileaceous cut flower comprising bright orange lantern-like flowers on wiry stems that also hold bright green lancolate leaves. There is only one species in the *Sandersonia* genus, and breeding initiatives have been undertaken to increase the genetic diversity of the crop in order to expand flower colour and form. This review will show that plant production, postharvest management and an ongoing breeding programme are all essential for success of sandersonia in the future market place. It will also review recent molecular research, showing how our understanding of the metabolic processes that influence the rate of flower senescence has advanced.

Keywords: breeding, flower senescence, postharvest, production

Abbreviations: 1-MCP, 1-methylcyclopropene; **AOA**, amino-oxyacetic acid; **AVG**, aminoethoxyvinylglycine; **BA**, benzyladenine; **BAP**, 6-benzylaminopurine; **CA**, controlled atmosphere; **DETA/NO**, diethylenetriamine/nitric oxide; **EAW**, electrolysed anode water; **GA**, gibberellic acid; **MAP**, modified atmosphere packaging; **NBD**, 2, 5-norbornadiene; **NO**, nitric oxide; **PRECIS**, Pretoria National Herbarium Computerised Information System; **STS**, silver thiosulphate; **TDZ**, thidiazuron

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INTRODUCTION: *SANDERSONIA AURANTIACA*: THE PLANT

Sandersonia aurantiaca (Hook.) is a deciduous monocotyledonous perennial herb (order Liliales, family *Colchicaceae*), which grows from a tuber to produce supple, striate, simple stems (0.3–2.74 m in height, PRECIS). Bright orange-coloured flowers occur in leafy racemes on the upper part of the stem, and are placed beside a leaf on a long arcuate pedicel (Vinnersten and Manning 2007). The older flowers occur at the base of the inflorescence. Commonly known as 'Christmas Bells' or 'Chinese Lantern Lily', sandersonia is native to South Africa where it grows in grassland areas of high summer and low winter rainfall at altitudes ranging from 45-1950 m (PRECIS, Brundell and Reyngoud 1985). The unique bright orange flowers (fused tepals) with their distinct shape and good vase life have made sandersonia a sought-after cut flower on the international market, particularly in Japan. In cultivation, the slender flowering stems may grow up to 100 cm in length. The orange lantern-shaped flowers hang from pedicels attached at the axil of lanceolate leaves that are attached alternately on wiry stems (**Fig. 1**). Attributes that determine the quality of this cut flower crop include: stem length, stem strength, number of flowers per stem, flower shape, pedicel length, flower colour, balance of stem internode length, lateral branching, leaf colour, and vase life (Catley *et al.* 2002a, 2002b).

Cut flower breeders appeal to the consumers of their product by supplying a continuous stream of novel products (colour, form, fragrance), but they must also satisfy the

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Invited Review

Stage	Description
1.	Immature green buds
2.	Swelling bud, tepals yellow/green
3.	Swollen bud, tepals orange/green
4.	Open aperture, tepals orange with green tips
5.	Orange tepals with green tips folded upwards **Physiologically mature flower**
6.	Orange tepals with yellow tips
7.	Full orange flower **Mature flower**
8.	Orange tepals with tips fading to yellow **Visible sign of tepal senescence – fading**
9.	Orange tepals with wilted aperture **Visible sign of tepal senescence – wilting**
10.	Wilted tepals **DNA degradation visible as ladders**
11.	Wilted and necrotic tepals **Visible sign of tepal senescence – necrosis**

Fig. 1 ***Sandersonia aurantiaca*** **flower development and senescence.** Sandersonia flowers are borne on slender pedicels (20-30 mm long). Six tepals are fused together to form a lantern-shaped, pendulous, bright orange perianth (20-25 mm long), with six prominent spurs on the base. The flowers expand from a green bud (stage 1) to a physiologically mature flower (stage 5) that will continue to mature to stage 7 and then senesce (stage 8-10) when detached and held in water. The first visible sign of senescence is colour fading then wilting at the base of the flower (tepal tips).

consumer's desire for excellent quality. This review will examine the production methods that are used to maximise 'at harvest' quality of sandersonia flowers, and the current postharvest technologies that maintain flower quality after harvest. In addition, recent molecular research will be reviewed, showing how our understanding of the metabolic processes that influence the rate of flower senescence has advanced. This review will also examine the successes and barriers that breeding programmes have reported in their drive to provide a wider range of colours and forms for sandersonia.

PRODUCTION AND CUT FLOWER QUALITY

Flowers senescence is a natural process that follows physiological maturity (Watada *et al.* 1984) and is often regulated by pollination in many species (O'Neill 1997). However, cut flowers are often harvested before floral maturation, and in these situations biotic and abiotic stresses (e.g. nutrient starvation, hormone imbalance, water stress, temperature stress, pathogen growth) confound the natural process and cause premature senescence (reviews: Halevy and Mayak 1979; Halevy and Mayak 1981; Teixeira da Silva 2006; van Doorn and Woltering 2008). As a general rule, cut flower quality can never be improved beyond the quality present in a stem at the time of harvest. Therefore it is prudent for growers to take care during cultivation to produce plants of the highest quality and health. To this end, plants should be grown in the most appropriate soil, have adequate fertility, suitable light levels, the correct temperature range for long healthy flowering stems, good moisture levels, and be free of pests and diseases at harvest. In addition, the harvest maturity of every cut flower crop should be empirically determined so that it will suit subsequent storage and transport options, and customer requirements.

Practical solutions for regulating the rate of flower senescence after harvest include; temperature control for reducing respiration, slowing metabolism, and inhibiting bacterial and fungal growth (reviews: Halevy and Mayak 1979; Halevy and Mayak 1981; Borochov and Woodson

1989; Teixeira da Silva 2006; van Doorn and Woltering 2008). Postharvest solutions are used to rehydrate harvested flowers and build up energy reserves to maintain quality. Packaging regimes are used to minimise dehydration and transport flowers to distant markets without physical damage. Various technologies are also available for the inhibition of ethylene biosynthesis and sensitivity. Postharvest treatment of flowers with liquid solutions of a low pH that contain nutrients in the form of carbohydrates, plant hormones (e.g. cytokinin, gibberellin), and anti-ethylene and antibacterial substances, assist in maintaining healthy tissues, and in delaying the onset of flower senescence. These treatments may occur immediately after harvest (pulse or loading solution) or during display (vase solution). The content, concentration, and length of exposure to postharvest solutions should be optimised for individual varieties of cut flowers.

Sandersonia flower stems grow from a tuberous storage organ. The flowering stems may grow from one of two meristematic points present on each whole tuber (Brundell and Reyngoud 1985). Early research found larger tubers (>3 g) generally produce longer flower stems (>100 cm) with a greater total number of flowers (>25) than smaller tubers (tubers of less than 2 g weight produced stems of less than 80 cm in length with less than 20 flowers per stem, Brundell and Reyngoud 1985), and this trend has been supported by more recent work (Clark and Reyngoud 1997; Clark and Burge 2002). Sandersonia tubers require a period of cool storage in order to break dormancy and initiate meristematic activity. Storage parameters (i.e. duration, temperature, and subsequent sprouting temperature) of sandersonia tubers influence flower stem size (Clark 1994). In general, cooler storage temperatures (e.g. 1°C) produce shorter flowering stems (ca. 449 mm) compared to higher storage temperatures (3-5°C, ca. 466 mm stem length), and flower stem length declines with increasing storage duration from 110 days (511 mm length) to 171 days (404 mm length) irrespective of temperature (Clark 1994). The recommended storage temperature for sandersonia tubers is 3-5°C (Clark 1994), and storage for 90-120 days is required to ensure rapid and even sprouting of sandersonia tubers (Clark 1995).

The practice of soaking tubers in plant growth regulator solutions (gibberellic acid (GA), uniconazole, benzyladenine (BA)) prior to planting is not recommended (Davies *et al.* 1998). GA_3 treatment increases flower stem length by 20 cm, but the effect is confined to the lower internodes, and GA_3 treatment drastically reduces flower numbers (decrease of ca. 5 flowers per stem with the late forming flowers high on the stem being most affected; Davies *et al.* 1998). Uniconazole treatment reduces stem length by ca. 15 cm and the effect is also confined to the lower internodes of the stem (Davies *et al.* 1998). BA treatment strongly promotes branching resulting in plants more suited to potted production than cut flower production (Davies *et al.* 1998). In New Zealand tubers are pre-sprouted in a warm environment (20-26°C) before planting for even crop production (Clark 1994).

The structure of sandersonia flowers may range from lantern-shaped to tubular-shaped, and researchers have shown that flower shape is strongly influenced by temperature and irradiance during production (Catley *et al.* 2002a, 2002b). There are, however, trade-offs in controlling production temperatures to optimise flower shape because there is no temperature regime best for all sandersonia flower quality parameters. For instance, flower numbers per stem increase linearly with increasing temperature (to 27°C). Whereas stem length increases to a maximum when plants are grown at 21-24°C but then declines at higher temperatures (24-27°C, Davies *et al.* 2002). In addition, the most desirable floral shape (a lantern on a short pedicel) is achieved with a relatively low mean temperature (23°C), minimal night/day temperature differentials, and high irradiance levels (Catley *et al.* 2002a, 2002b).

Sandersonia has a low to moderate nutritional requirement, and at high nitrogen rates cut flower quality is reduced; plants have shorter stems and reduced weight (Clark and Burge 1999). Clark and Burge (1999) found an increase in nitrogen fertilisation from 14.2 to 113.6 g/m^2 reduced sandersonia stem length by 40 cm and stem weight by 0.6 g. In addition, media pH levels above 6 reduce flower quality, inducing leaf chlorosis and leaf tip browning, and also result in shorter flowering stems (Clark *et al.* 2004).

HARVEST MATURITY

Postharvest researchers use empirical analyses to identify specific aspects of postharvest care that are required for maintaining quality and delaying senescence in cut flowers. Such research will identify the variables that optimise postharvest quality e.g. harvest maturity, storage temperature, sensitivity to ethylene, pulsing solution components, optimum packaging regime, and should provide growers with a matrix of technologies that they may choose from that will enable supply of cut stems to their customers with a guaranteed display life (Halevy and Mayak 1981; Kader 2003).

Harvest maturity is the term used to describe the stage at which a flowering stem may be cut that will enable a full floral display (after postharvest storage and transport) for the consumer. New Zealand-grown sandersonia flowers are exported to countries in the northern hemisphere in their off-season (e.g. Japan). During peak production cut stems are generally harvested daily, cool-stored on the grower's property, and then packed and transported via road and air to New Zealand exporters, and then on to export destinations. The stems must be harvested so they have 'good colour' and a long vase life when they reach the wholesaler/florist. Sandersonia stems are harvested when the oldest flowers at the base of the stem are fully open with maximum colour, and the young flowers at the meristematic tip of the stem are visible among the young leaves (**Fig. 1**). If the stems are harvested at a less mature stage, the young buds at the tip of the stem will not mature to full colour and some may abort (anecdotal evidence), thereby reducing the potential floral display of the stem. On the other hand, if the stems are harvested at a later stage, the most mature flowers will senesce during transit (anecdotal evidence). Individual flowers are physiologically mature at stage 5 (Eason and Webster 1995). Flowers detached from the parent plant at this stage or later and held in water will continue to expand and develop full colour in the tepal tissue before senescence (wilting and fading) starts, whereas younger flowers require additional supplements to reach a mature shape, size and colour (Eason and Webster 1995). This correlation between flower age and nutritional/hormonal requirements to reach maturation is paralleled by flowers on the cut stems, and is the basis for using carbohydrate and hormone-containing postharvest solutions to maximise vase life (outlined below).

Research on potted ornamental plants has shown that pre-stressing plants during production produces plants with greater drought tolerance during post-production periods when plants encounter water stress during transport and while displayed by the consumer (Andersen *et al.* 2004). Cultivation practices that enable the production of 'stress-resilient' cut flowers have not been widely reported but may provide opportunities to market cut flowers that are overly sensitive to postharvest stresses. In the case of sandersonia, the leaves of cut stems become dehydrated during transport and are visibly wilted requiring rehydration at the buyer (unpublished data). Stems with less sensitivity to wilting would demand a higher premium due to their improved postharvest quality.

New Zealand-grown sandersonia is harvested daily and the resources of the growers dictate the time of the day that flowering stems are cut. Although, there is no published literature quantifying the effect that 'time of harvest' has on vase life of cut sandersonia, it is likely to be a factor and certainly warrants further study. Indeed a wider understanding of the impact of 'time of harvest' on vase life may reduce the need for postharvest pulsing solutions for certain cut flowers.

STORAGE TEMPERATURE

Good temperature management is fundamental to the postharvest handling of all fresh produce, and lowering the temperature of harvested stems is recognised as one of the most important factors for successful storage of cut flowers (van Doorn and de Witte 1991). Storing cut flowers at low temperatures reduces both plant metabolic processes and microbial growth rates (van Doorn and de Witte 1991). Optimum storage temperatures will vary depending on the nature of the flowering plant (e.g. tropical, sub-tropical, or temperate), with tropical and sub-tropical cut flowers showing chilling damage after low temperature storage (Joyce *et al.* 2000; Redman *et al.* 2001). In addition, packaging and duration of storage will influence the appropriate storage temperature for a particular crop.

Sandersonia stems can withstand storage temperatures as low as 5°C after harvest without tissue damage (Eason 2002). Higher storage temperatures (>10°C) allow the young flower buds and immature leaves at the apex of the stem to develop during storage, producing a less desirable stem with lighter green-coloured leaves at the end of the flower stem (unpublished data). Thus these storage temperatures (>5°C) should be avoided to maintain stem quality. *Gloriosa* is closely related to sandersonia (Vinnersten and Manning 2007), and shows chilling damage when stored at low temperatures (Jones and Truett 1992). *Gloriosa* flowers stored at 1°C developed signs of chilling injury within 3 days, but chilling symptoms were not displayed in stems stored at 10°C for 10 days (Jones and Truett 1992). Chilling injury has not been reported for sandersonia flowers, however, any difference between these two cut flower crops should be further investigated, as new cultivars produced from crossing sandersonia and *Gloriosa* (Kuwayama *et al.* 2005; Nakamura *et al.* 2005; Amano *et al.* 2008; Burge *et al.* 2008) may have the propensity to be chilling sensitive, a feature sandersonia producers have not reported in their current crop.

PULSING SOLUTION COMPONENTS

Most practical approaches for maintaining quality in cut flowers after harvest involve management of hygiene, energy reserves and water balance within the harvested stem to slow harvest-induced tissue senescence, with the additional requirement for the immature flower buds on the cut stem to first grow to maturity (review: Halevy and Mayak 1981). Good postharvest care of cut flowers requires that the harvested stems are placed immediately into liquid solutions free of bacterial contamination to minimise water stress and vascular clogging. Stems should be held at low temperature after harvest (Kader 2003) to reduce respiration, to slow cellular metabolism, and to retain internal carbohydrate reserves (Halevy and Mayak 1981, van Doorn and de Witte 1991).

Cut flowers may be held in liquid solutions after harvest for a few hours to a few days prior to packaging; this postharvest technology is called 'pulsing' or 'loading' (Halevy and Mayak 1981). Consumers, on the other hand, may hold cut flowers in liquid solutions made from commercially available mixed chemical sachets; these solutions are called 'vase solutions'. The two solutions often contain similar compounds, but vase solutions provide chemicals at lower concentrations to the flowering stem, as the stems are held in vase solutions continuously during display (Halevy and Mayak 1981). Although vase solutions can often increase the display life of flowers (in laboratory trials), cut flower producers should not depend on the use of vase solutions for maintaining quality in their produce when it reaches the consumer, as the correct use of vase life solutions by customers cannot be guaranteed.

Postharvest solutions (pulse and vase) may contain sources of carbohydrates (e.g. sucrose, glucose) and plant growth hormones (e.g. cytokinin, gibberellin) for growth and development of flower buds, and anti-ethylene compounds (e.g. silver thiosulphate (STS), aminoethoxyvinylglycine (AVG)) to minimise the deleterious effect of the pre-senescence hormone (Halevy and Mayak 1981). Pulsing solutions may also contain bacteriocides and/or may be acidified (low pH reduces bacterial growth and may aid in water uptake, Halevy and Mayak 1981). If none of the above are required, clean water is essential for hydration of cut flower stems, and the impurities in tap water have been reported to provide additional benefits over deionised water (van Meeteren *et al.* 2000).

The 'at-harvest' quality of sandersonia stems will determine whether postharvest pulsing treatments are effective, and some postharvest solutions may not further enhance the quality of strong sandersonia stems that are harvested with bright green leaves and large healthy flowers. However, flowers grown out-of-season are often weaker and require solutions containing sucrose to ensure full colour and complete bud development is achieved after harvest. In addition, the leaves of weaker stems may be more susceptible to postharvest chlorosis, which can be prevented by treating the cut stems with plant growth regulators (e.g. cytokinins, gibberellin, Eason 2002).

Carbohydrates

The beneficial effect of supplying carbohydrates to cut flowering stems is well known (van Doorn 2004). The addition of sucrose to vase solutions of sandersonia promotes the development of young flower buds and delays the senescence of mature flowers (Eason and Webster 1995). In addition, sucrose treatment causes earlier maturation of sandersonia flowers, producing larger, firmer and brighter orange flowers (higher carotenoid content mg/flower) compared with flowers held in water (Eason *et al.* 1997). Further, the senescence of mature flowers is delayed by approximately 2 days, and the starch reserves of tepal tissue that are normally exhausted before flowers reach full maturity are not fully depleted in sucrose-treated flowers (Eason *et al.* 1997).

Genetic analyses suggest that sugars have a role not only as an energy source but also in regulating gene expression in plant tissues. Studies show that sugar-feeding treatments alter the expression of senescence-related genes in sanderonia flowers (Eason *et al.* 2002; O'Donoghue *et al.* 2005). In sandersonia tepals, sucrose treatment delays the senescence-associated expression of proteases (Eason *et al.* 2002), B-galactosidases (O'Donoghue *et al.* 2002), asparagine synthase and glutamine synthase (Eason *et al.* 2000). Therefore, the integration of sugar-containing pulsing solutions into postharvest regimes is effective as both an energy source and for delaying the expression of senescence-related genes.

Plant growth regulators

Ethylene

Ethylene plays a crucial role in the senescence of a group of so-called "ethylene-sensitive" flowers, coordinating senescence pathways and regulating floral abscission. The molecular regulation of ethylene biosynthesis, control of tissue sensitivity to ethylene, and postharvest tools to inhibit ethylene action have been widely studied (Müller and Stummann 2003; Shibuya and Clark 2006; Lers and Burd 2007; Martinez-Romero *et al.* 2007). Chemical inhibitors of ethylene biosynthesis and activity include: AVG, amino-oxyacetic acid (AOA), STS, 2, 5-norbornadiene (NBD), and 1-methylcyclopropene (1-MCP). Genes that have a role in the control of ethylene production, and tissue sensitivity to ethylene have been identified in a number of cut flower species including carnation (Kosugi *et al.* 2000; Iordachescu and Verlinden 2005) and rose (Muller *et al.* 2002). Recent comparative analyses of senescence of transgenic and wild-type carnations showed that genetic modification for ethylene-insensitivity was more effective than chemical treat-

ment for vase life extension (Bovy *et al.* 1999), and therefore a potential molecular tool for the industry to avoid postharvest chemical treatments. Horticultural performance of transgenic ethylene-insensitive petunias, however, has provided valuable information about the effect of ethylene on developmental programmes other than senescence. Plants with low sensitivity to ethylene also had poor rooting (Clark *et al.* 1999), and lower disease resistance (Shaw *et al.* 2002), reducing their viability as commercial crops of the future.

Sandersonia flower senescence however, has been shown to be relatively insensitive to ethylene (Eason and De Vre 1995). Treating detached, physiologically mature flowers with propylene (0.5%, 24 h) does not alter the pattern of senescence (colour change, loss of fresh weight, decline in respiration) that is normally associated with flower senescence. In addition, STS (1 mM) does not extend the vase life of the flowers (Eason and De Vre 1995). Postharvest ethylene production by flowers is also reported to be negligible, even after flowers have been exposed to propylene. In addition, the senescence of *Gloriosa* flowers (close relative to sandersonia, family *Colchicaceae*) is also reported to be insensitive to exogenous ethylene (Jones and Truett 1992; Tabuchi *et al.* 2005). Therefore technologies for minimising ethylene-related senescence processes are unlikely to improve the postharvest performance of sandersonia flowers.

The beneficial effect of nitric oxide (NO) gas in extending the postharvest life of flowers is thought to be due to its action in modulating endogenous ethylene activity (Badiyan *et al.* 2004). However, DETA/NO (diethylenetriamine/nitric oxide; a nitric oxide donor compound added to vase water) is effective in delaying the senescence of both ethylene-sensitive and ethylene-insensitive cut flowers. Further research to elucidate the mode of action of NO at the molecular level is required, and it may assist in realising DETA/NO's potential as a significant commercial application in the future (Badiyan *et al.* 2004).

Gibberellin

Gibberellic acid compounds delay chlorophyll loss in leaves of cut flowers (Jordi *et al.* 1995), and effectively inhibit the occurrence of cell death that occurs in apical buds of pea (Wang *et al*. 2007). GA_3 is effective in extending sandersonia vase life by delaying the onset of tepal fading and wilting (Eason 2002). Postharvest treatment of sandersonia with pulses of GA_3 (24 h, 7°C) increased the average vase life of stems from 13 days (water control) to 16 days (1 mM GA_3). Analysis of tepal tissue showed that GA_3 treatment resulted in firmer, brighter coloured flowers that wilted later than flowers that were held in water. In addition, protease activity, a commonly used marker for plant senescence (Eason *et al.* 2002), was significantly reduced in GA_3 treated flowers. GA_3 also improves the postharvest performance of *Gloriosa* by maintaining green healthy leaves (Tabuchi *et al.* 2005). Anatomical studies of *Gloriosa* leaves treated with GA revealed more compact palisade and spongy tissue that became filled with starch grains and chloroplasts as flower development proceeded (Tabuchi *et al.* 2005). Similar anatomical studies of sandersonia tepals treated with GA have not been reported, but they may provide some insight into the cellular modifications that GA causes during flower development and senescence in sandersonia.

Cytokinin

Cytokinins promote cell division and differentiation and are primarily produced in roots, young fruits, and in seeds. They enter the shoot organs *via* the xylem (Letham 1994). Organs that are cut off from a continuous cytokinin supply (e.g. cut flowers) age faster than those that are connected to their roots. This is most obvious for leafy liliaceous cut flowers, where premature leaf yellowing reduces postharvest quality in a range of cultivars, and the addition of cytokinin can stop degreening (Han 1995). Elevated endogenous cytokinin in petunia has also been linked to improved drought tolerance (Clark and Dervinis *et al.* 2004), and reduced sensitivity to exogenous application of ethylene (Chang *et al.* 2003). The response of tissues to cytokinin depends on the type and concentration of cytokinin, mode of application, and the developmental stage of the flowers (Chang *et al.* 2003).

Sandersonia stems develop leaf chlorosis after harvest as the flowers senesce (Eason 2002). Eighty percent of the stems held in water were chlorotic at the end of vase life (ca. 10.2 days, Eason 2002). Leaf chlorosis was significantly reduced using commercially available pulsing solutions, with Chrysal SVB (double the recommended dose) preventing chlorosis for up to 13.8 days (Eason 2002). This treatment, however, was reported to be relatively expensive and cheaper alternatives need to be found. Treatment of the *Sandersonia* x *Littonia* hybrid Santonia with 6-benzylamino purine (BAP), is also effective at delaying leaf yellowing after harvest (Eason *et al.* 2001). In addition, cytokinin treatment (100 ppm BAP, 24 h) of *Gloriosa* is effective at delaying leaf chlorosis, but BAP treatment was been found to cause necrosis of leaves (Tabuchi *et al.* 2005).

Thidiazuron (TDZ) is a substituted phenylurea, and effective at inducing responses associated with adenine-based endogenous cytokinins. TDZ has been shown to be a potent inhibitor of leaf senescence, retarding leaf yellowing in a range of other cut flowers (e.g. alstroemeria, lily, stock, tulip, iris) (Ferrante *et al.* 2002). On a concentration basis, TDZ is 100-fold more active than the synthetic adenine-based BAP in growth of carnation explants (Genkov *et al.* 1997), and 10,000-fold more active than BAP and kinetin in stimulating soybean callus growth (Thomas and Katterman 1986). TDZ is registered in the US as an agricultural chemical (for defoliation of cotton under the trade name 'Dropp'), and its efficacy at low concentrations makes it a potential and perhaps more economically viable commercial treatment for delaying leaf senescence in cut flower species (Ferrante *et al.* 2002). Postharvest assessment of TDZ for prevention of postharvest sandersonia leaf chlorosis should be examined further.

Water quality

Solutions developed for use in vases normally have a low pH that may reduce bacterial growth and improve water uptake (Halevy and Mayak 1981). Recent research has highlighted the importance of other aspects of water quality that may affect cut flower senescence. For instance, electrolysed anode water (EAW) extends the vase life of cut carnation flowers (Harada and Yasui 2003), and *in vitro* experimentation indicates that the positive effect of EAW may be related to its ability to decompose ethylene to ethylene chlorohydrine. A certain level of "impurity" in water (calcium chloride, copper, sodium bicarbonate) has been shown to improve the vase life of chrysanthemum flowers (van Meeteren *et al.* 2000). However, a thorough understanding of the effects of water quality on flower senescence is necessary, especially when tap water contains additives for human health that may be toxic to plant tissues e.g. fluoride. Fluoridated water is commonly associated with city water supplies, and in Palmerston North, New Zealand, tap water averages 0.9 ppm fluoride. Fluoride (0.5 pm) causes leaf tip browning of sandersonia (**Fig. 2**). Higher fluoride levels or extended exposure of sandersonia stems to low levels of fluoride increases tissue necrosis (**Fig. 2**). Fluoride-induced tissue necrosis has also been reported for the *Sandersonia* x *Littonia* hybrid Santonia (Eason *et al.* 2001), *Gentiana* (Eason *et al.* 2004), gerbera (Tjia *et al.* 1987), gladiolus (Marousky and Woltz 1975) and rose (Lohr and Pearson-Mims 1990).

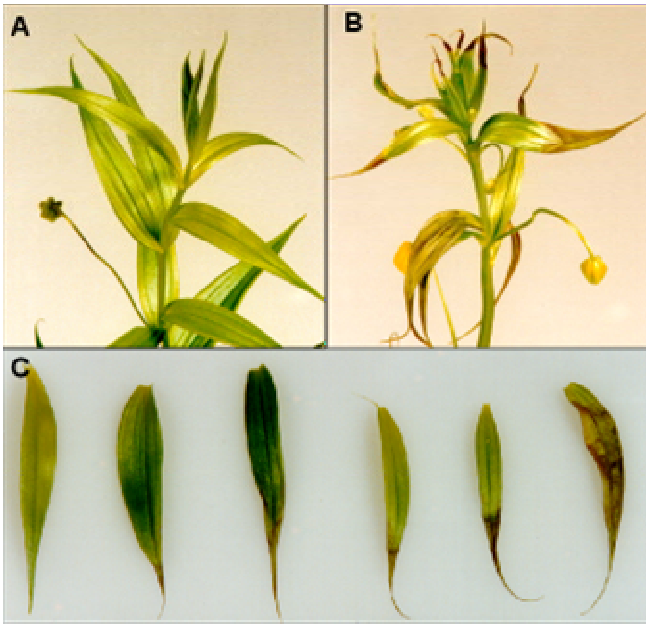

Fig. 2 Fluoride damage to *Sandersonia aurantiaca* leaves. Stems were held in dionized water (**A**) or in solutions of 0.5 ppm NaF (**B**). Leaf damage was progressively greater on the stems held in higher fluoride concentrations (**C**).

PACKAGING

Packaging materials can help to maintain cut flower quality after harvest. Cut flower boxes should be lightweight, and strong enough to enable temperature-controlled storage and prevent crushing damage during transit. Various packaging technologies are available that will suit a particular flower crop, grower, and/or marketplace (review: Kader 2003). Packaging must take into account the metabolism of the packed plant tissue (e.g. respiration rate, ethylene sensitivity, sensitivity to dehydration or humidity requirements; Teixeira da Silva 2006). Packaging materials may be impregnated with ethylene absorbing chemicals (Wills and Warton 2004) or anti-microbial compounds (Guillen *et al*. 2007) to reduce senescence and postharvest disease.

Controlled atmosphere packaging and modified atmosphere packaging are being developed for use with several cut flower crops that are produced in large quantities and shipped long distances (Zeltzer *et al.* 2001; de Pascale *et al*. 2005; Bishop *et al.* 2007). On a smaller scale *Gloriosa* flowers are transported and stored short-term in sealed, air-filled bags to protect the flowers from physical damage, and researchers have shown that some atmosphere modification occurs within the bags (Jones and Truett 1992), although the relevance of the modification to vase life has not been defined. Both MAP and CA have been shown to prevent leaf yellowing in horticultural produce, and although their use during storage and transport has been investigated for a number of horticultural crops (review: Kader 1986), there have not been any reports on the use of this technology for sandersonia flower storage.

New Zealand-grown sandersonia flowers are cooled prior to transportation and bunched sleeved flowers are packed tightly in cardboard boxes and transported by air to export destinations (primarily Japan). Examinations of alternative packaging technologies have not been reported for this flower crop but may provide market flexibility for growers.

GENE PRODUCTS THAT REGULATE FLOWER SENESCENCE

The process of flower senescence in sandersonia is a genetically programmed event that results in cell death (Eason and Bucknell 1999). Cell-death in flowers is thought to be regulated by anti- and pro-death proteins expressed throughout the life of the flower, providing a highly regulated homeostatic balance (Rubinstein 2000; Thomas *et al.* 2003; van Doorn and Woltering 2004). Genome-wide searches for regulatory flower senescence genes have now been undertaken in several cut flower species, namely *Alstroemeria* (Wagstaff *et al.* 2002; Breeze *et al.* 2004), carnation (Verlinden *et al.* 2002), chrysanthemum (Narumi *et al.* 2005), daffodil (Hunter *et al.* 2002), *Iris* (van Doorn *et al.* 2003), rose (Channeliere *et al.* 2002), and sandersonia (Eason *et al.* 2000, 2002). The researchers have isolated and identified senescence-associated genes from these crops and identified common processes that appear linked to the progression of cell death in flowers (e.g. carbohydrate metabolism, proteolysis, ethylene biosynthesis and signalling). The processes are common between ethylene-sensitive and ethylene-insensitive cut flowers, and cross-talk between the various pathways has been reported. All senescence-associated genes isolated from sandersonia are also associated with senescence in other cut flowers (**Table 1**). The next challenge for researchers is to determine the function and understand the

Table 1 DNA sequences isolated from *Sandersonia aurantiaca* and associated function.

Accession №	Putative protein function	Reference
Senescence-associated genes		
AY280500	β-galactosidase	O'Donoghue *et al.* 2005
AY280499	β-galactosidase	O'Donoghue *et al.* 2005
AY280498	β-galactosidase	O'Donoghue *et al.* 2005
AF411121	cysteine proteinase precursor	Eason *et al.* 2002
AF133839	papain-like cysteine protease	Eason *et al.* 2002
AF133838	papain-like cysteine protease	Eason *et al.* 2002
AF130882	glutamine synthetase	Eason *et al.* 2000
AF005724	asparagine synthetase	Eason *et al.* 2000
AF469485	cystatin	Not published
AF479060	serine threonine kinase	Not published
AF479059	copper/zinc superoxide dismutase	Not published
AF479058	70 kDa heat shock protein	Not published
EU436762	Cyclic nucleotide gated ion channel	Not published
EU436759	Nitrilase-associated protein	Not published
EU436760	26S proteasome regulatory complex	Not published
Pigment metabolism		
AY077687	β-carotene hydroxylase	Nielsen *et al.* 2003
AY077686	phytoene desaturase	Nielsen *et al.* 2003
AF489520	β-lycopene cyclase	Nielsen *et al.* 2003
AJ551236	chloroplast rps16 gene for ribosomal protein S16	Vinnersten and Reeves 2003

significance of specific gene expression patterns (and the products) during flower senescence. To this end, readily transformable model flower systems have been sought (e.g. petunia; Clark and Dervinis *et al.* 2004; Jones *et al.* 2005). Future analyses of floral senescence may identify the protein(s) that function to maintain a non-senescent "youthful" state, and such regulatory proteins might then be used as genetic markers in breeding programmes to select for lines with improved vase life.

BREEDING AND GENETIC MODIFICATION FOR EXPANDING SANDERSONIA MARKET SHARE

Releasing sandersonia cultivars with novel colours and forms is essential for maintaining and growing market share of sandersonia in the fashion-driven industry of cut flowers. Buyers are always looking for 'novel' traits and although orange-flowering sandersonia are highly sought after in Japan, the lack of colour range (Neilsen *et al.* 2003) reduces further expansion of this crop into the wider market place.

The absence of other species within the sandersonia genus means that wide crosses with related genera must be considered as a way to develop new germplasm. Sandersonia is in the Colchicaceae family and closely related genera include *Littonia* and *Gloriosa* (Vinnersten and Manning 2007). Hybrids have been produced between sandersonia and both *Littonia* and *Gloriosa* (Morgan *et al.* 2001, 2003; Kuwayama *et al.* 2005; Nakamura *et al.* 2005; Amano *et al.* 2008; Burge *et al*. 2008). Wide crosses between *Sandersonia aurantica* and *Littonia modesta* produced the hybrid Santonia, a cut flower with features midway between each parent (Morgan *et al.* 2001; 2003). More recently *Sandersonia aurantiaca* x *Gloriosa* hybrids have been reported (Kuwayama *et al.* 2005; Nakamura *et al.* 2005; Amano *et al*. 2008; Burge *et al*. 2008). The new hybrid Santonia brings with it postharvest disorders not evident in the sandersonia parent (i.e. more serious leaf yellowing, leaf necrosis, Eason *et al.* 2001). Therefore, ongoing postharvest assessment during selection is required in order to successfully release the new hybrids into commerce.

The use of techniques such as genetic transformation, also offer opportunities for colour modification in sandersonia. A prerequisite for such colour modification is knowledge of the pigments present in floral tissue. Both carotenoid and flavonoid pigments are present in sandersonia tepal tissue, and several strategies for colour modification have been suggested (Lewis *et al.* 1998). The work of Nielsen *et al.* (2003) shows that inhibition of the carotenoid pathway gives a paler flower colour. Alternatively, modification of the concentration and types of carotenoids present in sandersonia could move the flower colour from yellow and orange to red. Transient expression of genes in sandersonia has been demonstrated using a biolistic technique (John Seelye, pers. comm.), but stable transformation of the species has not been reported.

CONCLUSIONS

Sandersonia plants grow from underground tubers that produce supple, simple stems with bright orange-coloured flowers occurring in leafy racemes on the upper part of the stem. Flower buds grow to maturation then senesce to leave a dry shell of tepal tissue covering the developing ovary (sandersonia tepals do not abscise). New Zealand growers of these cut flowers harvest the stems when the oldest flowers (at the base of the stem) are fully mature and the young flowers at the meristematic tip of the stem are visible among the young leaves (**Fig. 1**). The individual flowers on cut stems will continue to mature and senesce in a progression similar to that observed for attached stems, although the process is more rapid as detached stems are exposed to stresses resulting from the act of harvest that attached stems do not experience. The act of harvest also removes an essential source of carbohydrate, plant hormones and other nutrients from the cut stem. Although flower tepals are programmed to die, it is possible through optimisation of cultivation, harvest, and postharvest storage conditions to maximise the potential postharvest life of sandersonia flowers delaying tepal senescence and thus extending their marketability. The postharvest performance of sandersonia flowers is improved with low temperature storage, and pulsing solutions containing sucrose, cytokinin and gibberellic acid (Eason 2002). However, the optimum postharvest storage temperature for this crop has not been fully investigated, and the efficacy of the cytokinin alternative TDZ for preventing postharvest leaf chlorosis should also be examined. Further examination of packaging technologies for sandersonia is warranted, although the technologies must be cost effective for growers.

A thorough understanding of the requirements of postharvest floral maturation, and the abiotic and biotic stresses that lead to premature death of floral organs, is integral to achieving a long vase life and the return custom of buyers. To this end genetic research has been undertaken to study the mechanisms involved in sandersonia senescence (Eason and Bucknell 1999; Eason *et al.* 2000, 2002; O'Donoghue *et al.* 2005). This is particularly useful as sandersonia flowers have been shown to be insensitive to ethylene (Eason and de Vre 1995) and standard postharvest anti-ethylene treatments are not effective.

Maximising preharvest quality through optimised growing conditions (Brundell and Reyngould 1985; Clark 1994, 1995; Clark and Burge 1999; Catley *et al.* 2002a, 2002b; Davies *et al.* 2002; Clark *et al.* 2004), and controlling the onset and rate of postharvest senescence with low temperature storage, and optimum pulsing treatments (Eason 2002), have enabled New Zealand's cut flower growers to successfully distribute a highly perishable horticultural product from the southern hemisphere to northern hemisphere export markets.

There is little doubt that postharvest technologies are essential for maintaining postharvest quality of cut flowers. The results of a good vs bad postharvest chain are immediately evident for the consumer, who will preferentially purchase high quality flowers. The challenge for the sandersonia industry is to develop further cultivars of this successful cut flower crop using breeding programmes in New Zealand and Japan. Postharvest assessments will be integral to the selection process to ensure any new selections are devoid of postharvest disorders and as successful as the parent cut flower crop.

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