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The Cut Flower: Postharvest Considerations

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Abstract: Cut flowers are the big revenue creators of fresh commodities. In this review, the current status of postharvest technology applied to cut flowers and foliage is discussed. Also included are considerations of the physical, biochemical and genetic mechanisms underlying some of the processes central to cut flower and foliage deterioration, such as abscission, senescence and programmed cell death. Moreover, through examples, solutions to increasing longevity through improvement of cultural practices and sanitation and through genetic engineering are covered, providing practical solutions to the global cut flower market.

Key words: Chlorophyll, cut flower, ethylene, plant cell death, reactive oxygen species, senescence

Cut flowers

Cuttings from ornamental plants, particularly cut flowers, have a limited shelf life. Methods of maintaining the quality of these fresh products over time, such that the consumer may be able to still enjoy them after harvest, have improved dramatically. It is the ever-changing nature of human emotion, the dynamic evolution of the society we live in and the situations that govern our lives that are the primary catalysts for consumer-driven cut flower markets. As consumer and florists' demands and interest in new species increase, so the quality and longevity of this consumption product need to improve, with regulations and evaluating parameters constantly in need of adaptation to meet the need of an evolving flower market. These parameters differ between European and American markets with respect to colour, size, fragrance and decorum. The appearance, quality, and longevity of cut flowers depend upon the conditions of cultivation, the proper harvest time, product transport conditions and postharvest handling, which are dependent on the stresses imposed upon them: decrease in water uptake, transpiration, hydraulic conductivity, fresh weight, water content of flowers and water potential.

Plants cultivated under optimal conditions will exhibit the highest quality, and depending on distance to the target market, flowers are generally harvested with a certain frequency and at a particular harvesting date and physiological or developmental stage of the flower (Monteiro ***et al.***, 2001). This is commonly exemplified in flowers that have been cut too early, resulting in 'bent neck' in roses or scape bending in gerbera, resulting from insufficient lignification of the peduncles' vascular tissue. Often cold storage before marketing is inevitable, especially in trans-continental sales, where the duration and temperature of storage can vary greatly. Moreover,

symptoms of leaf disorders are not immediately evident following removal from the cold storage room, but only in the interior environment, providing little indication of cut stem quality at time of purchase.

The most important cut flowers grown and used throughout the Western World are standard and spray carnations, glasshouse roses, disbudded and spray chrysanthemums, forced spring bulbs and lilies, gerber as, asparagus fern and other foliage, gladioli and orchids (cattleyas, cymbidiums, dendrobiums and paphilopedilums), although 'Spider Orchids' (***Aeres***, ***Aerides***, ***Oncidium*** and ***Renanthera***) are being increasingly exported from Malaysia and Thailand. The present global market sees an increase in cut flowers relative to house plants, potted foliage or flowering plants, despite the fact that flowers are transient and perishable. Flowers are also commercialized as dried cut flowers.

The practical culture of cut flowers and their handling

The handling, storage, and marketing of plants and plant parts is one of the major preoccupations of human societies. Postharvest physiology deals with the functional processes in plant material after it has been harvested, from harvest or removal of the plant from its natural growing environment to the time of ultimate utilization, deterioration, or death. General requirements for a cut flower holding exist including sorting and grading, even if picked and bunched in the field. Initially, flower care and hygiene commences prior to harvest, including correct nutrition (conventional or hydroponic), appropriate lighting and irrigation practices, marginal to the discussion within this review.

Cut flower packing material varies from flower to flower, and is normally determined based on the necessities of the wholesaler, the flower market, and the distance of transport of the material. A factor that needs to be considered by producers, distributors or retailers is the maintenance of flower and foliage at cool temperatures, ensuring a slowing of metabolism and reduction of heat caused by respiring/transpiring tissues, resulting in longer life and subsequent consumer satisfaction.

Flowers are of no value to the producer until they are sold, while the ultimate purchaser expects to receive a product that lasts well in the home. Ultimate vase-life, longevity of the product, care and attention are all features making a floricultural product attractive to the wholesale market. An understanding of the plant's physiological requirements after harvest assists the grower in taking the appropriate actions to ensure that the product is satisfactory, with each crop requiring specific conditions. This review attempts to understand these various mechanisms of action as well as the physiological and genetic basis of cut flower postharvest changes. The effects of light and temperature in flower induction, the transition from the vegetative state to the floral state, ***in vitro*** flowering, and floral genetics, and pre-harvest condition-related topics, although all closely related to this review lie beyond its scope and are covered elsewhere (Teixeira da Silva and Nhut, 2003a).

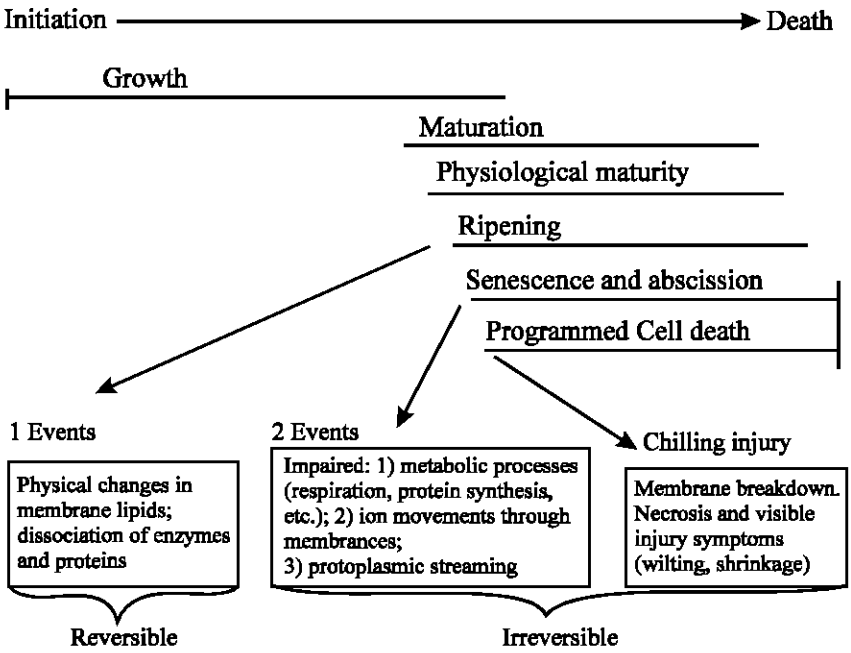

Fig. 1: Simplified scheme of the mobilization of senescence-related macromolecule components. TCA, Tricarboxylic acid. Onset of senescence and chilling during floral development

Metabolism and metabolic pathways affecting cut flower quality

Metabolism represents the entirety of the many chemical activities that occur within cells. The acquisition and storage of energy (photosynthesis) and its inverse, the utilization of this stored energy (respiration) are two of the central processes in the control of the overall metabolism of plants. Respiration is a central process in living cells that mediates the release of energy through the oxidative breakdown of carbon compounds (starch, sugars and organic acids) and the formation of carbon skeletons necessary for maintenance and synthetic reactions after harvest (Wills ***et al.***, 1998). Respiration of glucose, for example, occurs through two main reaction sequences: firstly glucose → pyruvate (in glycolysis or EMP pathway) and then pyruvate → CO_2 by the TCA cycle (Fig. 1). The oxidative pentose phosphate pathway (OPPP), another respiratory pathway, can account for significant tissue respiration in ornamentals (Wills ***et al.***, 1998). The synthesis and degradation of carbohydrates, organic acids, proteins, lipids, pigments, aromatic compounds, phenolics, vitamins, and phytohormones are classified as secondary processes (relative to photosynthesis and respiration), but which are vital and influential to the quality of cut flowers, as many of these changes are not desirable. In fact the greatest quantitative change associated with ripening is the breakdown of carbohydrate polymers, especially the

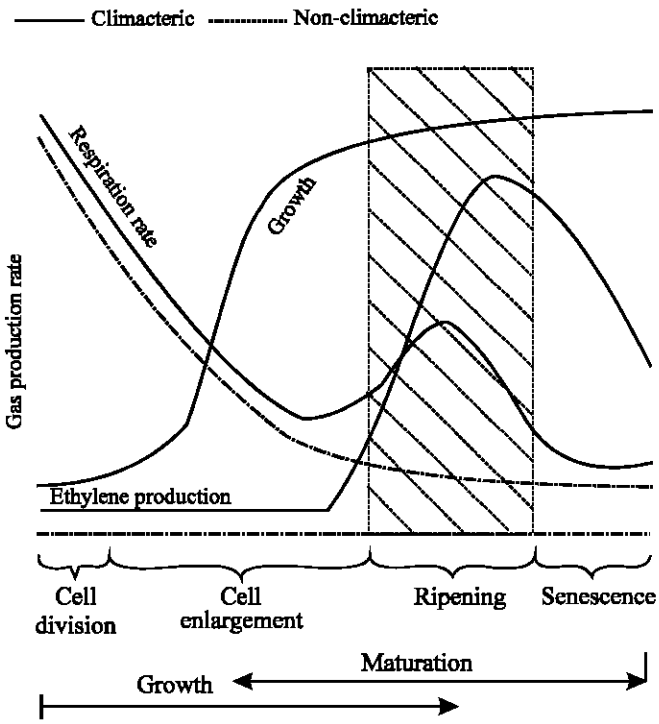

Fig. 2: Growth and respiration in climacteric and non-climacteric species.

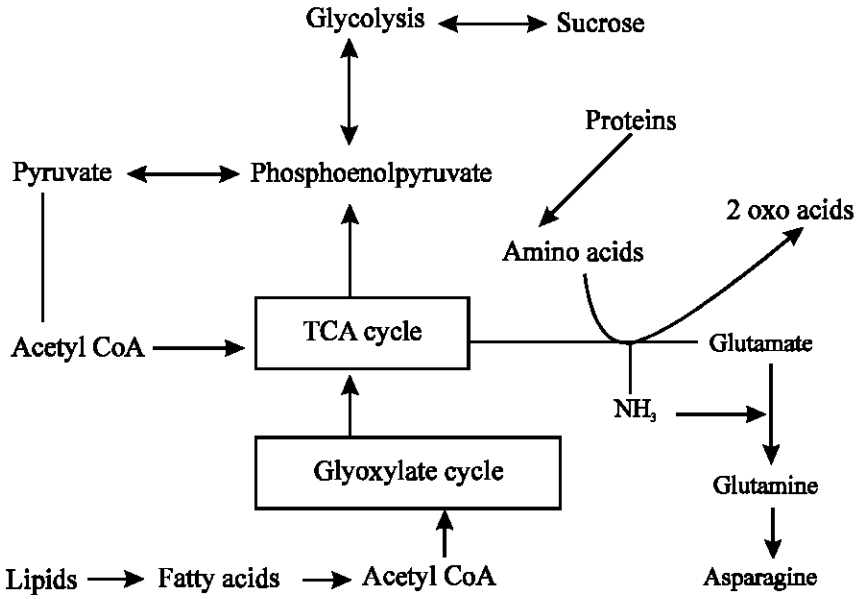

Fig. 3: The evolution of changes occurring from growth through to senescence.

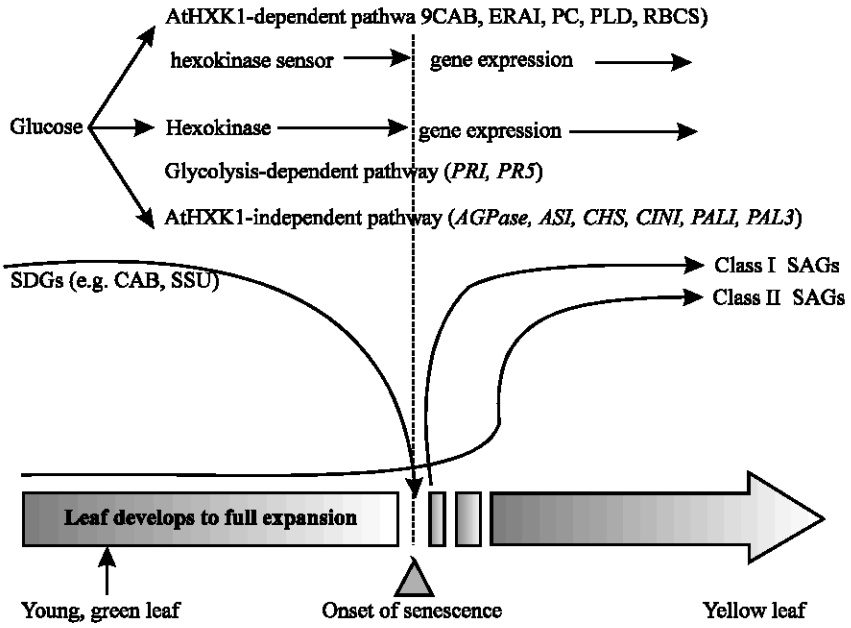

Fig. 4: Leaf senescence, senescence-associated gene expression and its link to sugar-controlled gene expression. *AS1*, asparagine synthetase; At, *Arabidopsis thaliana*; *CAB*, chlorophyll *a*/*b*-binding protein; *CHS*, chalcone synthase; *CIN1*, cell wall invertase; *ERA1*, enhanced response to ABA; HXK, Hexokinase; *PAL*, phenylalanine ammonia lyase; *PC*, plastocyanin; *PLD*, phospholipase D; *PR*, pathogenesis-related; *RBCS*, ribulose-1,5-bisphosphate; *SAG*, senescence-associated gene; *SSU*, Rubisco small subunit.

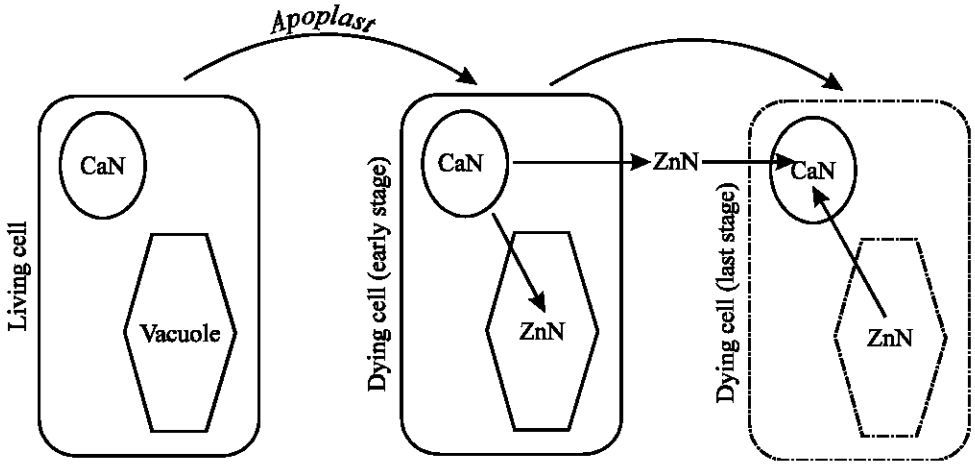

Fig. 5.1: Programmed cell death (PCD) in plants. DNA is hydrolysed during PCD involving different endonucleases (CaN, ZnN)

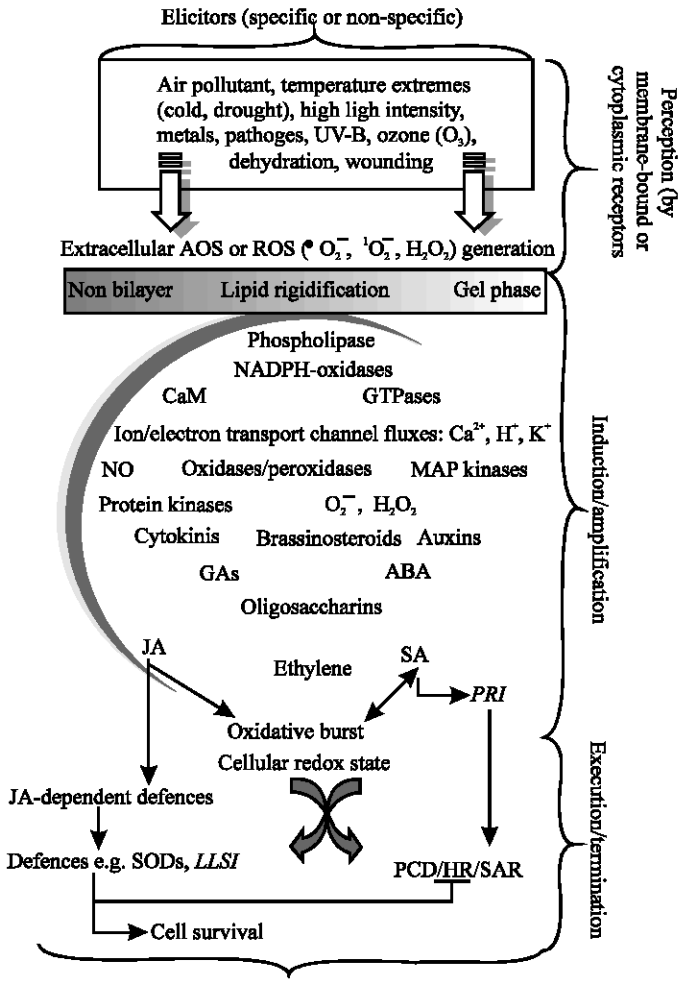

Fig. 5.2: Various signalling components may act in concert or antagonistically to influence plant defence responses to a wide variety of stimuli that generate ROS/AOS, which oxidize membrane lipids, causing 'leaky membranes'. The AOS-induced changes in the physichochemical properties of the plasma membrane modify phospholipase activity by altering the ion fluxes, Ca^{2+} channels, GTPases, MAP kinases, and others, which in turn influence the NOS activity, generating NO. These changes, including the presence of ozone, then also influence the biosynthesis of signaling molecules such as SA, JA, ethylene and/or other PGRs. These signals act together to amplify the signal and influence the cellular redox state, influencing the transcription of defense genes and induction of PCD. *ABA*, abscisic acid; *AOS*, active oxygen species; *CaM*, calmodulin; CaN, Ca^{2+}-dependent endonuclease; *GA*, giberellic acid; *HR*, hypersensitive response; *JA*, jasmonic acid; *LLS1*, *lethal leaf spot 1* gene; *NO*, nitric oxide; *PR1*, pathogenesis-related protein; *ROS*, reactive oxygen species; *SA*, salicylic acid; *SOD*, superoxide dismutase; *UV-B*, ultraviolet B radiation; ZnN, Zn^{2+}-dependent endonuclease; $^{\bullet}O_2^-$, superoxide; $^1O_2^-$, singlet oxygen; H_2O_2, hydrogen peroxide.

near total conversion of starch to sugars. The breakdown of polymeric carbohydrates, especially pectic substances and hemicelluloses, weakens cell walls and the cohesive forces binding cell walls together.

Senescence, abscission and plant cell death

Senescence and abscission

Senescence and death are important processes in the life cycle of an organism and is an active process during which nutrients are broken down and metabolised from senescing organs to actively growing ones. Senescence of organs such as leaves appears to differ from typical apoptosis (or PCD) in a number of significant ways. The cells in senescing organs undergo a gradual, orderly disassembly and the cytoplasm does not boil or bud. More substantially, nuclei do not show substantial structural changes until relatively late in the senescence process (Nooden ***et al.***, 1997). Whole plant (monocarpic) senescence that follows the reproductive phase of many plants, is one of the most dramatic and probably the most complex form of senescence, and is usually induced by the reproductive structures. PGRs, especially cytokinins, appear to control the monocarpic senescence process, GA controls apex senescence in peas while ethylene stimulates leaf and petal senescence, resulting in drying of sepals, abscission, floret abscission, in-rolling of petals or corollas, wilting and even colour changes (Davies, 1995). Flowers are referred to as climacteric or non-climacteric depending on the occurrence of an ethylene and respiratory peak during petal senescence (Fig. 2). In climacteric species ethylene production is centrally involved in petal senescence, which is induced in response to ethylene, suggesting its involvement in both initiation and regulation of senescence, while ACC synthase and ACC oxidase increase dramatically preceding the onset of senescence, something that does not occur in non-climacteric species (Williams ***et al.***, 1995).

Petal senescence

In petals of cut flowers undergoing senescence, protein content falls, protease activity increases, lipid fluidity in the membranes declines, and respiration rate increases (van Doorn and Stead, 1997). Aging of petals is accompanied by a morphological, biochemical and biophysical deterioration (Fig. 3). Senescing carnation flowers exhibit a climacteric-like rise in ethylene production and exposure of carnation flowers to exogenous ethylene induces inrolling of petals, triggering ethylene synthesis, and inducing chemical and physical changes in microsomal membrane lipids of senescing petals (Bartoli ***et al.***, 1996). In chrysanthemum, which is non-climacteric, ethylene does not play a role in flower senescence, with only minor changes in protein content and the proportion of major polypeptides being observed (Williams ***et al.***, 1995), explaining the long post-harvest life of chrysanthemum. Conditions inhibiting the action of, i.e. by the supply of silver salts, sodium benzoate or boric acid, or the synthesis of ethylene, i.e. by the supply of α-aminooxyacetic acid (AOA), prolong the vase-life of carnations (Serrano ***et al.***, 2001); an invertase inhibitor, apparently synthesized in wilting petals of a number of flowers (***Ipomoea***, alstroemeria, carnation, dahlia, gladiolus, petunia and rose) affects the senescence of petals by blocking sucrose hydrolysis to glucose and fructose in the senescing tissue, which

may control the translocation of sucrose from wilted petals to other organs of the flower. Petal abscission in rose petals is not affected by the water status unless the plants reach a low water potential early on during vase life, nor is it inhibited by low light intensity nor affected by the Pr/Pfr ratio (Van Doorn ***et al.***, 1996).

Leaf senescence

On the stems of many cut flowers exist numerous leaves which also suffer the degenerative process of senescence, offset by developmental age, external factors, including temperature, drought, nutrient deficiency, shading, wounding and pathogen infection, and by internal factors, including developmental stage and PGR levels. Leaf senescence, although part of the natural life cycle of the plant, can be triggered by stress conditions (salinity, removal of roots, and low light conditions), resulting in a large number of metabolic changes: increased activity of proteases, glyoxysomal enzymes, nucleases and chlorophyllases, resulting in an overall decrease in the amount of protein, RNA and chlorophyll (Chl). Activation of abscission by ethylene involves the expression of specific hydrolases (such as endo-ß-1,4-glucanases and polygalacturonases) whose activity weakens (loss of cell adhesion and cell separation) the structure of cell walls at the abscission zone (Casadoro ***et al.***, 1999; van Doorn and Stead, 1997; Fig. 4). The co-ordinated expression of senescence-associated genes (SAGs) appear to regulate leaf senescence, and whose gene products are primarily involved in degradation or remobilization of biomolecules, and in the protection of cell viability for completion of senescence (Buchanan-Wollaston, 1997). Stress remains central to the understanding of the reaction of the plant or plant part, and the physiological, biochemical and genetic reaction to stress has been well documented (e.g. Storey, 1999).

Programmed cell death

Recently, and with expanded recent interest, apoptosis, or programmed cell death (PCD) has been studied in plant systems (Rubinstein, 2000). PCD is a broad term describing the process by which cells promote their own death through the activation of self-destruction systems. PCD, suicidal cell death or apoptosis is an area of research that has only just commenced in detail in plants, and has already been shown to be essential in processes such as xylem differentiation and tapetal cell degeneration. PCD in plants has a structural role (formation of fibres or ducts for nutrient transport), adaptive roles (reallocation of resources and preventing water loss, aerenchyma formation), or defensive roles (halting the spread of pathogens). In the case of xylem differentiation (Fukuda, 2000), PCD may be important in increasing water flow in embolized cut flower stems. Moreover, PCD is considered to be the endpoint of senescence, enabling the plant to recycle nutrients in an ordered fashion (Swidzinski ***et al.***, 2002). The plasma membrane is considered to be one of the primary sites for stress signal recognition, whose activation initiates signalling cascades, leading to the induction of many plant defence mechanisms, including the accumulation of the signalling molecule salicylic acid (SA), synthesis of pathogenesis related (PR) protein, thickening and hardening of cell walls, and an increased production of antibiotic compounds, the phytoalexins (Kuriyama and Fukuda, 2002). Moreover, PCD-specific hydrolytic

Table 1: Some aspects of change in senescence and programmed cell death in petals

Location	modification
Cellular structural changes	
Membrane	Rupturing and increase in cytoplasmic debris; loss of permeability and fluidity (due to oxidation)
Tonoplast	Invagination and endocytosis of cytoplasmic contents; cortical microtubules disappear
Cytoplasm	Reduction in volume; cessation of cytoplasmic streaming; change in proton flux across plasma membrane
Organelles	Degeneration and collapse (e.g. of protoplasts); increase in number of peroxisomes
Change	Enzyme/molecule
Biochemical and structural molecular changes	
Increase	Proteinases (e.g. caspases); nucleases; up-regulation of phospholipases, acyl hydrolases, lipoxygenase Neutral lipids; sterol/phospholipid ratio; lipid peroxidation; reactive oxygen species (ROS) Water leakage; cell wall cross-linking
Decrease	Phospholipids; chlorophyll; proteins; thiol groups; nucleic acids and RNA
Change	Resulting reaction
Countering PCD	
Increase	Catalase, ascorbate peroxidase or superoxide dismutase lower H_2O_2 and protects build-up of ROS Use of antioxidants (ascorbate, glutathionine, α-tocopherol)

enzymes (e.g. S1-nuclease, RNases and cysteine proteases) are synthesized and accumulate in the vacuole. The transport of organic anions into the enlarging vacuole is inhibited. The vacuole then bursts, shrinks and fragments, causing hydrolytic enzymes to invade the cytoplasm and attack various organelles, resulting in the degradation of cell contents and part of the cell walls (Kuriyama and Fukuda, 2002).

A distinguishing feature of plant cells is the prominent vacuole, which contains many catabolic enzymes such as proteases and nucleases (Table 1). Self-ingestion of cells destined for PCD is probably common among plants, but the actual sequence and resulting morphological changes may differ depending on the particular inductive death signal (developmental, pathogen- or ROS-activated, Fig. 5). Plant 'apoptosis' relies on a cascade of enzymes, caspase-like proteases that are activated by cleavage at specific peptide bonds after the binding of an extracellular death signal (stress, pathogen or other) to its receptor on the cell surface (Beers ***et al.***, 2000; Estelle, 2001; Teixeira da Silva and Nhut, 2003b). Superoxide dismutases (SODs) constitute the first line of defence against ROS (Alscher ***et al.***, 2002), while the presence of the ***LLS1*** (***lethal leaf spot 1***) gene acts to eliminate a phenolic effector of Chl swelling and PCD (Buckner ***et al.***, 2000).

The action of PGRs in senescence and abscission

ABA

Abscisic acid (ABA) is generally known as a strong growth inhibitor and a senescence-stimulating factor, but it also controls stomata closure in certain plants. In vegetative tissues, ABA appears to be involved in the response and adaptation of plants to environmental stresses, especially in drought, salinity and cold conditions (as may occur in storage conditions of cut flowers). It has also been proposed that under water stress, turgor pressure declines and it results in an increase in cytosolic and apoplastic ABA levels (Patterson, 2001). This increase leads

to: a) the closure of stomata to avoid further water stress, and b) the induction and accumulation of compatible solutes, such as proline, for water stress tolerance (Shen ***et al.***, 1997). Exogenous applications of ABA can serve also to increase the cold hardiness of plants. Provision of exogenous ABA in the vase solution effectively reduces vase solution usage and extends flower life. The expression of ABA genes results in the formation of, amongst other gene products, LEAs (late embryogenesis abundant), which are neither enzymes nor storage proteins but rather serve to protect proteins and membranes from damages during water loss in the cytoplasm due to desiccation. Reid (1985) hypothesized that a gradient of auxin from the subtended organ to the plant axis maintains the abscission zone in a non-sensitive state. A reduction or reversal of the auxin gradient causes the abscission zone to become sensitive to ethylene. Consequently, senescence and abscission could be altered by factors like shading, low irradiance, high temperature or water stress and poor nutrition, which alter auxin gradients by exposure to ethylene, and by stresses that enhance ethylene production.

Ethylene

Ethylene (C_2H_4), the simplest unsaturated hydrocarbon, is involved in the control of growth and developmental processes that range from germination to senescence (Lilievre ***et al.***, 1997). Ethylene plays a crucial role in the senescence of flowers, but ethylene sensitivity can vary depending on the cut flower species (Redman ***et al.***, 2002). Ethylene is synthesized when L-methionine → S-adenosyl-L-methionine (SAM) → ACC (1-aminocyclopropane-1-carboxylate, produced in the Yang cycle) → ethylene, the last two reactions being catalyzed by ACC synthase and ACC oxidase (Mathooko, 1995; Fig. 6). SAM is also a precursor for the synthesis of the polyamines spermidine and spermine, which are related to young or actively growing tissues (Walden ***et al.***, 1997; Pandey ***et al.***, 2000). Ethylene probably binds to specific receptors to form a complex that then triggers ripening. In carnation, where the effect of ethylene on senescence has been well-studied, ethylene is first produced in the pistil and the evolved ethylene acts on petals and induces the expression of genes for ACC synthase, ACC oxidase and cysteine proteinase, resulting in the auto-catalytic ethylene production from the petals, in-rolling of petals and wilting of the flowers (ten Have and Woltering, 1997). The gynoecium has been shown to produce a significant amount of ethylene before its production in the petals, possibly induced by factors like ABA or IAA, suggesting its importance in controlling ethylene production in the flower during natural and pollination-induced senescence, with emasculation hastening the release of ethylene (Shibuya ***et al.***, 2001). Daffodil (***Narcissus pseudonarcissus***) flowers adversely affect the vase life of other flowers through an ethylene-mediated effect and a bacterial-growth-inducing effect created by daffodil mucilage (van Doorn, 1998).

Others

Gibberellins (GAs) are a large family of diterpenoid compounds, some of which are bioactive growth regulators, controlling such diverse processes as germination, stem elongation, and flowering. GA biosynthesis branches from the general terpene biosynthetic pathway at geranylgeranyl diphosphate, which is a common precursor for carotenoids, ABA and the phytol

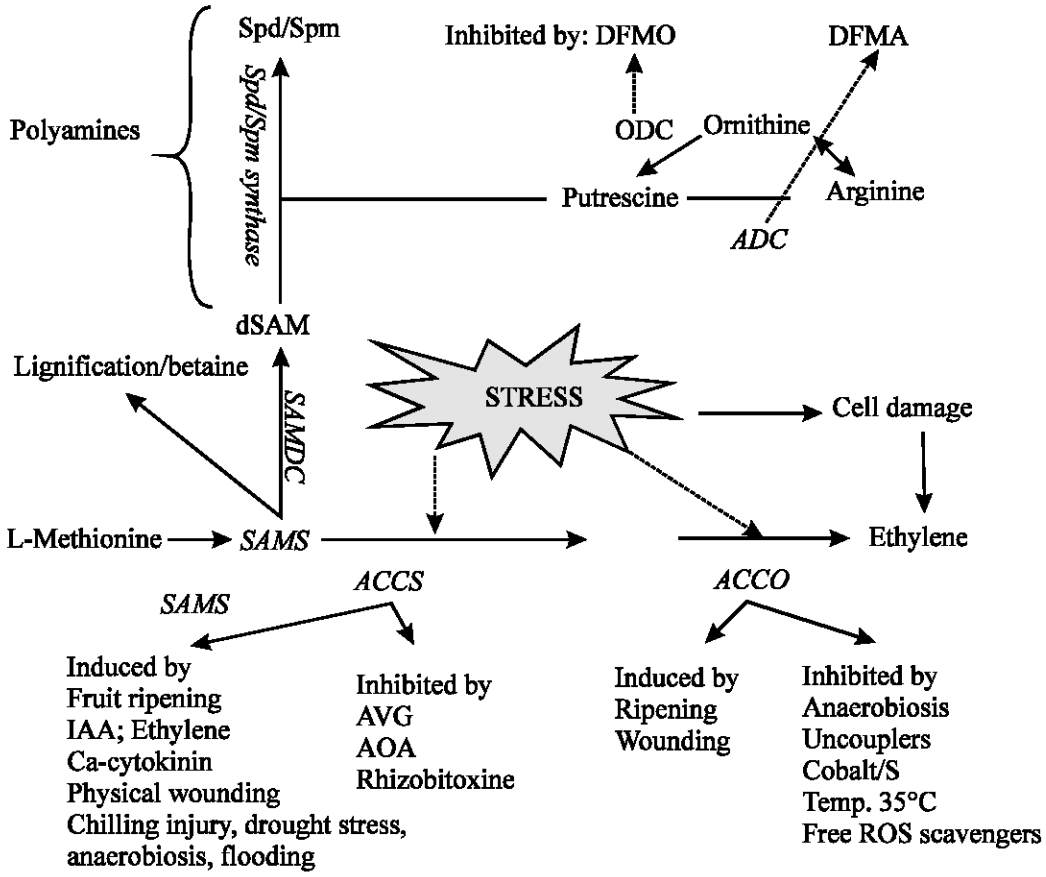

Fig. 6: Ethylene biosynthetic pathway: a generalized scheme. *ACCO*, 1-aminocyclopropane-1-carboxylic acid oxidase; *ACCS*, 1-aminocyclopropane-1-carboxylic acid synthase; *ADC*, arginine decarboxylase; *AOA*, aminooxyacetic acid; *AVG*, aminoethoxyvinylglycine; *DFMA*, DL-difluoromethyl arginine; DFMO, DL-difluoromethyl ornithine; *ODC*, ornithine decarboxylase; *SA*, salicylic acid; *SAM*, S-adenosyl-L-methionine; *SAMDC*, SAM decarboxylase; *SAMS*, SAM synthase; *Spd*, spermidine; *Spm*, spermine

chain of Chl. The large number of metabolic changes which occur during leaf senescence, such as the increase in enzyme activity of proteases, glyxosomal enzymes, nucleases and chlorophyllases, result in a decrease of protein, RNA and Chl. Light and phytohormones influence leaf senescence. Cytokinins, and in some cases GAs (such as GA_3, GA_4 and GA_7 in ***Alstroemeria*** cut flowers; Jordi ***et al.***, 1994, 1996) delay the loss of Chl whereas ethylene and ABA enhance the rate of Chl loss; the application of BA and GAs together improved the postharvest quality of cut Asiatic and Oriental lilies (Han, 2001). Jasmonic acid can induce senescence while polyamines delay foliar senescence. In geralton waxflower, the foliage of cut flowers often desiccates before flowers on the same sprig become senescent, since leaves have relatively higher turgor

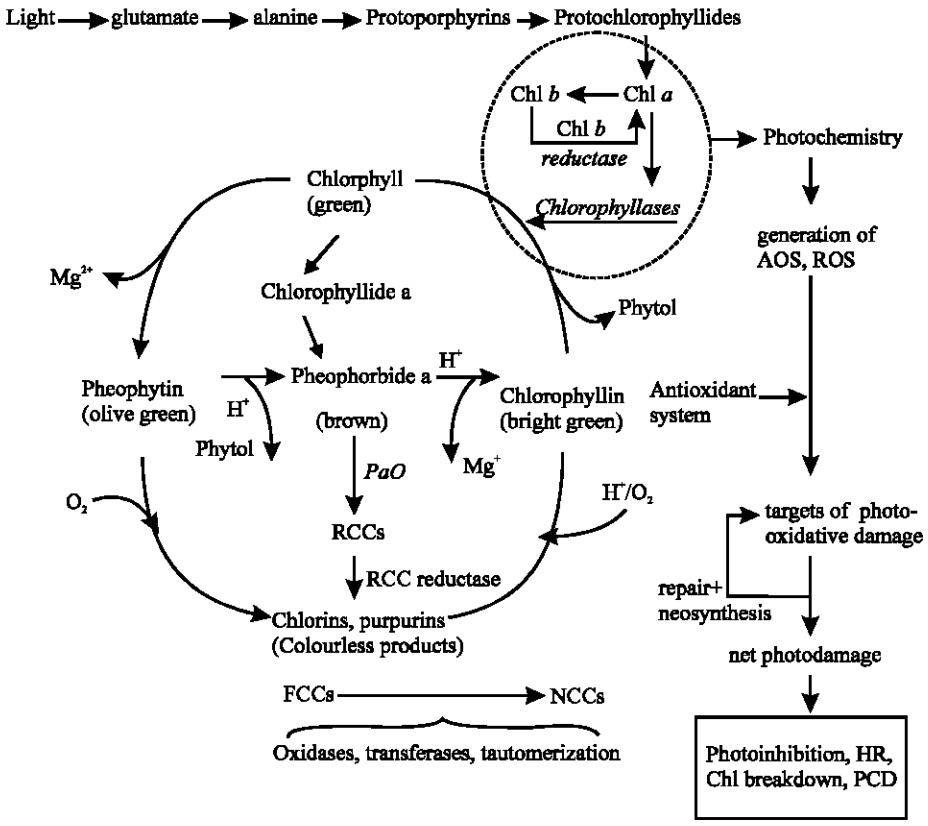

Fig. 7: Chlorophyll breakdown. *AOS*, active oxygen species; *Chl*, chlorophyll; *FCC*, fluorescent Chl catabolite; *HR*, hypersensitive response; *NCC*, nonfluorescent Chl catabolite; *PaO*, phaeophorbide *a* oxygenase; *PCD*, plant cell death; *RCC*, red-coloured catabolite; *ROI*, reactive oxygen intermediates

and lower osmotic potentials than flowers, and are less elastic (Joyce *et al.*, 2000). Brassinosteroids induce PCD and the formation of secondary walls (Kuriyama and Fukuda, 2002).

Growth retardants (e.g. uniconazole, ancymidol, paclobutrazol) reduce shoot elongation normally through inhibition of endogenous GA. GA effectively retains Chl, while the addition of IAA in vase water has little effect on leaf yellowing, while kinetin delays it (Van Doorn *et al.*, 1992). The cytokinin benzyladenine (BA) improved the vase life of anthurium, heliconia, and ginger (*Alpinia purpurata*) when applied as a spray or a dip, but inhibited that of bird-of-paradise (*Strelizia reginae*), beehive ginger (*Zinziber spectabilis*), and Uluhe fern curls (*Dicranopteris linearis*), bamboo orchid (*Arundina bambusifolia*) and fern lycopodium (*Lycopodium cernuum*) cut leaves (Paull and Chantrachit, 2001). Jasmonic acid and methyl jasmonate, natural PGRs are involved in plant defense responses, exhibit direct antifungal activity as well as increase numerous antifungal compounds in plant tissues when applied exogenously. They also activate many inducible genes leading to the synthesis of secondary plant products that funtion as

antimicrobial compounds (Meir ***et al.***, 1998).

Inhibition of ethylene action

The prime requirement to ensure the absence of ethylene is by adequate ventilation, and by keeping ethylene-inducing products such as ripe fruits separate from floral products. Since silver nitrate ($AgNO_3$) and acetate move slowly in plant tissue and are photodegradable, silver thiosulphate (STS), an ethylene antagonistic, is used instead. STS doubles the longevity of carnations, excellent for gypsophila and other herbaceous plants that produce flowers in a spike such as ***Antirrhinum*** or ***Phalaenopsis***, but is less effective with roses or cymbidiums. STS toxicity is species- and cultivar-dependent.

STS pre-treatment is obligatory in Dutch flower auctions. The use of $AgNO_3$ proved superior to STS in maximizing vase life in ***Dendrobium*** and chrysanthemum, although did not act as an inhibitor of ethylene synthesis, but rather as an antimicrobial agent (Ketsa ***et al.***, 1995). A similar pattern of senescence is observed in attached and detached petals of carnation; patterns of senescence are not altered by the addition of STS, and the basal region of the petal is important in the regulation of petal senescence (Altman ***et al.***, 1995). The longevity of freesia buds can be prolonged by the addition of sucrose to vase solutions, whereas STS does not affect the production of ethylene in cut flowers (Spikman, 1989). RNA-Ag+tris (a ribonucleic acid-silver complex and trishydroxymethylaminomethane) was superior to STS in increasing longevity of cut rose flowers (Ohkawa ***et al.***, 1999).

STS has not been able to extend the vase life of irradiated cut flowers in a number of species, including chrysanthemum, but has been successful in snapdragon (Lee ***et al.***, 1995). 8-Hydroxy quinoline sulphate (8HQS), $AgNO_3$, carbonated water (20-30%) and 1-Methylcyclopropene (1-MCP; Serek ***et al.***, 1995) can all extend the vase-life of cut chrysanthemums (Lee ***et al.***, 1996). 8HQS, an effective germistat, reduces the number of bacteria in the water and increases the conductivity of the stem (Ichimura ***et al.***, 1999). 1-MCP also extended the vase life of a number of Australian cut flowers, but only in the presence of exogenous ethylene (Macnish ***et al.***, 2000). 1-MCP and Promalin® (a commercial mixture of 1.8% gibberellin (GA_{4+7}) + 1.8% BA) or Accel® (GA_{4+7} to BA ratio 1:10), when used together effectively eliminate the post-harvest effects of ethylene on Oriental lily cut flowers, namely accelerated flower bud and open flower abscission, and yellowing and abscission of leaves (Çelikel ***et al.***, 2002). Since 1-MCP acts as a competitive and apparently irreversible inhibitor of ethylene binding, and treatment at low concentrations eliminates the effect of ethylene on ethylene sensitive potted plants and cut flowers of geraldton waxflower (Serek ***et al.***, 1995).

Many of the processes involved in the response of cut flowers to water stress, including accelerated ethylene production, membrane modifications, and water and solute loss can be prevented by a transient exposure (24h) of cut carnation flowers to cycloheximide (Drory ***et al.***, 1995). Wilting in ***Iris*** tepals (indistinct outer whorl sepals and inner whorl petals) is delayed by the addition of cycloheximide, which acts by causing rapid stomatal closure and a decrease in the rates of respiration and water uptake (van Doorn ***et al.***, 1995). Aminotriazole, although also inhibiting the climacteric peak of ethylene in carnation, is also a putative carcinogen (Serrano

et al., 2001). AOA, also an inhibitor of ACC synthase activity, has certain toxicological risks, and a more inexpensive and effective substitute is boric acid (Serrano ***et al.***, 2001). Glyphosate, a herbicide used by the floriculture industry in devitalisation of cut carnations and roses to prevent bud outgrowth from the nodes, inhibits the shikimate pathway enzyme ESPS synthase due to its metal-chelating properties, thus interfering with aromatic amino acid (phenylalanine, tyrosine, tryptophan) metabolism, resulting in delayed senescence of ***Sandersonia*** flowers (Eason ***et al.***, 2000).

Another substance, diazocyclopentadiene (DACP) has been shown to be an ethylene antagonist, and successful in increasing vase life, decreasing leaf and bud drop in rose and miniature rose (Serek ***et al.***, 1994). α-Aminoisobutyric acid (AIB) has been shown to be a successful replacement for STS, replacing the existence of heavy metal ions in the preserving solution (Shimamura ***et al.***, 1997). AVG, an ethylene biosynthetic inhibitor has been shown to be superior in its effect than STS or AIB in prolonging vase life of cut ***Cymbidium*** flowers. No visible signs of senescence such as lip reddening, petal wilting and abscission of individual flowers on inflorescences could be observed once cut flowers were pre-treated with AVG (Kwack ***et al.***, 1996).

Endogenous polyamines (especially spermine and spermidine; Walden ***et al.***, 1997; Pandey ***et al.***, 2000) possibly suppress ethylene production (Lee ***et al.***, 1997). Spermine delays the senescence of cut carnation flowers and reduces ethylene production, endogenous ACC content and the activities and the transcript amounts of ACC synthase and ACC oxidase in petals. Methylglyoxal bis-(guanylhydrazone), an inhibitor of polyamine biosynthesis, elevates ethylene production, increases the activities and amounts of transcripts for ACC synthase and ACC oxidase, shifting the climacteric pattern of ethylene production.

Lysophosphatidylethanolamine (LPE), a natural phospholipid, retards senescence and increases vase life of snapdragons (Kaur and Palta, 1997), while 1,1-dimethyl-4-(phenylsulfonyl) semicarbazide is a new commercially utilized antisenescence preservative in Japan (Satoh ***et al.***, 1999).

Ozone (O_3) and activated charcoal are other agents for oxidizing ethylene (Wills ***et al.***, 1998). The use of free-radical scavengers sodium benzoate and ***n***-propyl gallate delayed wilting in cut gladiolus florets (Yamane ***et al.***, 1999).

Flower colour, pigmentation: changes and biochemical degradation

Chlorophyll (Chl) is the principle green foliage pigment. Carotenoids constitute many of the yellow, orange and red pigments, while anthocyanins and related compounds (flavonoids) are responsible for red, purple and blue colours in most flowers (Tyrach, 1997), related to pH. Anthocyanins, often masking carotenoids and Chl, are red at a more acidic pH (<7), whereas they tend to be blue pH >7. This gives rise to a phenomenon termed 'blueing', where a shift from red to blue colouration occurs with ageing (Wills ***et al.***, 1998), resulting from a depletion of sugars as a respiratory substrate and the switch to catabolism of proteins (Estelle, 2001), with the release of free amino groups resulting in a shift to a more alkaline pH in the cell. The colour white is due to the reflectance of the visible spectrum and often results from the presence of

highly aerated tissues (Wills ***et al.***, 1998). Variegation is due to areas devoid of Chl, but which may be white or orange/yellow, resulting from the carotenoids. Cellular pH is very important in the regulation of metabolism. Most of the cellular volume may be occupied by the vacuole, which is usually very acidic (pH <5). The cytosolic functions are however optimal at a pH near neutral (~ 7.4). In order to maintain cytoplasmic pH, metabolic processes consume or produce protons, and H^+-pumps operate in the plasmalemma and in the tonoplast. The genetic mechanisms underlying flavonoid biosynthesis have been reviewed (Teixeira da Silva and Nhut, 2003a, 2003b; Winkel-Shirley, 2001).

Carbon income and expenditure over the life of a leaf (and in principle a petal) is related to the productivity benefits of altering the timing of senescence initiation. Senescence is normally apparent to the eye as a loss of Chl. Unlike the de-etiolation of seedling organs, where biogenesis of chloroplasts (CPs) involves the development of thylakoids and expression of genes for assembly of the photosynthetic apparatus, in senescing leaves, disassembly of CPs is a programmed process and thylakoid proteins are immobilized (Buchanan-Wollaston, 1997; Thomas, 1997).

Breakdown of the CP is an important aspect of the senescence syndrome, but leaf cells do not die when CPs are lost, and the existence of proteolysis does not account for the whole process of senescence. CP breakdown results in the release of stored N (Fig. 7), and these resources are generally reallocated elsewhere, such as developing seeds (Matile ***et al.***, 1999). Partly dismantled CPs function to salvage or compartmentalize degraded material. Concomitantly there is a loss of photosynthetic capacity of the cells, beginning with an orderly disassembly of the thylakoids. Senescent leaves contain partially dismantled CPs that function to salvage or compartmentalize degraded material. These senescent plastids, the 'chromoplasts' due to their residual pigments, or 'gerontoplasts' in the case of senescing leaves are smaller than green CPs, with degenerated membrane systems and stroma, and larger plastoglobuli. In regreening plastids however there is the redevelopment of grana and stroma (Zavaleta-Mancera ***et al.***, 1999b). Gerontoplasts and chromoplasts, despite having a common thylakoid system and prominent plastoglobuli, however, chropmoplasts that develop from proplastids, amyloplasts or young CPs retain the capacity for division and biosynthesis, whereas gerontoplasts have lost these capacities.

Chl degradation can be slowed by a treatment with GAs or cytokinins and, ironically, by thidiazuron (TDZ), a defoliant, which has also been shown to delay leaf senescence in lilies, tulip and iris (Ferrante ***et al.***, 2002). Ethanol, methanol and paclobutrazol (a kaurene oxidase inhibitor with an anti-gibberellin activity) retarded senescence and improved the vase life of cut chrysanthemum flowers by limiting fresh weight loss and increasing Chl content, especially causing a decrease in the Chl ***a***: Chl ***b*** ratio, resulting in a better adaptation of the photosynthetic apparatus to low light regimes and interior environments (Petridou ***et al.***, 2001). Reversing or stopping yellowing, and re-instating a green state, or regreening, of a cut flower's leaf may be achieved by iron chelators since they target an iron-dependent step in Chl degradation (Thomas and Howarth, 2000). In regreening of yellow leaves, protochlorophyllide is photoreduced to chlorophyllide, catalyzed by NADPH-protochlorophyllide oxidoreductase (POR)

late in the Chl biosynthetic pathway (Thomas, 1997). POR, being the predominant enzyme in the prolamellar body of etioplasts, rapidly disappears with illumination (Zavaleta-Mancera ***et al.***, 1999a). Expression of senescence genes that have been cloned may be modified by transgenic intervention or mutagenesis, and about 50 genes (***Sees***) have been associated with leaf senescence (Buchanan-Wollaston, 1997). In regreening, the formation of a functional thylakoid membrane was indicated by the reappearance of the thylakoid component, light-harvesting Chl ***a/b***-binding protein.

Cytokinin application can also induce regreening (Zavaleta-Mancera ***et al.***, 1999a), and attenuate the promoters of senescence-induced proteases, which are the most readily detectable senescence-induced genes (Gan and Amasino, 1997; Buchanan-Wollaston, 1997). Many proteas suffer the postharvest problem of leaf blackening, caused directly by polymerisation and oxidation of the abundant hydroxyphenols and tannins, occurring when cell compartmentalization breaks down (McConchie ***et al.***, 1993). Chilling injury, anoxia, ethylene, water stress and shortage of carbohydrates all contribute to the disruption of plant cell compartmentation (Bieleski and Reid, 1992), countered by placing cut stems in a sucrose solution (i.e. increased carbohydrate pools), retarding blackening. Polyphenol oxidase and peroxidase have been proposed as the enzymes responsible for leaf blackening symptoms (McConchie ***et al.***, 1994).

'Stay-green' genetic variants have delayed senescence, and deconstruction of the photosynthetic apparatus during leaf senescence is partially or completely prevented or disabled in five different ways based on function and speed (Thomas and Howarth, 2000): 1) delayed initiation, normal rate; 2) normal initiation, slower rate; 3) normal initiation and rate, lesion in Chl degradation; 4) rapid tissue death and 5) enhanced greenness, initiation and proportional rate as normal. In the case of any stay-green, outside interference perturbs a particular biochemical or physiological process, which in turn will be specified by one or more genes. Manipulating such a gene in order to disable pigment degradation by knockout mutants is the most common way to produce stay-greens. The control of senescence can be through nuclear genes or through non-nuclear genes, such as the CP senescence-associated gene, soybean stay green gene ***cytG*** (Thomas and Howarth, 2000).

Secondary metabolites: changes and biochemical degradation

Phenological, genetic and environmental factors affect the production of extract and volatiles after harvest (MacTavish and Menary, 1998). In brown boronia (***Boronia megastigma***), an Australian endemic commercially grown for its valued floral extract (ionones, jasmonates and dodecyl acetate) used in the food industry to enhance fruit flavours (MacTavish and Menary, 2000), as flowers become visibly senescent, their ability to produce volatiles after harvest declines, suggesting that respiratory activity and photosynthesis may regulate postharvest biosynthesis or accumulation of volatiles. As flowers senesce, non-enzymatic degradation and regulated catabolism of floral volatiles may supersede the action of ***de novo*** biosynthesis and production. Prolonged postharvest incubation results in a decline in the concentration of extract and volatiles, but incubation at 12-25°C in the presence of additional O_2 results in

increases of up to 25% in the concentration of floral extract (% dry-weight) and that of ß-ionone by 300% (MacTavish and Menary, 2000), perhaps by carotenoid degradation (Enzell, 1985). In rose flower oils production is proportional to respiratory activity, and non-respiratory oxidative reactions deplete oil yield (Tyutyunnik and Ponomaryova, 1977).

The cut flower milieu

Water and humidity in storage and growth, and water uptake

The quality of water is important for the maintenance of cut flowers. A steady water supply, which is removed at harvest, is essential to the physical development of a cut flower. This physical development is made possible in part by positive turgor, which drives cell expansion and provides support. Water potential is composed of turgor and osmotic potential. In intact plants, the xylem water is often under tension due to transpirational pull (arising from increased temperature and decreased RH), and water moves from the xylem into cells down an osmotic (water potential) gradient. If the xylem water potential falls below the water potential of adjacent cells, water may be withdrawn from these cells, resulting in shrinkage and then wilting, when turgor falls to zero (Wills ***et al.***, 1998). At a molecular/biochemical level, plant aquaporins, membrane proteins that can mediate a bi-directional water flow across membranes, cells, tissues and even organs, may be involved in the increased water uptake in the life of a cut flower (Tyerman ***et al.***, 1999).

Pure, clean water is a requisite, where normally there exist limited amounts of dissolved salts, although temporary alkalinity may occur due to soluble bicarbonates. Moreover, there are differences in the composition of tap water, de-ionized or distilled water that can cause differences in the keeping quality of cut flowers, as well as the efficacy of chemical solutions used for holding, pulsing, or bud-opening (van Meeteren ***et al.***, 2000). Saline water improves cut flower quality and yield in ***Trachelium*** and lisianthus (***Eustoma grandiflorum***), and this may be important in arid and semiarid regions used for cut flower production (Shillo ***et al.***, 2002).

The stems of some plants exude sap, containing various cations, anions and amino and organic acids (van Meeteren ***et al.***, 2000), or chemicals like phenols that can be harmful to other cut flowers or to themselves. Such water needs regular replacement. Acidic solutions move more readily up the stems than neutral or alkaline solutions. Alkalinity is negatively correlated with the action of flower food and preservative solutions, the suitable pH being 3.5-4.5. Fluoride, a mineral found in tap water, can harm the flower, causing yellowing of leaves and petal discoloration in some flower types (Wills ***et al.***, 1998).

Water is continually being lost in cut flowers through transpiration and decreasing water conductance in the stem, resulting in drooping of flowers and the premature wilting of both flowers and leaves, symptoms of water deficit stress as a result of a decrease in water uptake, transpiration, hydraulic conductivity, fresh weight, water content and water potential, making them unacceptable to consumers. In some flowers stomata are absent, consequently they do not transpire and thus heat up, especially when bunched. Leafy, actively respiring and transpiring material, such as ***Rosa*** and ***Pittosporum*** will generate more heat than almost leafless or small leafed stems like those of carnation (***Dianthus caryophyllus***) or ***Thryptomene***. When the stem is

blocked, continuing transpiration by the leaves results in net loss of water by flower and stem tissues. Water loss also enhances ripening, senescence, browning and chilling-injury. Water stress thus limits vase life and a reduction in the rate of water loss relies mainly on maintaining a high relative humidity (90-98%) either through the use of packaging or by storage at low temperature (Wills ***et al.***, 1998). The emission of nitric oxide (NO), a free radical gas, in plants increases with short-term environmental stress such as water deficit, heat and salinity (Ku ***et al.***, 2000). NO, believed to act as a natural stress-alleviating agent, reduces water loss and transpiration in Christmas bush, chrysanthemum, carnation, rose and gerbera, since it inhibits the action of ethylene (Ku ***et al.***, 2000).

Inferior cut flower performance during vase life may also result from insufficient water uptake caused by xylem occlusion, itself caused by: microbial growth, deposition of materials such as gums and mucilage in the lumen of xylem vessels, formation of tyloses (balloon-shaped outgrowths of cells adjacent to a conduit), the presence of air emboli in the vascular system, physiological responses of stems to cutting, and PCD (van Doorn, 1997; Ichimura ***et al.***, 1999; van Doorn and Cruz, 2000; van Doorn ***et al.***, 2002). Air emboli may be due to air that is aspired into the conduits that are cut open and to cavitation in xylem conduits that remain unopened. The reversion (by removal) of air emboli present in vessels in the bases of cut flower stems partly results in restoration of water uptake and a positive water balance during vase life (van Meeteren and van Gelder, 1999). Almost all vessels that are opened by cutting fill with air and embolize or clog, while no air passes into non-cut xylem vessels since air-water interfaces cannot pass vessel-to-vessel connections at low-pressure differences. Since air cannot be simply pressed out of the cut open vessels, it will be trapped between the entering water column and the pit membranes of the vessel-to-vessel connections. Consequently, in the first few hours after placement in water, only a part of the vessels are completely refilled with water. The trapped air must dissolve into the surrounding water, while the hydraulic conductance and subsequent water uptake must be re-established, for which mathematical models using chrysanthemum cut stems have been devised (van Ieperen ***et al.***, 2002). This repair of cut open vessels and embolism occurs by two processes, its speed depending on the diameter. Firstly there is a fast reconnection between vase water and non-cut xylem vessels above the cut surface by redistribution of air and water, followed by a relatively slow dissolution of trapped air and diffusion of dissolved air to the environment.

A high number of cavitations (filling of xylem conduits with air) may occur in non-cut stems of rose plants, or cut stems of other cut flower species leading to low water uptake immediately after excision, depending on the cultivar and the weather, while the low rate of water uptake after a period of dry storage is correlated with the presence of a high number of cavitated xylem elements (van Doorn and Suiro, 1996) since air is immediately aspired into xylem elements that are opened by cutting.

Air quality

The use of controlled atmospheres (increasing CO_2 or nitrogen concentrations and decreasing that of O_2) and modified atmosphere packaging decreases polyphenol oxidase (PPO)

activity, and ethylene and ethanol production (Tian ***et al.***, 2002). High levels of O_2 or of colourless quinones may inhibit PPO, resulting in the inhibition of enzymatic discolouration (Day, 1996). Reduced O_2 (5 kPa; hypoxia) and elevated CO_2 (5-10 kPa) concentrations delay and reduce the magnitude of the climateric rise in respiration by suppressing the onset of climacteric rise in CO_2 evolution. If O_2 levels fall below those supporting aerobic respiration, glycolytic conversion of pyruvate to acetaldehyde and ethanol occurs. The O_2 level at which tissue fermentation is induced may be taken as the lower O_2 limit. Although tissue tolerance to anaerobic conditions is variable, extended exposure to these conditions leads to tissue fermentation, browning, and a loss of economic value (Gran and Beaudry, 1993). There is an increasing variation in internal O_2 concentrations with factors that increase O_2 gradients by reducing their cuticular permeability. Flowers or leaves with lower cuticular permeabilities would tend to have more variable internal O_2 partial pressures relative to flowers with highly permeable cuticles/epidermises. Increased variability in the internal atmospheres of flowers under low O_2 storage would likely result in an increased percentage of flowers with internal O_2 partial pressures below the lower O_2limit, and a greater incidence of cell/tissue damage. For those flowers having relatively high epidermal permeabilities and, therefore, more homogeneous internal atmospheres, fewer flowers would exhibit damage symptoms at the lower O_2 limit. The influence of tissue permeability upon low O_2 damage would likely be accentuated with increasing temperature.

Light

Light intensity directly influences the efficiency of photosynthesis, which determines the carbohydrate content of flowers. Flowers containing relatively high amounts of carbohydrates, especially mobile sugars, last longer in the vase. Petal colour is also affected by shading/low light intensity, and thus depends on the availability of carbohydrates in surrounding tissues, resulting in tissue blueing in the presence of low light intensities. In shipping, darkness or low light intensity greatly reduces plant and consequently flower quality due to leaf and flower abscission (Cushman ***et al.***, 1998).

Dark-held plants stored at low temperatures, once moved to higher ambient temperatures undergo a number of changes, including a rapid loss of Chl, proteolysis, increased lipid peroxidation, loss of catalase activity and increased membrane permeability (Ranwala and Miller, 2000). When plants are exposed to supplemental lighting during low temperature storage, soluble carbohydrate concentration increases. This abrupt increase in metabolic activities, accompanied by oxidative stress in leaves already depleted in reserves results in leaf senescence in dark-held plants. Reactive oxygen species (ROS) generated under oxidative stress conditions can react with cellular components leading to the disruption of cellular metabolism, and anti-oxidative enzymes (e.g. catalase and superoxide dismutase) function as a defence system against oxidative stress by scavenging ROS, as do antioxidant molecules such as carotenoids, tocopherols, ascorbate, glutathionine and scavenging enzymes such as SOD (Niyogi, 1999).

Temperature in storage

Temperature is the most important environmental factor influencing the deterioration of cut

flower commodities, since these must be able to withstand storage, either cold in a fridge or warm if a fridge is not available. Most perishable horticultural commodities last longer at temperatures near 0°C, since low temperatures reduce both metabolic processes and microbial growth rate and germination (van Doorn and de Witte, 1991). Temperatures outside the physiological norm can cause rapid deterioration due to: 1) freezing injury (perishable commodities which have a high water content and large, highly vacuolate cells have a high freezing point of the tissue, and disruption caused by freezing usually results in immediate collapse of the tissues and total loss); 2) heat injury (***in vivo*** transpiration normally maintains temperatures in the optimal range, but organs removed from the plant lack the protective effects of transpiration, and direct sources of heat can rapidly heat tissues to above the thermal death point of their cells, leading to localized bleaching, necrosis (sunburn or sunscald), or general collapse; 3) chilling injury: tropical and sub-tropical commodities cannot be stored at low temperatures, even if these are above the freezing point, resulting in a variety of symptoms such as discoloration, failure to ripen and heightened susceptibility to pathogen attack (Joyce ***et al.***, 2000).

Since temperature is the major factor affecting flower life, emphasis is laid on cool storage. Generally increased temperatures result in higher levels of respiration. Cooling is also essential in order to reduce other metabolic changes such as enzyme activity, and to slow the maturation of the product (flowers or foliage), although cold storage can increase ethylene production. Cooling prior to packaging and transport will also improve longevity prospects. Refrigeration, in addition to cooling, is a desiccating process, and thus cut flowers should be maintained cool without desiccation damage. Species of subtropical and tropical origin suffer chilling injury at low temperature storage, with symptoms such as browning. A few cut flowers such as daffodil (***Narcissus***) can be stored out of water for 24 hours (dry storage), as occurs in airfreight, and will recover. Most flowers, however, are best kept in water, or nutritive solutions. Polyethylene film usually retains a layer of moisture, reducing transpirational stress by retaining dampness around leaves.

Gerbera (***Gerbera jamesonii***) and sunflower (***Helianthus annuus***) cut flower respiration increases exponentially with increasing storage temperature, which also negatively affects post storage vase life and gravitropic bending of the neck (Çelikel and Reid, 2002).

Nutrients in growth and vase/floral solutions

Some countries require that any imported plant material be non-propagatable. This implies that the buds of most cut flowers must be devitalised in some way. Solutions exist in which disbudded stems of carnations, chrysanthemum or roses are stood, both to devitalise them as well as to act as a pulsing agent (a solution supplied via the transpiration stream). Bud opening solutions are of value where a complete crop is being removed or where immature flowers are being removed from the growing crop, such as carnations or chrysanthemums. The partially developed buds, too immature for marketing, are placed in this solution. Desirable quantities and developmental stage flowers can be thus achieved this way.

Flowers usually have high rates of respiration through glycolysis and the TCA cycle based on

sugar translocation from the leaves. For cut flowers, preservative solutions in the vase water contain sucrose or a carbohydrate source to help maintain the respiration rate and to extend storage flower postproduction longevity (Wills ***et al.***, 1998; Monteiro ***et al.***, 2002). Plant tissue requires sugar in order to carry on its vital functions, especially respiration, and in practical issues, supplying alcoholic drinks, sugar or lemonade is common practice, continuously, or as a pulse. Pulsing is a principle in which plant tissues are filled with carbohydrate to ensure that there is sufficient substrate for the flowers to mature and possess longevity. Furthermore the inclusion of a sugar may increase the osmotic concentration of flowers or leaves, subsequently improving water uptake (Iwaya-Inoue and Takata, 2001). Sugars have been shown to regulate numerous genes (reviewed in Teixeira da Silva and Nhut, 2003b; Fig. 4).

A loss of rigidity in the rose bent neck syndrome is correlated to a decrease in the levels of lignification, correlated to an increase in the activity of PAL synthase. The process of photosynthesis supplies sugars to the plant tissue both for growth and its activities. Cut flowers with considerable foliage such as alstroemeria, chrysanthemums, marguerite and daisies, and foliage material such as flax or conifers do not require sugar in the vase water while senescence in many cut flowers such as rose or carnation is delayed by the addition of sucrose. The term 'nutritive solution' is applied to those mixtures in which flowers stand continuously. In cut ***Dendrobium*** flowers, the higher the level of sugar content at harvest, the longer the keeping time. Since spikes are cut with more than half the flowers still in bud, an external, high level of sugar is required in the vase solution, with resulting larger proximal end (near cut base) flowers than the distal end flowers. The presence of sucrose in preservative solutions, or even the intensive greenhouse production employing supplemental lighting and CO_2, can have deleterious effects, unless there is the presence of ABA, as has been shown in cut rose (Markhart ***et al***, 1995) where 'leaf crisping', characterized by interveinal cell turgor loss, collapse and dehydration, is caused when sucrose accumulates in the mesophyll cell wall, thus decreasing apoplastic osmotic potential, leading to collapse and tissue death.

Trehalose, a non-reducing disaccharide consisting of two α-[1,1]-linked glucose units, markedly suppressed water loss, increased water retention and enhanced vase life and viability in gladiolus petals as compared to other mono- and di-saccharides (Otsubo and Iwaya-Inoue, 2000), and prolonged the vase life of tulips when used in conjunction with CAP (Iwaya-Inoue and Takata, 2001). Trehalose appears to be related to the survival of bacteria, yeast, fungi, algae and insects under stress conditions such as dessication and freezing (Iwaya-Inoue and Takata, 2001). In plants trehalose, which is present at low levels, may be hydrolysed by trehalase (Goddijn and Smeekens, 1998), and an excessive accumulation may be toxic to plant tissues. Consequently, trehalose may not act as an energy source as sucrose, which supplies the energy and carbon skeletons required for bud opening. Trehalose also suppressed ion leakage in gladiolus petals (Iwaya-Inoue ***et al.***, 1999), and protects biological membranes under drought stress, the integrity of which is necessary to help maintain cell turgour, thus reducing water loss.

An alternative source to sugar is by introducing CO_2 into the atmosphere. CO_2 enrichment has been shown to increase stem length, fresh weight, leaf number and vase life in cut ***Dendranthema*** flowers (Tanigawa ***et al.***, 1995) and influence the qualitative growth (length of

flower neck and number of tubular florets) of chrysanthemum (Tanigawa ***et al.***, 1997) but is dependant on day temperature and long-day period and results in a higher preservability of ***Phalaenopsis*** vase life (Endo and Ikusima, 1997). CO_2 enrichment of miniature roses does not improve the problem of postharvest chlorosis even though the carbon status of the plant increases and appears to cause disruption of mitochondrial membranes resulting in a loss of phospholipids and polyunsaturated fatty acids. CO_2 enrichment is more applicable to whole plant physiology and performance in ***in vitro*** and greenhouse conditions, outside the scope of this review.

The addition of cobalt to vase solutions inhibits vascular blockage in rose stems, maintains a high water flow rate through the stems, leading to an increased water uptake by cut flowers. Additionally cobalt partially closes the stomata, and maintains a high water potential in the cut flower (Reddy, 1988). Many municipalities worldwide add fluorine to water as an additive to prevent tooth decay in humans, but levels =1 ppm have injurious effects on rose cut flowers (Lohr ***et al.***, 1990). Addition of Mg did not affect flower quality or vase life, only the size of leaves (Shima ***et al.***, 1995) while the same could be concluded from addition of Ca (Kageyama ***et al.***, 1995).

Sanitation, disinfestation and postharvest pest and disease control

Floricultural commodities have pest problems unique among the agricultural crops. Most floral products are not consumed, except for edible garland chrysanthemum (***Chrysanthemum morifolium***), which allows some tolerance in chemical residues. The most frequently utilized methods for pest removal thus far include hand removal, irradiation, fumigation, insecticidal dips and sprays, cold storage, hot water baths, vapour heat, controlled atmospheres (CA, in which CO_2 or N_2 levels are increased and O_2 levels are decreased), and biological control agents (Hansen and Hara, 1994).

Hand removal

This is the most cost-effective way of eliminating insects from cut flowers and foliage, with a slight risk of damage due to handling.

Irradiation

Novel quarantine techniques include exposure of plants to ionizing radiation (gamma rays, 300 Gy), which not only destroys pests but also damages some kind of cut flowers (Hayashi and Todoriki, 1995) while also reducing ethylene production in cut flowers. Gamma irradiation disinfestation is rapid and effective, but both floral materials and pest species vary in their sensitivity to radiation, and when excessively high (100 kGy) can reduce vase life of chrysanthemum, accelerating bloom wilting and foliage yellowing and suppressing bud opening, while doses of over 2 kGy (minimal doses needed for 100% kill of insect pests) causes blackening of flower bracts and suppression of the rate and degree of opening blooms in various Australian cut flower species, ***Protea***, ***Leucospermum***, ***Chamelaucium***, ***Anigozanthos***, and ***Banksia*** (Seaton and Joyce, 1992). Aqueous solutions (2%) of sugars (sucrose, glucose, fructose or maltose) delay

bloom wilting and foliage yellowing caused by gamma irradiation in chrysanthemum (Hayashi and Todoriki, 1995). Although the exact mechanism of action remains to be elucidated, sucrose supplied to cut chrysanthemum flowers following irradiation prevents radiation-induced damage. Gamma irradiation increases respiratory rate and alters membrane structure and function of agricultural products, reactions prevented by the presence of sugars (sucrose, glucose, fructose or maltose at 2% w/v) up to a value of 750 Gy.

Vacuoles in higher plants play important roles in the maintenance and regulation of homeostasis of plants. They are involved in the transport and storage of ions and sequester metabolites and lytic enzymes, a balance regulated by the presence of H^+-ATPase in the tonoplast. Gamma irradiation inactivates this enzyme, causing deterioration of membrane lipids (Todoriki ***et al.***, 1994).

Electron-beam irradiation proves to be a cell-damaging alternative source of irradiation for reducing microbial (***B. cinerea***) populations (Chang ***et al.***, 1997), but is more advantageous than gamma rays in that: 1) it is a nonradioactive radiation source and 2) irradiation can be achieved at a much greater dose-rate that may reduce the potential for tissue damage by allowing less residence time in the irradiation facility. It has however shown to have a number of effects on flowering species, including: lack of lustre in petal colour in tulips, delayed flowering of upper florets and smaller florets or flower buds in prairie gentian and browning of the inflorescence core and inhibition of flowering in chrysanthemum (Tanabe and Dohino, 1993). The presence of sugar in floral preservative solutions reduces the effect of radiation damage in chrysanthemum (Hayashi and Todoriki, 1995).

Fumigation

Japan has a rigorous import quarantine check, and often the presence of insects, most commonly with larval, pupal and adult stages of aphids, mites and thrips are rejected. Fumigation with hydrogen cyanide, carbonyl sulphide and methyl bromide (MeBr) cause severe damage to ***Protea*** species (Weller and Graver, 1998). MeBr is not only detrimental to the ozone layer, but will also be phased out by 2010. Phosphine (PH_3) is highly toxic to insects, has a rapid rate of diffusion and desorption, has minute residues of phosphites and phosphates, and may thus be a suitable replacement for MeBr. PH_3 does not affect vase life of king protea (***Protea cynaroides***), tulip (***Tulipa gesneriana***), kangaroo paw (***Anigozanthos manglesii***) and geralton wax (***Chamelaucium uncinatum***) when applied at 4000 ppm for 6 hours (Karunaratne ***et al.***, 1997), while higher concentrations or longer application times affects the vase life. Despite MeBr, hydrogen cyanide and PH_3 being potent fumigants for insect disinfestations of cut flowers (Karunaratne ***et al.***, 1997), the former two have phytotoxic activity.

Biocidal and insecticidal dips and sprays

It has been suggested that the presence of micro organisms in water can: 1) cause physical plugging of the cut stem; 2) release toxic metabolites and/or enzymes or 3) evolve damaging levels of ethylene and 4) induce a hypersensitive response resulting in PCD (Alvarez, 2000). Pure water used in flower containers soon becomes contaminated with bacteria or fungi which breed on

plant tissue or debris. The organisms produce, or induce, the production of substances such as tannins that can block the conducting vessels of the stems. To inhibit their development, biocides or disinfectants are added to the water, but some, such as household disinfectants, especially those based on cetrimide or chlorhexidine, are phytotoxic (Knee, 2000). Freely available and safe materials for use with plants are calcium or sodium hypochlorite - domestic bleach - used at rates of 500-1000 ppm, can be used, even if they turn the water more alkaline. Cl-based disinfectants can be used while the effect of Br-based products are unknown. The use of MeBr together with PH_3 and CO_2 has been shown to be effective in the elimination of insect and arthropod pests on cut flowers of chrysanthemum and orchid (Kawakami ***et al.***, 1996). Other commonly used disinfectants include STS, dichlorphen, quaternary ammonium compounds (Ueyama and Ichimura, 1998), 8-hydroxyquinoline citrate (8HQC) or 2,2´-bipyridyl, chelating agents (Knee, 1996), 8HQS and citric acid.

The major cell-wall constituent of herbaceous plants that influences the water-holding capacity of the intact plant is pectin. A number of pectolytic enzymes are produced by pectolytic bacteria (***Pseudomonas***, ***Bacillus*** and ***Flavobacterium***) often found in the phyllosphere of healthy plants. Both the action of pectic enzymes as well as mechanical injury such as cutting or pruning can cause the release of phytoalexins by the host plant (Put and Rombouts, 1989). Although the use of antibiotics is not so common, chloramphenicol has been shown to be an effective antimicrobial agent in successful postharvest storage of ***Dendrobium*** cut flowers (Dai and Paull, 1991), inhibiting prokaryotic protein synthesis; however these, as well as 8HQC and 8HQS induce mutations and are toxic to humans (Iwaya-Inoue and Takata, 2001). These disinfectants improve water conductance by preventing bacterial growth and reducing occlusions (van Doorn, 1998). Cycloxehimide (CHI), a protein synthesis inhibitor on the 60S ribosome, despite improving the vase life of the first florets of cut gladiolus spikes, causes inhibition of florets further down the spike (Otsubo and Iwaya-Inoue, 2000). Bacterial peptides have been shown to control bacterial growth in solutions and increase the vase life of roses, but their cost remains high (Florack ***et al.***, 1996).

Fungicides are still one the major means to control postharvest diseases, but their effect on vase life and subsequent cut cultivated greens (such as leatherleaf fern, ***Rumohra adiantiformis***, the greatest cut cultivated green revenue-maker in the US) is negative (Stamps and McColley, 1997). Certain poorly soluble fungicide mixtures (benomyl, iprodione and furlaxyl, wettable powders; propiconazole, propamocarb, and procymidone, water miscible) increase the blockage of stems (Dubois and Joyce, 1992). Public concerns over health and environmental hazards associated with their use, development of fungicide-resistant strains of postharvest pathogens, and deregistration of some of the most effective fungicides have prompted the development of non-chemical methods, such as the use of citric acid (Jones and Hill, 1993).

Aminotriazole (ATA, amitrole or amizole), a low-molecular weight heterocyclic ring compound, is used as a post-emergence, nonselective, systemic herbicide. The spectrum of ATA's activities is broad and may include inhibition of catalase activity, purine biosynthesis, mitochondrial protein biosynthesis, and imidazol-glycerol-phosphate dehydratase activity, an essential enzyme in the histidine biosynthetic pathway of bacteria and fungi. ATA inhibits both

physiological and morphological aspects of floral senescence in carnations and may serve as an alternative floral preservative for carnation and other cut flowers (Altman ***et al.***, 1993). Other germicides such as DICA (sodium dichloroisocyanurate) and BCDMH (with 12 ppm active chlorine), amongst others are variable in their effect among species and variety (Jones and Hill, 1993). Methamidophos proved effective against flower thrips (***Frankliniella occidentalis***) in calendulas (***Calendula officinalis***) and chrysanthemums (Seaton ***et al.***, 1997).

Many plant species produce essential oils that contain complex mixtures of secondary metabolites, some of which, like the active compounds (aldehydes, ketones and terpenes), play a role in chemical defense, while several components of essential oils display strong antifungal and antibacterial activity (Smid ***et al.***, 1995).

Cold storage, hot water baths, vapour heat

Before any other treatment is given, the bases of the stems of certain plants have to be preconditioned by placing them in hot water, including: a) woody plants, foliage such as ***Lophomyrtus***, leafy shrubs and glasshouse roses where it is vital to prevent the condition 'bent neck'; b) chrysanthemums, dahlias and hollow-stemmed flowers; c) plants which produce latex, such as Iceland poppies and ***Euphorbia***. This treatment drives air out of the stems and also has biochemical effects within the tissues, improving subsequent water uptake, following which stems are placed in nutritive solutions rather than in just water. Warm water reconditioning is also applied to flowers that have been dry-stored, such as tulips, or to fresh unstored flowers that may have wilted in transit. Reconditioning follows i.e. the lowest end of the stem is initially cut off to ensure rapid active uptake of water.

Hot water treatment has been used as an effective disinfestation treatment but can also induce thermotolerance in plants due to the formation of heat shock proteins (Hara ***et al.***, 1997). A 100% death of adult flour beetles and Mediterranean fruit fly larvae occurs if kangaroo paw (***Anigozanthos rufus***), geraldton wax and acorn banksia (***Banksia prionotes***) are exposed to low temperatures (1°C) for 14 days; an exposure of the same three species to the same temperature but with increased CO_2 concentrations led to a reduction in pest eradication, without an effect on cut flower life (Seaton and Joyce, 1993). Heat treatments of hot water dips (46°C for 30 min or 56°C for 10 min) and vapour heat (66°C for 10 min) killed 100% of the above mentioned pests but damaged and shortened the vase lives of geraldton wax and banksia. Cool storage slows deterioration without predisposing the cut flower to abnormal ripening or other undesirable changes (Fig. 3). Depending on the commodity, cooling may occur by cold air (room cooling, forced-air or pressure cooling), cold water (hydro-cooling), ice and evaporation of water (evaporative cooling or vacuum cooling; Wills ***et al.***, 1998).

Nitrous oxide (N_2O) is a chemically neutral, non-toxic, naturally occurring atmospheric gas, stable and highly soluble, similar to CO_2, capable of suppressing fungal growth through interference of methionine biosynthesis and is a competitive inhibitor of ethylene production and accumulation (Qadir and Hashinaga, 2001), making it an efficient as a fungicidal or fungistatic compound.

Vapour heat has been used with a number of Hawaiian floral commodities, large heliconias, red ginger (***Alpinia purpurata***) and bird-of-paradise (***Strelizia reginae***), treating, at 45-46°C, nymphs and adults of aphids, soft and armoured scales, mealy bugs and thrips (Hansen ***et al.***, 1992).

Biological control agents

A number of fungal or yeast biocontrol agents or microbial antagonists have been developed (Spadaro ***et al.***, 2002) in order to substitute environmentally unfriendly fungicides and chemicals, often as part of integrated pest management. Yeasts are generally poorly sensitive to fungicides, and due to their slow growth and prolonged permanence in tissues may be effective biocontrol agents, working primarily by competing for nutrients and space (Daniell, 1999).

Floral preservative and forcing solutions and rehydration

Some fresh cut flowers are pulsed (the supply of a solution via the transpiration stream) to re-hydrate tissues using water with a wetting agent, and also a carbohydrate source. The water permeability of a bio membrane, together with the presence of aquaporins, is necessary for plant cellular water movement (Eckert ***et al.***, 1999). Cut flowers are also pulsed with dyes, such as food grade blue dyes used on white carnations to give interesting visual effects (Wills ***et al.***, 1998). Occasionally it is important to delay or speed up flowering to suit a market requirement, as occurs with carnations for Mother or Valentine's Day. If flowering can be controlled it allows for predictability of crops and marketability of flowers. Floral preservative solutions can contain germicides or bactericides, a carbohydrate, usually sucrose, surfactants, acidifiers (such as citric, benzoic, or ascorbic acid: antibacterial compounds that indirectly promote water flow in the xylem; Jones ***et al.***, 1993; van Doorn and Cruz, 2000; van Doorn ***et al.***, 2002), growth regulators and silver, and are effective in preventing deterioration of irradiated cut flowers of protea and chrysanthemum, even though cultivar-specific. Surfactants improve water uptake and balance and germicides prevent the plugging of stems caused by microbial growth. The lack of effects of SDS (sodium dodecylbenzenesulfonate) and PLE (polyoxyethylene lauryl ether), surfactants, and 8HQS and potassium sorbate (germicides) on irradiated chrysanthemums indicates that neither poor water uptake nor microbial growth is responsible for the deterioration of chrysanthemum caused by irradiation. The addition of surfactants to the cut flower water speed up rehydration in dry-stored cut flowers. In modern cut-flower markets and auctions, the effectiveness of flower water uptake at the lowest possible surfactant concentration must consider their high biodegradability and absence of toxicity to both humans and the aquatic environment, such as in alkylethoxylate surfactants (van Doorn ***et al.***, 2002). Forcing in carnation (Koyama and Uda, 1994) is affected by temperature (at higher temperatures, days to anthesis is shortened and vase life is extended), light intensity (different cultivars require different light intensities, both weak and strong, to force normal petal colour flowers) and sucrose concentration (increasing concentration until 15% → increase in flower diameter and extended vase life).

Vase life is often used as an indicator of postharvest longevity in cut flowers, and is

determined by the number of days from harvest until flower senescence, whether or not senescence is considered premature (Wernett ***et al.***, 1996). Similar to bent neck in cut roses, knicking, folding, neck droop or stem break are terms used to describe the sudden bending of the stem in cut gerberas, where bending of the flower stalk, also termed the scape, occurs (van Doorn ***et al.***, 1994), incapable of supporting the weight of the composite flower (capitulum). This senescence contrasts with normal/conventional senescence, where the ligulae of an inflorescence on an upright stem have visibly lost their turgidity.

When cut flowering stems are kept in air an occlusion develops in the lowermost stem segment. The mechanical wounding induced by stem cutting increases the expression of numerous genes and stimulates the activity of a range of enzymes such as phenylalanine ammonia lyase, peroxidase, and ACC oxidase, several of which are involved in the biosynthesis of compounds related to lignin and suberin, serving to impede the entry of micro-organisms into the opened tissue (van Doorn and Cruz, 2000). Traditional rehydration of dried stems has often involved STS, often without result. Regaining turgidity can be improved by the inclusion of a surfactant (Tween-20, Tween-80, Triton X-100 or Nonoxynol-8.5) as has been achieved with roses, ***Bouvardia*** and Cattleya (van Doorn ***et al.***, 1993), although some of them are known to be phytotoxic. $Al_2(SO_4)_3$ has been shown to effectively increase vase-life of tuberose (Reddy and Singh, 1996) while the same compound resulted in an increased respiration rate, reduced rate of photosynthesis and respiration and Chl content of leaves, and damage of both flower and leaf in 'Sonia' rose (Son ***et al.***, 1994). The addition of BA to the latter resulted in a much better and extended vase life of cut roses or chrysanthemum (Petridou ***et al.***, 2001) by retarding the senescence of both leaf and flower, and by increasing fresh weight.

Lysophosphatidylethanolamine (LPE) has been shown to prolong the vase life of cut snapdragon flowers, delaying fresh mass loss, lowering endogenous ethylene levels and reducing ion leaks (Kaur and Palta, 1997). A number of chemical agents inhibit either auxin signal transduction pathway or ethylene formation in plant cells have been effective in controlling the gravitropic response of cut snapdragon flowers (Kim ***et al.***, 1997). The application of ***o***-vanadate, CDTA or $CoCl_2$ application resulted in, in increasing level of effectiveness, the elimination of the gravitropic response.

Cut flowers and foliage destined for desiccation are pulsed with a humectant (such as 20-30% v/v glycerol or glycerine), a process known as uptake preservation (Wills ***et al.***, 1998). Thus, instead of desiccating completely, plant material treated in this way retains a degree of suppleness (plasticity) associated with the humectant and its attraction of water vapour from the atmosphere into the tissue, but often with a resultant browning of tissue, countered by the inclusion of synthetic dyes allowing the flower to look like the fresh product. Effective preservation of plant material by glycerol uptake is achieved through the maintenance of a large VPD through control of atmospheric humidity.

Molecular strategies of extending cut-flower life and countering senescence or PCD

Conventional breeding is still a practical form of increasing the number of flowering buds, extending the longevity of an inflorescence, and improving its postharvest performance, as has

been demonstrated in ***Lilium*** (van der Meulen-Muisers ***et al.***, 1999). Many of the molecular mechanisms underlying senescence, and the respective genes involved in protein degradation, nucleic acid and Chl breakdown, and lipid and nitrogen remobilisation have been extensively covered in other reviews (Buchanan-Wollaston, 1997; Gan and Amasino, 1997). An understanding of these mechanisms is vital to the use of molecular techniques to clone genes of interest to reverse, for example through antisense technology, the detrimental effects of senescence, ageing or PCD. Maternal inheritance of herbicide resistance via chloroplast engineering, or hyper expression of lethal insecticidal proteins (other than the Bt (***Bacillus thuringiensis***) gene product) provide new genetic solutions to bio control of infectious agents in development of phytosanitary control.

PCD in plants is well documented, and not only is it synonymous with senescence (leaf and flower), but is also a fundamental part of a plant's adaptation to stresses, such as ROS. The termination of a flower involves two overlapping mechanisms (Rubinstein, 2000), one being petals that abscise before the majority of their cells initiate a cell death program, and where abscission may occur before or during the mobilization of food reserves to other parts of the plant. In the second, the petals are more persistent, and cell deterioration and food remobilisation occur while the petals are still part of the flower. One way of countering the effects of pathogen-induced PCD is through the use of caspase inhibitors in the cut flower medium (Richael ***et al.***, 2001).

Numerous ethylene-insensitive mutants, such as ***Arabidopsis thaliana etr1-1*** or ***ein-2***, or ***Never ripe*** tomato mutants exist (Zacarias ***et al.***, 1999). Flowers could be engineered to produce reduced levels of ethylene by introduction of an antisense ACC oxidase transgene, as occurs in tomatoes (FLAVR SAVR®), driven by a flower or senescence-specific promoter (John ***et al.***, 1995; Wilkinson ***et al.***, 1997; Bleecker ***et al.***, 1998; Zacarias ***et al.***, 1999). Transgenic fruits containing ACC deaminase and antisense ACC synthase, ACC oxidase and polyphenoloxidase have been produced, the first three reducing ethylene production and slowing ripening, the last reducing browning of damaged tissue (Flores ***et al.***, 2001).

When the endogenous cytokinin status is manipulated through transgenic intervention, a stay-green phenotype can be obtained, as occurred in the fusion of ***ipt***, an ***Agrobacterium*** gene encoding a limiting step in cytokinin biosynthesis, to an ***Arabidopsis See*** (***SAG12***) promoter (Gan and Amasino, 1997). Greenness can also be altered (delay in leaf senescence) by down-regulating the production of a senescence-promoting hormone, as seen in tomato plants in which ethylene biosynthesis is inhibited by antisense suppression of the gene for ACC oxidase (John ***et al.***, 1995).

Concluding remarks

The utilization of optimal flower handling procedures (increased sanitation and innovative preservation through the use of inexpensive and environmentally-friendly products) will result in better appearance and longer life for cut flowers and foliage, and potted plants. Flowers of long-lasting quality mean fewer losses through the handling cycle. Ultimately they mean heightened enjoyment and more satisfaction for and by the consumer. Understanding the biophysical and genetic mechanisms that control the physiological processes in both the flower

parts and leaves will allow for engineering of new, transgenic varieties with longer cut flower life and superior postharvest traits (sustained colour, fragrance, form).

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Abbreviations: abscisic acid, ABA; α-aminooxyacetic acid, AOA; chloroplast, CP; chlorophyll, Chl; gibberellic acid, GA; phaeophorbide ***a*** oxygenase, PaO; plant growth regulator, PGR; plant cell death, PCD; PGR; relative humidity RH; reactive oxygen species, ROS; silver thiosulphate, STS; vapour pressure deficit VPD.