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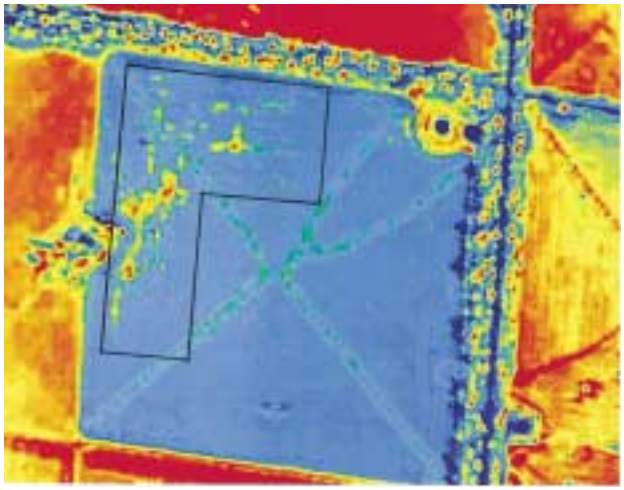

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Review

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A review of the flower characteristics of Geraldton waxflower and factors influencing their abscission from harvested stems

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Abstract. Geraldton waxflower (*Chamelaucium uncinatum* Schauer) is Australia's most economically important cut-flower export. Its small, attractive flowers make it particularly suitable as a filler in floral arrangements. However, postharvest bud and flower abscission is a major problem during transport, handling and marketing. Abscission may be caused by wound-induced endogenous ethylene production brought about by flower tissue infection with fungal pathogens such as *Botrytis cinerea*. Botany and postharvest characteristics are discussed in relation to flower abscission and how resultant postharvest losses may be minimised.

Introduction

Geraldton waxflower (*Chamelaucium uncinatum* Schauer) is an Australian native plant that belongs to the Myrtaceae family (Lamont 1985). Related genera include *Eucalyptus*, *Callistemon* and *Melaleuca*. *Chamelaucium uncinatum* is the most widely cultivated *Chamelaucium* species. It is indigenous to Western Australia and grows best in areas with winter rainfall and hot, dry summers (Lamont 1985). Commercial plantings of waxflower can be found throughout Australia and in Israel, Peru, Thailand and California (Lamont 1985; Wearing and Joyce 1994). Waxflower can be difficult to cultivate in south-eastern Queensland due to disease associated with summer rainfall (Lamont 1985). The plant flowers from early winter to early summer (Faragher 1989).

Flower characteristics and floral biology

The *C. uncinatum* inflorescence is a corymb (Slater and Beardsell 1991). Flowers are about 12–25 mm in diameter and borne in clusters of 2–5 (Lamont 1985). *Chamelaucium* stems bear flowers at all stages of development, ranging from tight buds to senescent flowers (Olley *et al.* 1996). *Chamelaucium uncinatum* flowers consist of 5 minute sepals, 5 broad waxy petals and 10 stamens (Slater and Beardsell 1991). The flowers vary in colour from white to cream, pink, mauve and purple, and typically become darker with age (Lamont 1985). The hypanthium is cup-shaped and contains nectiferous tissue (Slater and Beardsell 1991). Floral nectaries produce up to 5 μL nectar per day (O'Brien 1995). Nectar production starts at anthesis and continues for 7–10 days from the time when the petals start to separate until the hypanthium changes colour, turning pink (O'Brien 1995; Olley *et al.* 1996).

Chamelaucium uncinatum has also inconspicuous extrafloral nectaries in the axils of all leaves. These are most active on new growth (O'Brien 1995). It is thought that extrafloral nectaries maintain the pollen-vector population (e.g. bees) throughout the year to ensure efficient pollination during flowering (O'Brien 1995). Insects switch from foraging extrafloral nectaries to floral nectaries once a large number of flowers become available (O'Brien 1995).

Chamelaucium uncinatum flowers are protandrous. Pollen is shed from the anthers before the stigma becomes receptive, thereby avoiding self-pollination (Slater and Beardsell 1991). A secondary pollen-presentation system exists and has been described in detail by Slater and Beardsell (1991). The stigma becomes receptive about 7 days after anthesis and remains receptive until 20 days after anthesis (O'Brien 1995). Foraging insects, such as the Australian native bee, *Trigona carbonaria*, and the European honey bee, *Apis mellifera*, are pollen vectors. They are advantageous to the reproductive success of *Chamelaucium uncinatum* (O'Brien 1995).

Postharvest characteristics

High-quality waxflower stems are about 60 cm long, and straight, with little vegetative growth past the flower clusters. Stems must have good leaf colour, acceptable vase life, and minimal leaf, bud and flower abscission (Maier *et al.* 1996). Waxflower flowers have a non-climacteric senescence pattern (Olley *et al.* 1996). The vase life of different waxflower cultivars varies considerably, generally being

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about 11 or 12 days (Manning 1996). Flower vase life generally exceeds foliage vase life by about 1 day (Joyce *et al.* 1996). However, leaves can desiccate even before flowers start to close (Joyce and Jones 1992). Vase life was reduced by about 8.1 days for leaves and about 7.4 days for flowers after storage for 14 days at 0°C (Manning 1996).

Flower abscission

Flower fall after harvest can occur as a result of physical or mechanical damage, water stress, exposure to exogenous ethylene or infection by fungal pathogens, such as *Botrytis cinerea* (Joyce 1992). Flower abscission is a problem during the transport and handling of waxflower (Faragher 1989). Abscission of the flowers results in low prices in overseas markets and reduced importer confidence (Joyce 1993).

Ethylene exposure

The plant-growth regulator, ethylene, causes abscission and/or accelerated senescence of floral organs of many traditional ornamental plants, including roses and carnations (Serek *et al.* 1995*a*), and Australian native ornamentals, such as tea tree (*Leptospernum* sp.) (Zieslin and Gottesman 1983) and waxflower (Joyce 1992). Accumulation of exogenous ethylene in the postharvest environment results in flower abscission from waxflower (Joyce 1988*a*, 1992). However, it is believed that flower abscission from waxflower is due more to endogenous ethylene than to accumulation of exogenous ethylene (Joyce 1993).

Water stress

Leaving waxflower sprigs out of water for lengthy periods can result in excessive moisture loss and reduced vase life (Seaton and Joyce 1996). Water stress may cause endogenous ethylene production and associated flower abscission (Joyce 1993). Waxflower leaves are seemingly more influenced by water loss than flowers. Leaf cells are less elastic and turgor loss occurs sooner than in flower cells (Joyce and Jones 1992).

Disease

Flower abscission may be caused by pathogen-related endogenous ethylene production associated with infection by fungi. *Alternaria alternata* has recently been shown to cause flower abscission in waxflower (Taylor *et al.* 1998). However, the primary fungal pathogen associated with flower abscission in waxflower is thought to be *Botrytis cinerea*, the causal agent of grey mould disease (Wearing and Joyce 1994; Tomas *et al.* 1995). Outbreaks of *Botrytis cinerea* on waxflower are favoured by cool and moist conditions, which are also experienced during handling and transport of flowers (Ogle 1994). Visible signs of infection of waxflower flowers can become evident as early as 2 days after inoculation (D. Beasley unpublished data). Waxflower flowers infected with *Botrytis cinerea* are characterised by brown necrotic lesions at the base of petals and the presence of superficial grey fungal mycelium (Fig. 1*A*; Tomas *et al.* 1995; Joyce and Wearing 1996). Sporulation can be observed about 4 days after inoculation (Fig. 1*B*). However, flower abscission often occurs before visual symptoms of the disease appear (Joyce and Wearing 1996).

Botrytis cinerea infection has been studied at the cellular level by light microscopy (D. Beasley unpublished data). Evidence of *Botrytis cinerea* infection was observed inside the pistil as early as 4 days after inoculation. Infection was characterised by rapid cellular degradation, which became progressively more severe with increasing time after inoculation (Fig. 2*A*, *B*).

The severity of *Botrytis cinerea* infection in waxflower is related to weather conditions, including temperature and relative humidity, during flower development (Joyce 1988*a*). Quiescent infections established before harvest can remain undetected until postharvest conditions, such as high relative humidity or free water (e.g. condensation), promote growth (Joyce 1993). Similarly, quiescent infections of strawberry and raspberry flowers can result in the development of grey mould disease of fruit after harvest (Powelson 1960; Jarvis 1964; Williamson *et al.* 1987). Water impermeable plastic films used in packaging can exacerbate disease problems by creating more-favourable conditions for fungal growth (Joyce 1992). *Botrytis cinerea* sporulates prolifically on abscised flowers in cartons and may, thereby, infect healthy flowers (Tomas *et al.* 1995). Inoculation of waxflower flowers with *Botrytis cinerea* spore suspension can result in flower abscission as early as 2 days after inoculation, although 4 days is an average time taken for waxflower flowers to abscise (Table 1). Within 5–6 days, flowers can become necrotic and covered in *Botrytis cinerea* mycelium, as confirmed by the findings of Wearing and Joyce (1994).

Control of flower abscission

Flower abscission can be greatly reduced by ensuring that the cold chain is maintained throughout transport and handling (Joyce 1997; Taylor *et al.* 1997). However, temperature abuse is common, both in domestic and export trades (Orlikowski 1991). Management to avoid water stress, removal of ethylene and use of effective disease-control measures can also help to ensure acceptable vase life and minimum flower abscission (Taylor *et al.* 1997).

Maintainance of low temperature

Botrytis cinerea can grow at temperatures below 5°C (Couey and Follstad 1966). Nonetheless, storing flowers at low temperatures will delay disease development. Disease severity in waxflower was found to be lower for flowers stored at 5°C than for those stored at either 10 or 20°C (Taylor *et al.* 1997). Furthermore, flower abscission can be delayed significantly by storing flowers at 10°C (Table 2). Interestingly, high temperatures (30°C) also delayed flower

abscission, although this was thought to be the result of other fungal species such as *Nigrospora* sp. interfering with *Botrytis cinerea* infection (Table 2). Temperature fluctuations associated with poor cold-chain management may result in condensation inside packages. Condensation provides free water that may promote spore germination (Hammer and Marois 1989; Joyce 1992).

Management of water stress

Wrapping waxflower bunches in plastic (e.g. polyethylene) sleeves after harvest is beneficial in reducing water loss (Joyce 1988*b*). However, plastic wrapping can increase the relative humidity (vapour pressure) around the flowers and, thereby, provide a more suitable environment for fungal growth. Wrapping may also allow the accumulation of condensate and ethylene (Joyce 1992).

Packaging modifications to improve ventilation could result in reduced disease severity and flower abscission in waxflower without significantly increasing water loss (Taylor *et al.* 1997). Maintaining waxflowers at a reduced relative humidity of about 75% prevented the growth of *Botrytis cinerea* (Taylor *et al.* 1997). A novel packaging system suggested by Taylor *et al.* (1997) involves wrapping stems and foliage to minimise desiccation, while allowing ventilation around the flowers. Also simply leaving forced-air cooling holes open in commercial packages can reduce disease severity (Taylor *et al.* 2001).

Removal or blocking of ethylene

Ethylene accumulation in packaging can be prevented by ensuring adequate ventilation or by including chemical scrubbers such as potassium permanganate (Reid 1985; Elad 1993). Ornamentals can also be treated with various chemicals, including binding site blockers, to reduce sensitivity to ethylene (Cameron and Reid 1981; Serek *et al.* 1994).

Silver thiosulfate (STS) is commonly used to prevent ethylene-induced flower abscission in waxflower after harvest (Joyce 1992). This chemical is a liquid that is typically applied as a postharvest pulsing treatment (Joyce 1988*a*). STS treatments generally have no beneficial effect on waxflower vase life unless flowers are exposed to ethylene (Joyce 1988*a*). For example, an 8 h pulse treatment with 0.5 mmol/L STS at 22°C significantly delayed abscission of

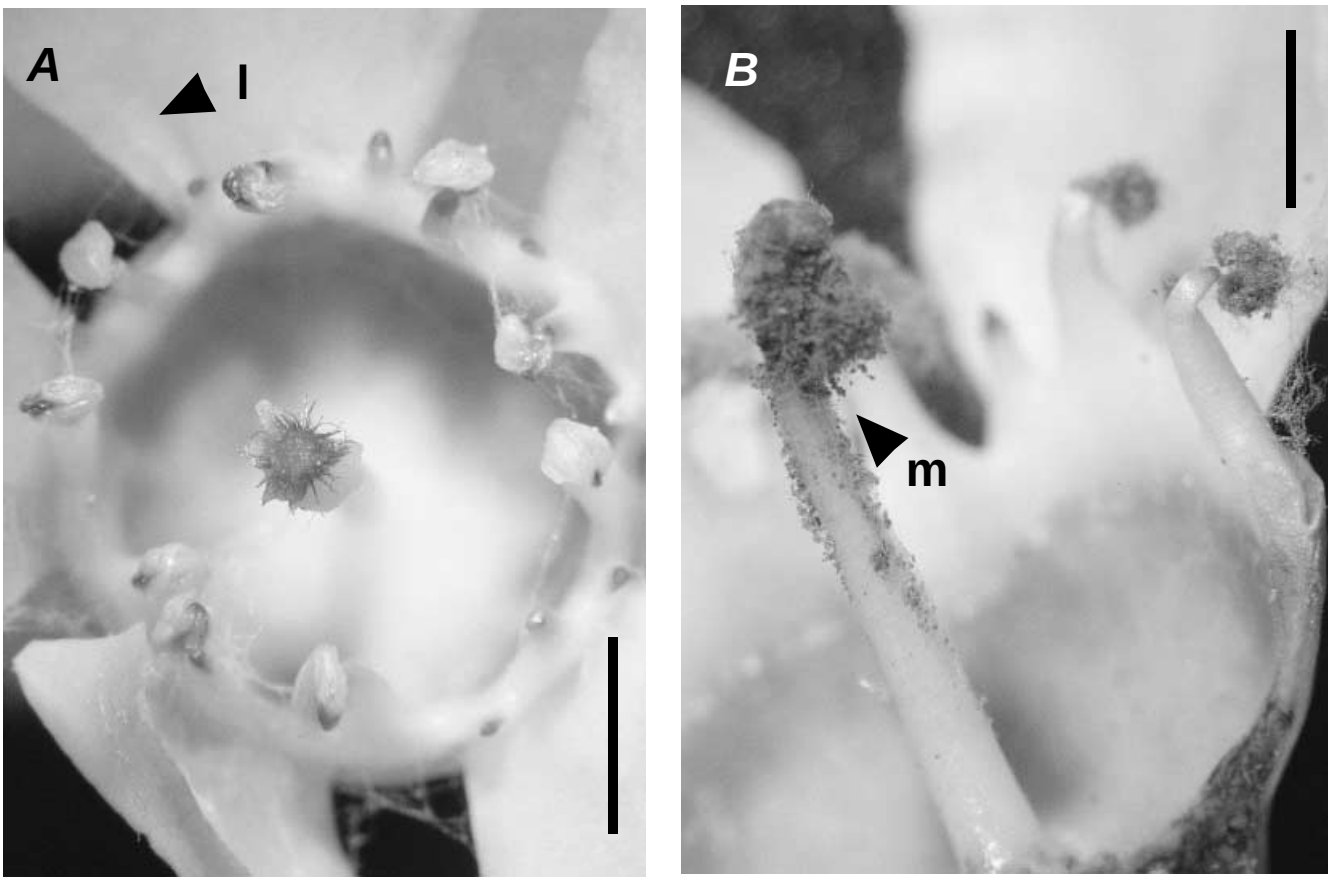

Figure 1. Visible symptoms associated with the colonisation and infection of waxflower flowers by *Botrytis cinerea.* (*A*) Waxflower flower 2 days after inoculation displaying small lesions (l) at the base of a petal and mycelial growth. Scale bar = 2 mm. (*B*) Waxflower flower with sporulating *Botrytis cinerea* mycelium (m) on the stigma and anthers 4 days after inoculation. Scale bar = 1 mm.

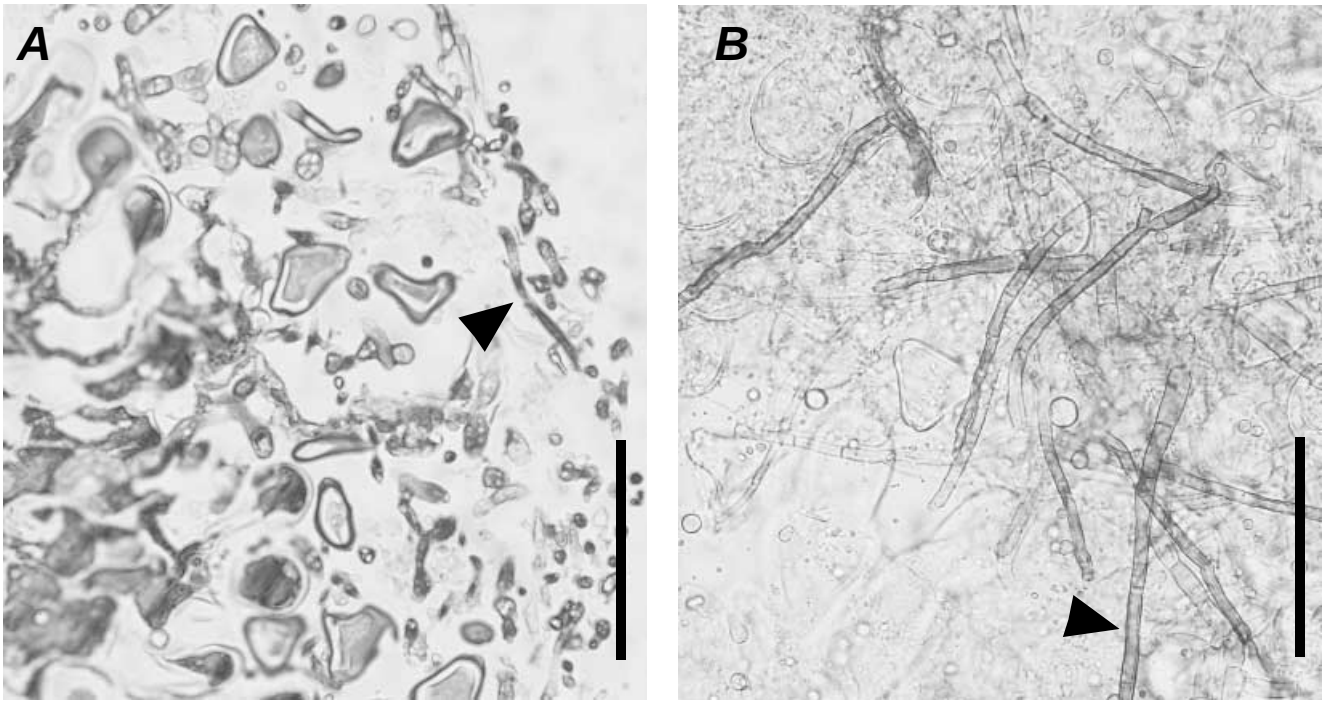

Figure 2. Light micrographs showing (*A*) a cross-section of waxflower stigmas 6 days after inoculation with *Botrytis cinerea* and (*B*) a squash mount of a waxflower stigma and pollen kit 6 days after inoculation. Scale bar = 100 μm (*A* and *B*). The section in (*A*) was stained with 0.5% toluidine blue in 0.1% sodium carbonate (Na_2CO_3), pH 11.1 for 1–6 min at 60°C, while the squash mount in (*B*) was stained with 0.1% w/v water-soluble aniline blue in 0.1 mol/L potassium phosphate (KH_2PO_4), pH 8.5. The arrowheads in (*A*) and (*B*) point to a fungal hypha.

flowers from waxflower pre-treated with ethylene at 2 μL/L (Table 3). Similarly, Joyce (1989) reported that a 30 min pulse treatment with 4 mmol/L STS at 22°C was effective in preventing ethylene-induced flower abscission in waxflower. STS treatments have been found to reduce disease severity in waxflower (Taylor *et al.* 1996).

1-methylcyclopropene (1-MCP) is a novel non-toxic ethylene inhibitor (Serek *et al.* 1995*a*). Its discovery was timely, as there is public concern over the use of STS (Joyce 1993). This relatively new gaseous ethylene-binding inhibitor is active at very low (e.g. nL/L) concentrations (Sisler *et al.* 1996). Pre-treatment of native flowers, such a *Boronia* sp. and *Grevillea* sp., can reduce the adverse affects of ethylene (Macnish *et al.* 1999, 2000). Treatment with 1-MCP at 200 nL/L for 13 h at 21°C can prevent flower abscission in waxflower when applied before ethylene exposure (Serek *et al.* 1995*b*). Also Macnish *et al.* (2000) found that treatment of waxflower sprigs with 1-MCP at 10 nL/L for 12 h at 20°C afforded the flowers up to 4 days protection from ethylene.

Table 1. Effect of inoculation of the pistil with *Botrytis cinerea* on waxflower cv. 'CWA Pink', cv. 'Purple Pride' and cv. 'Lollipop' flower abscission from the petiole when incubated at 20°C and >95% relative humidity (D. Beasley unpublished data)

Means in the same column followed by different letters are significantly different at $P = 0.05$; $n = 10$

Treatment	Time to flower abscission (days)[A]		
	CWA Pink	Purple Pride	Lollipop
Control	12.1a	13.3a	7.1a
Inoculated	4.1b	4.5b	3.2b

[A]± Inoculation (CWA Pink), $P<0.001$; ± inoculation (Purple Pride), $P<0.001$; ± inoculation (Lollipop), $P<0.001$.

Table 2. Effect of holding at 10, 15, 20, 25 and 30°C on waxflower cv. 'CWA Pink' flower abscission from the petiole in the presence and absence of *Botrytis cinerea* inoculum (D. Beasley unpublished data)

Row and column means followed by different letters are significantly different at $P = 0.05$

Temperature (°C)	Time to flower abscission (days)[A] Control (n =10)	Inocul. (n =10)	Row mean (n = 20)
10	12.7	7.6	10.2a[A]
15	6.6	5.3	6.0c
20	9.4	3.7	6.6c
25	11.2	3.4	7.3bc
30	12.4	6.4	9.4ab
Column mean (n = 50)	10.5a[A]	5.3b	

[A]Temperature, $P<0.001$; inoculation, $P<0.001$; temperature × inoculation, $P = 0.066$.

Table 3. Number of days to flower abscission for untreated waxflower cv. 'CWA Pink' and those pulsed with 0.5 mmol/L STS for 8 h at 22°C with and without subsequent exposure to 2 µL/L ethylene (D. Beasley unpublished data)

Means followed by different letters are significantly different ($P = 0.05$)

Treatment	Time to flower abscission (days)[A]		Row mean
	Control (n =10)	Ethylene (n =10)	(n = 20)
Control	13.9ab	3.1c	8.5
Silver thiosulfate	14.9a	12.6b	13.8
Column mean (n = 20)	14.4	7.9	

[A]STS treatment, $P<0.001$; ethylene exposure, $P<0.001$; STS treatment × ethylene exposure, $P<0.001$.

Disease control

Control can be achieved by practising strict field hygiene, maintaining the cold chain throughout postharvest handling and using cartons designed to provide ventilation and moisture control (Taylor *et al.* 1997). Fungicides for control of *Botrytis cinerea* are also very important to limit postharvest flower abscission. Preharvest fungicide sprays are beneficial and virtually essential under cool, moist growing conditions (Joyce 1988*b*). Waxflowers should also be treated with fungicides immediately after harvest to improve storage performance (Jones and Faragher 1991) and vase life (Joyce 1988*b*).

Commonly used fungicides include Benlate (500 g benomyl/kg), Rovral (500 g iprodione/kg) (Taylor *et al.* 1996) and Ronilan (500 g vinclozolin/L) (Joyce and Wearing 1996). Postharvest fungicide-dip or spray treatments reduce fungal lesions caused by *Botrytis cinerea* and also the pathogenesis-induced ethylene production that results in flower abscission (Joyce 1993). However, development of resistance to fungicides by *Botrytis cinerea* on many crops has reduced the efficacy of chemical control measures (Taylor *et al.* 1996). More recently developed fungicides with activity against *Botrytis cinerea*, such as the strobilurin group and pyrimethanil (Taylor *et al.* 1999), may prove commercially useful for waxflower.

Calcium treatment may provide an alternative to fungicide sprays. Spraying rose flowers with calcium before harvest inhibited ethylene production (Elad and Volpin 1988). Treating roses with $CaSO_4$ or $CaCl_2$ solution postharvest reduced disease severity by up to 45% (Volpin and Elad 1991). For waxflower, however, preharvest calcium sprays were ineffective in reducing disease severity and flower abscission (Taylor *et al.* 1996). Postharvest treatments with calcium were similarly ineffective (Taylor 2000).

Biological control is a potentially viable alternative to chemical control of *Botrytis cinerea*. Biological control of *Botrytis cinerea* has been utilised on horticultural crops such as strawberry, cucumber and grapes (Peng and Sutton 1991; Elad *et al.* 1993; Elad 1994). There are significant incentives for developing biological control systems for waxflower. As noted earlier, chemical control of *Botrytis cinerea* with preharvest fungicide sprays is problematic. In addition to the cost and inconvenience of repeated spraying, strains of *Botrytis cinerea* that are resistant to fungicides have been isolated from waxflower (Taylor *et al.* 1996). More importantly, new and, therefore, unprotected flowers open daily on each flowering stem. Potential for biological control of *Botrytis cinerea* on waxflower has been demonstrated by Beasley *et al.* (2001). They reported that several bacteria and filamentous fungi isolated from waxflower flowers displayed antagonism towards *Botrytis cinerea in vitro*. When applied to waxflower flowers under controlled conditions, flower abscission was also delayed in some cases.

Another strategy may be natural disease resistance. All plant tissues possess natural disease resistance mechanisms in the form of physical barriers and antifungal compounds. These resistance mechanisms limit damage caused by fungal pathogens and, therefore, manipulation can result in improved disease resistance (Lamb *et al.* 1989). Concentrations of antifungal compounds in plant tissues can be enhanced by various means. Salicylic acid is one of the potential 'inducer' chemicals that has been shown to enhance natural disease resistance (Frey and Carver 1998). Beasley *et al.* (1999) reported that salicylic-acid treatment significantly reduced the extent and delayed the onset of fungal colonisation in the flower tissue of waxflower.

Conclusion

Bud and flower abscission from waxflowers can result in major postharvest losses during transport, handling and marketing. However, postharvest losses can be minimised by maintaining low temperatures and preventing periods of water stress during handling. Removal or blocking of ethylene is another important factor that can delay or prevent flower abscission. In addition, infection of waxflower flowers by *Botrytis cinerea* can lead to flower abscission. Strategies that can be employed to control this fungal pathogen include the maintenance of field hygiene and application of pre- and postharvest fungicides. However, exacerbation of fungicide resistance problems is a cause for concern. Therefore, alternative control strategies, such as biological control and the enhancement of host-plant disease resistance, should be considered.

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