

Flower Development: From Bud to Bloom

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Abstract

In many commercial cut flowers, particularly those with spike or compound inflorescences, postharvest life and quality are highly dependent on the continued development of small buds to open blooms. Buds may be separated into two major types – those enclosed by a calyx, where petal growth is largely complete before the calyx opens or is shed, and those where the petals are naked and expand rapidly prior to opening. Plants employ an interesting range of mechanical systems to facilitate the rapid opening of the petals at anthesis, from the calyptrium of the poppies where the calyx encloses the fully expanded petals until the moment of opening, through the inverted umbrella of the cyclamen, where dramatic changes in cell size result in unfurling and reorientation of the fully grown petals. Growth of young buds of many different cut flowers can be sustained by the simple preservative solutions used in commercial floriculture, indicating that the primary components of the bud are present from very early in development, and that a sugar supply is all that is required to drive floral development. The rapid expansion that precedes or accompanies flower opening is usually associated with increased soluble sugar content of the petal cells. This change, which presumably provides the turgor necessary for growth, may be at the expense of stored complex carbohydrates (starch or inulin), or may reflect import of sugars from the plant or the vase solution. We have demonstrated changes in the expression of invertase genes during floral development of the ephemeral flowers of Four O'clock (*Mirabilis jalapa*) that correlate with the onset of rapid flower growth and suggest that sucrose metabolism may be a key component of the sink strength of the developing bud. Rapid growth of floral organs requires changes in the size and shape of the cell walls, and we have also demonstrated dramatic changes in the expression of genes encoding expansins, proteins associated with rapid expansion growth in other plant organs, during the growth of *M. jalapa* corollas.

INTRODUCTION

The phase of flower development from mature bud to open flower encompasses one of the most active growth periods in all of plant development. Calyces unzip, abscise or burst, stamens extend, anthers dehisce, and petals expand and re-orientate. The net result, for animal-pollinated flowers, is the deployment of an apparatus to attract the attention of desired pollinators. For horticulturists and consumers, too, flower development and opening is critical to providing attractive blooms. The vase life and quality of many flowers, particularly those cut as spikes or tight buds is a function of continued and adequate development and opening of young buds (Evans and Reid, 1986). van Doorn and van Meeteren (2003) recently published a comprehensive review of the anatomy, physiology, and biochemistry of flower opening. In this paper I briefly review the findings of research in this area that have been conducted at Davis over the past two decades.

RESULTS

Timing

Floral opening is timed to ensure optimum exposure to the preferred pollinators, and flowers therefore show precise control of opening, anther dehiscence, and stigma

receptivity, usually in response to environmental cues such as light, temperature, or relative humidity. In many flowers, opening is under some type of photoperiodic control. Daylilies (*Hemerocallis*) open at midnight (Lukaszewski and Reid, 1989), Four O'clock (*Mirabilis*) in the late afternoon (Gookin et al., 2003), and roses open just before dawn. In a detailed analysis of rose opening, Evans (1987) demonstrated that petal expansion in the multi-whorled commercial rose was sequential, commencing with the outer whorl of petals, and involved both re-orientation of the petals and petal expansion. Opening was cyclical, commencing just before dawn and continuing for a few hours, then re-commencing at the end of the following dark period. The rhythm could be entrained to different photoperiods, although an underlying diurnal rhythm tended to persist. Continuous light or darkness resulted in a loss of the cyclic rhythm, and a failure of the flowers to open fully. The photoperiod was apparently perceived in the petals, since removing or covering the leaves did not change the rhythm, and disks cut from young petals continued to show the rhythm in expansion.

Release from the Calyx

For many flowers, the deployment of the corolla is a remarkably rapid event following release from the enveloping calyx. This is perhaps most spectacular in the poppies. In the California poppy, *Eschscholzia californica*, the fused calyx or calyptra abscises at its base, resulting in rapid release of the fully expanded petals (Fig. 1). In many flowers, the calyx splits between the lobes, probably with the development of an abscission zone. In *Iris*, growth of the pedicel and ovary tissues pushes the fusiform bud through the enveloping leaves, thereby permitting the tepals to unfold (Evans and Reid, 1986).

Expansion

Expansion of the petals, which may occur before or after release from the calyx, is often extremely rapid, particularly in ephemeral flowers (Gookin et al., 2003). For example, the opening of *Mirabilis* flowers is accompanied by a doubling in flower fresh weight in a matter of a few hours (Fig. 2). This rapid growth, clearly a result of increased cell volume, results from an increase in this rapid growth, clearly a result of increased cell volume, results from an increase in solutes in the petal cells and may also involve loosening of the cell wall. In rose petals, changes in solute concentrations (largely the result of hydrolysis of petal starch to sugar) were largely independent of the cyclic pattern of growth of the petals (Evans and Reid, 1988), indicating that either wall extensibility or hydraulic conductance of the cells were responsible for the cyclic growth pattern. Wall extensibility and wall pH both showed cyclic changes consistent with an acid-mediated wall loosening during rose petal growth (Evans, 1987).

In Four 'clock flowers, the onset of rapid growth is associated with a dramatic increase in expression of genes with high homology to Type 2 expansins (Gookin et al., 2003). Expansins are wall-associated proteins that have been shown to be associated with wall loosening in rapid growth responses (Cosgrove, 2000), and the dramatic increase in their transcript abundance in expanding four o'clock corollas is further evidence that wall loosening is an important part of cell growth during flower opening.

The carbohydrates required to drive petal expansion may derive from stored carbohydrate (as in rose petals) and/or imported carbohydrate. In daylilies, petal opening involves the hydrolysis of a stored fructan (Bialeski, 1993), whereas the sugars in Four O'clock flowers are primarily imported just prior to and during corolla growth (Meir et al., in preparation). In the latter case, it appears probable that changes in invertase, shown years ago to be associated with the opening of morning glory flowers (Winkenbach, 1971), are associated with increased sink strength and sugar import into the developing corolla (Meir et al., In preparation).

Unfolding

The unfolding of flower petals often involves differential growth of corolla

tissues, changes in orientation at the base of the petals, or even a separation process. In oriental lilies, an intricate 'tongue and groove' system joins the outer and inner tepals (Fig 3) and opening involves separation of the tissues in a fashion not dissimilar to the opening of a zip lock bag. Cyclamen flowers open with an unfurling and remarkable reorientation of the petals (Fig 4 a,b). During this process, tissues at the base of the corolla reflex through more than 270° (Fig 4 c,d), due, apparently to rapid expansion of a layer of cells on the adaxial epidermis at the base of the corolla (Fig 4 e,f).

DISCUSSION

Much has been learned about the biologically and commercially important processes of bud opening and development. However, the diversity of floral behavior cataloged here, and in van Doorn and van Meeteren's (2003) review makes it clear that model systems will illuminate only the most general features of floral opening. Detailed anatomical, physiological, biochemical, and molecular studies will be required to fully understand the control of flower development in individual genera, species, and perhaps even cultivars.

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Figures

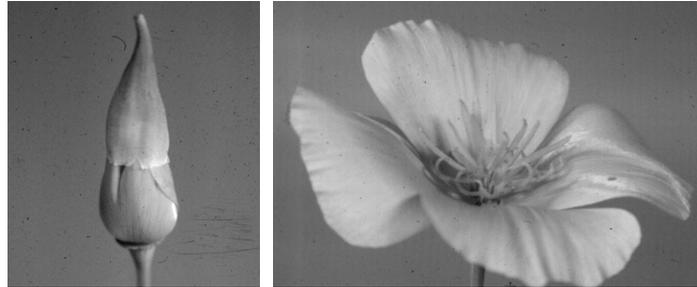


Fig. 1. The opening of California poppies involves abscission at the base of the calpytra.

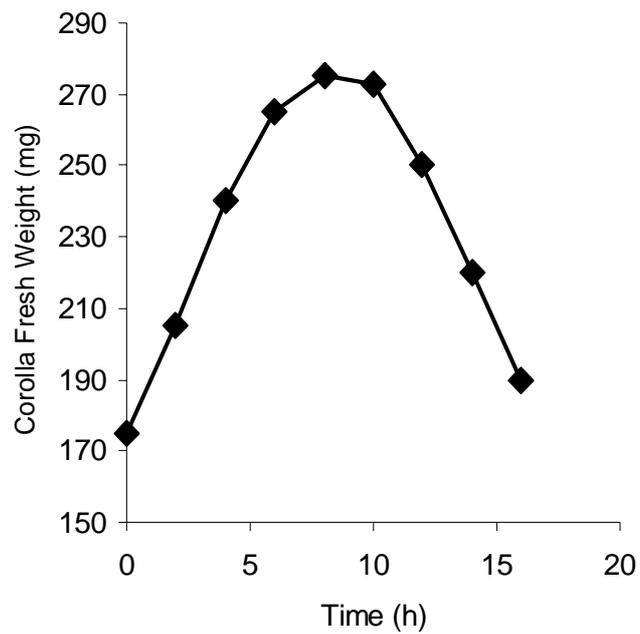


Fig. 2. Changes in fresh weight during the opening of corollas of Four O'clock (*Mirabilis jalapa*) flowers

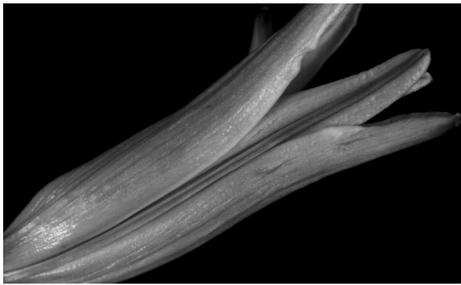


Fig. 3. The inner and outer tepals of Oriental lilies are joined, in the bud, by a tongue and groove system. Lower image is a micrograph of a transverse section of the junction.

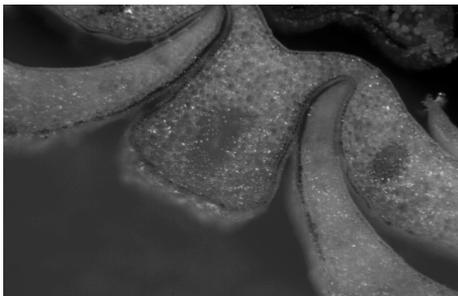


Fig. 4. When cyclamen buds open, the petals unfurl and reflex (a,b), associated with bending of the basal petal tissues (c,d), probably as a result of rapid growth of cells in the adaxial epidermis (e, f, insert). Left panels from buds, right panels from open flowers.

