Some Observations on the Very Rapid Abscission of the Petals of *Geranium robertianum* L.

R. Sexton*,1, W. A. Struthers1, and L. N. Lewis2

1 Department of Biology, University of Stirling, Stirling
2 University of California Systemwide Administration, U.C. Berkeley, Berkeley, California

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Summary

The petals of young flowers of *Geranium robertianum* L. start to be shed 2.25 hours after exposure to 20 ppm ethylene whilst controls kept in air take approximately 8 hours longer. The detachment of the petal takes place at its junction with the receptacle. The cells in the region show evidence of cell wall degradation and fracture takes place by loss of cell cohesion along the line of the middle lamella. The petal base is surrounded by a canal of receptacle tissues which alter shape either during or immediately after fracture. It is proposed that these structural changes may produce stresses which facilitate fracture.

Keywords: Abscission; Ethylene; Petals; *Geranium robertianum*; Cell-wall breakdown.

1. Introduction

The term abscission refers to the mechanism whereby a wide variety of structures can be shed from the main plants axis. This process not only includes the more familiar loss of leaves, fruits and floral parts (Addicott 1982) but also structures which range in size from the complete aerial system of tumble weeds (Becker 1968) down to the shedding of individual glands and hairs from developing leaves (Sifton 1963). Most workers in this field have come to believe that a common weakening process is involved in the majority of these examples. This depends on the breakdown of cell walls and loss of cell cohesion in a separation layer across the base of the structure to be shed (Webster 1973, Addicott and Wiatr 1977, Sexton and Roberts 1982). Both β1:4 glucan 4 glucan hydrolases and polygalacturonases have been implicated in the wall hydrolysis (reviewed, Abeles et al. 1971, Osborne 1973, Addicott and Wiatr 1977, Huberman and Goren 1979, Sexton and Roberts 1982) and the removal of calcium may also play some part (Stösser et al. 1969).

The synthesis and secretion of these wall degrading enzymes depends on a period of essential RNA and protein synthesis which precedes their appearance in the cytoplasm (reviewed, Abeles et al. 1971, Abeles 1973, Osborne 1973, Addicott and Wiatr 1977, Sexton and Roberts 1982).

Over the last 80 years the majority of observations have been consistent with the idea that enzyme hydrolysis was of central importance in wall breakdown, however the literature has consistently ignored the observations of Fitting (1911) which challenge this view. Fitting demonstrated that the petals of a wide variety of plant species were shed only a few minutes after administering a range of inductive stimuli (i.e., illuminating gas, tobacco smoke, high temperatures, high CO₂, chloroform, mechanical wounding). He pointed out that it was very unlikely that enzyme synthesis and breakdown of the wall could take place in so short a time, a conclusion which few would challenge some 70 years later.

Darwin (1877) had earlier demonstrated that corolla...
abscission in *Verbascum thapsus* would take place some 2-3 minutes after shaking the plant. This rapid abscission was attributed to the fact that the process was well under way when the stimulus was given. *Fitting* was therefore aware that the same criticism could be levelled at his own findings. As a consequence he took great care to use very young flowers with unopened stigmatic surfaces. The latter were chosen because they were insensitive to pollination, a process known to accelerate natural petal fall (*Fitting* 1911, *Kendall* 1918, *Stead* and *Moore* 1979).

Another explanation for these anomalous findings was that mechanical forces were responsible for fracture rather than breakdown of the cell walls. *Reiche* (1885) had shown that the sudden growth of the ovary after fertilisation without a parallel expansion of the petal bases could lead to the development of forces across the transition region which would tear the tissues apart. *Fitting* demonstrated however that if geranium petals were torn away from their point of attachment the cells on the fracture surfaces were broken in contrast to the rounded turgid cells found after abscission. He concluded that the cells separated along the line of the middle lamella though he could find no evidence of the wall swelling or gelatinisation that characterised wall breakdown.

In view of the controversial nature of these results we have attempted to repeat *Fitting’s* findings using *Geranium robertianum* L. as an experimental material. *Geranium* species were used in the majority of *Fitting’s* experiments, indeed the ease with which they shed their flowers is a problem for commercial growers (*Armitage et al.* 1980).

### 2. Materials and Methods

Flowering shoots of *Geranium robertianum* L. were gathered from the Stirling University campus at approximately 7.30 a.m. every morning throughout June and July 1981. Flower buds that were just opening were selected and carried back to the laboratory with their cut ends in water. Approximately one hour later the shoots were placed in beakers of water in perspex chambers 24.4 dm³ in volume through which ethylene 20 ppm or ethylene free air were passed at the rate of 1 dm³ hr⁻¹ (*Durbin et al.* 1980). The numbers of petals that had fallen were recorded at 15 minutes intervals. Between 50 and 100 flowering shoots were used in each time course. Sections for light microscopy were prepared and stained for carbohydrates with the periodic acid Schiff’s method (*Sexton* 1979). Uncoated frozen specimens were used for scanning electron microscopy (*Sexton* 1976) since critical point drying was judged to cause considerable distortion to the surface topography. The methods for TEM have also been described previously (*Sexton et al.* 1977).

### 3. Results

#### 3.1. The Time Course

The results depicted in Fig. 1 show a typical time course of petal abscission in the presence and absence of 20 ppm ethylene. Ethylene rapidly accelerates the abscission process, all the petals being shed in 4 hours whilst controls took 24-36 hours to reach the same end point. Under the conditions of this experiment the first petals fell between 2.25 hours and 2.5 hours, a rather longer time course than those recorded by *Fitting* (1911). Attempts were made to shorten this time by increasing the temperature to 30 °C and increasing the ethylene concentration to 100 ppm. Whilst these treatments marginally shortened the lag before first petal fall, significant numbers were never shed before 2.25 hours.

![Fig. 1. Plot of percentage abscission of *G. robertianum* petals against time. The stems were exposed to either 20 ppm ethylene or ethylene free air which was pumped through perspex cabinets at the rate of 11 min⁻¹. This experiment was carried out at 23 °C.](image)

#### 3.2. Morphological Observations

Abscission occurs as a result of a fracture line which forms where the petal base joins the tissues of the receptacle (*cf.*, Figs. 2 with 3, Figs. 6 with 7). Some 150 µm above this junction the petal base is swollen, the bulbous outgrowth being confined to the petal face away from the centre of the flower (Figs. 2, 6, and 9).