

SHORT COMMUNICATION

Anther dehiscence in two-rowed barley (*Hordeum distichum*) triggered by mechanical stimulation

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Abstract

Pricking or pressing an ovary can induce anther dehiscence in cleistogamous two-rowed barley in the absence of lodicule swelling. This response is considered to be inherited from a chasmogamous ancestor in which anther dehiscence is induced by the stimulus given to the pistil by the lodicule swelling, which causes floret opening.

Key words: Anther dehiscence, floret opening, sensory organ, trigger, two-rowed barley.

Introduction

In many plants, including some poaceous plants such as rice and wheat, anthers dehisce at the time of flower opening. Historically, it has been believed that anther dehiscence is a consequence of desiccation (Schmid, 1976), probably because of the synchrony between anther exposure to ambient air and dehiscence. However, it has been proposed (Cheng *et al.*, 1979, 1986), on the basis of SEM and TEM observations of the anther cuticle, that in *Zea mays* the tensile force generated by a shortening of the outer circumference of the microsporangia is the driving force for septum rupture. Bonner and Dickinson concluded that in *Lycopersicon esculentum*, anther dehiscence is not a simple desiccatory process (Bonner and Dickinson, 1990) and Keijzer showed that in liliaceous plants swelling of pollen, imbibition of anther wall cells, and lysis of the septum are responsible for anther dehiscence (Keijzer, 1987). Recently, Matsui *et al.* demonstrated that rapid swelling (within a few minutes) of pollen grains in response to artificial floret opening is the driving force to open the locules and results in anther

dehiscence in *Oryza sativa* (Matsui *et al.*, 1999a, b) and *Hordeum distichum* (Matsui *et al.*, 2000). Detailed studies have clarified that desiccation of the anther is not the direct driving force for anther dehiscence (see review by Keijzer, 1999) and the mechanism responsible for co-ordinating the phenomenon with the time of flower opening remains unknown.

The observations by Matsui *et al.* (Matsui *et al.*, 1999a, b, 2000) suggests that synchrony between anther exposure and dehiscence is due to some stimulus associated with floret opening. A relationship between mechanical stimuli and anthesis was first reported in the Poaceae over a century ago (Tschermak, 1890). It is reported here that a stimulus, similar to removal of the lemma, induces anther dehiscence in cleistogamous two-rowed barley. How this might trigger anther dehiscence and the phenomenon synchronized with floret opening is discussed.

Materials and methods

Plant materials

Cleistogamous two-rowed barley (*Hordeum distichum* L. emend. LAM. cv. Saikaikawa-24), grown under field conditions (Kyoto University, Experimental Farm, Osaka, Japan) from November to May was used. The heading period was from the end of March to mid-April. Florets with indehisced anthers that can dehisce in response to the removal of the lemma (referred to as mature anthers hereafter) were selected for this experiment. Such florets were selected by observing the sequence of anthesis on a panicle. In the same panicle, anthesis occurs from the middle position toward both apical and basal ends (Hoshikawa, 1980). This sequence of anthesis corresponds with the order of anther maturity: the anthers in the florets that pollinate earlier have a higher ability to dehisce than those in the florets that pollinate later (Matsui *et al.*, 2000). Anther maturity was determined as follows. A floret in which the anthers had not dehisced was detached from the panicle, the lemma of the floret

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was removed and the anthers that dehisced within 5 min were regarded as mature anthers.

Search for triggers and sensory organs of the anther dehiscence

The following treatments were given to the florets with mature anthers without detaching them from the panicle (Fig. 1). (1) Cut the glumes above the anthers with scissors, (2) pierce the glumes above the anthers with a needle, (3) pierce the glumes beside the anthers with a needle, (4) prick the anther through the lemma with a needle, (5) prick the ovary through the lemma with a needle, and (6) press the pistil from the side over the lemma at 10, 20, 30, 40, and 50 g per 28 mm² (a circle 3 mm in diameter). Five minutes after the treatments, the dehiscence of the anthers was examined. The test was repeated 10 times for each treatment.

Results and discussion

Matsui *et al.* reported that, in the florets of two-rowed barley, the removal of the lemma induces the pollen swelling that causes anther dehiscence (Matsui *et al.*, 2000). This suggests that some stimulus given to the floral organs at the time of lemma removal induces anther dehiscence. The stimulus may be classified into the following three categories. (1) Injury around the base of the pistil; (2) friction between the lemma and the palea; (3) changes of gaseous and light conditions inside the floret. In the experiments in Table 1, pricking of an anther and the ovary induced dehiscence whereas cutting or piercing of the glumes did not. These results rule out the possibility that any change in exogenous gaseous or light conditions in the floret or the mechanical stimulation given to the glumes *per se* induces dehiscence, and suggest that the

removal of the lemma triggers the phenomenon through injury of the base of the pistil.

A maize anther dehisces at the time of floret opening and it has been proposed that the endogenous carbon dioxide concentration in the flower bud of maize determines the time of anthesis and that production of the gas from the respiring pollen might provide an explanation of why the septum and stomium should be open just before anthesis (Keijzer, 1999). Despite such a possible role in anthesis, the present results suggest that carbon dioxide would not be the trigger of anther dehiscence. However, any role of ethylene, produced due to damaging the ovular base, cannot be excluded.

Anther dehiscence induced by removal of the lemma was observed also in rice (Matsui *et al.*, 1999b). This indicates that similar mechanisms may trigger anther dehiscence in rice and two-rowed barley. In natural flowering of rice, swelling of the lodicules at the base of the pistil is considered to force the glumes to open, but it also may press the pistil, causing anther dehiscence at the time of floret opening. A similar mechanism may be involved in the synchronous floret opening and anther dehiscence in wheat. To test the possibility that such pressure to the base of the pistil can trigger anther dehiscence, the effect of pressure applied to the pistil on barley dehiscence was examined. As shown in Table 2, pressure applied to the pistil induced anther dehiscence. Although the percentage of dehisced anthers increased gradually as the pressure applied to the pistil was increased, the percentage of dehisced anthers in each floret was either 0% or 100%. This suggests that a threshold pressure applied to the pistil may trigger anther dehiscence. If the pressure given by the swelling of lodicules to the pistil is above the threshold level, it may induce anther dehiscence. This may explain the synchrony in rice between anther dehiscence and floret opening.

The mature anthers of rice dehisce in response to cutting of the glume tip (Matsui *et al.*, 1999a). In two-rowed barley, cutting of the glume tip did not cause anther dehiscence (Table 1), but cutting with blunt scissors induced anther dehiscence (data not shown). This is probably because the pulling of the glumes act as a stimulus at the base of pistil. It is, therefore, supposed that the rice floret is more susceptible to a mechanical stimulus given to the base of pistil. It is generally known that, just before anthesis, the lodicules of rice are very sensitive to mechanical stimuli given to the glume, such as rubbing, vibration and even air pressure and that the lodicules swell rapidly in these cases. The rice lodicules may respond to a slight stimulus given to the glume, and transmit the information to the pistil as pressure thus causing anther dehiscence.

Lodicules in the cleistogamous two-rowed barley have no swelling ability. Therefore, mechanical stimulation that triggers anther dehiscence may not be given to the

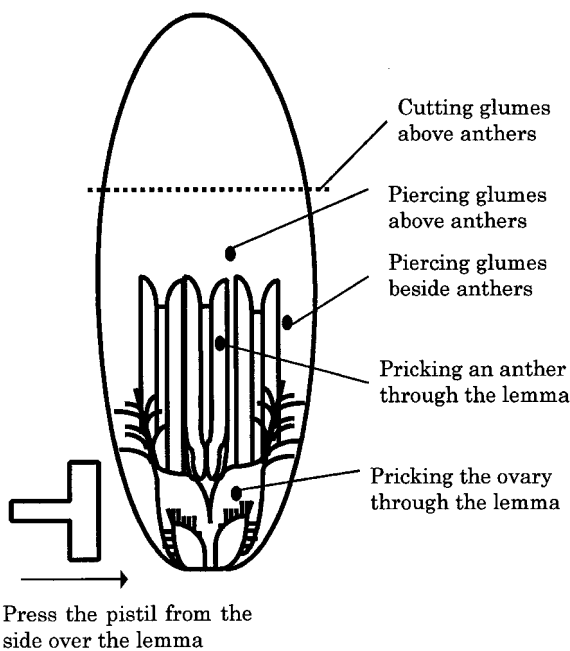


Fig. 1. The stimuli given to the floral organs.

Table 1. The effect of injury to floral organs on anther dehiscence

Treatment/position	Cutting glumes		Piercing glumes		Pricking through lemma	
	Above anthers		Above anthers	Beside anthers	Anther	Ovary
Percentage of dehisced anthers	0	0	0	0	100	100

Table 2. The effect of pressure applied to the pistil over lemma on anther dehiscence

Pressure applied (g per 28 mm ²)	Percentage of florets		
	All anthers indehisced	All anthers dehisced	Others ^a
10	100	0	0
20	90	10	0
30	60	40	0
40	30	70	0
50	0	100	0

^aFlorets of which anthers partly dehisced.

pistil or stamen in the two-rowed barley under natural conditions. The two-rowed barley may not require rapid anther dehiscence (because it is cleistogamous). Nevertheless, the anther of two-rowed barley dehisced rapidly in response to the mechanical stimulus applied to the pistil or stamen. The ability of anthers to dehisce in response to such mechanical stimuli seems to be inherited from a chasmogamous ancestor. Actually, a floret of four-rowed barley (*H. tetrastichum*) opens and its anthers dehisce just after opening.

In some poaceous autogamous crops, such as rice, anthers dehisce at the time of floret opening under natural conditions probably by the mechanism mentioned above. The synchrony between anther dehiscence and floret opening would be favoured to maintain a high self-fertilization rate (Hoshikawa, 1993). Plants may have evolved to increase their self-pollination rate if the decrease of viability by inbreeding depression is small relative to the costs of cross pollination, because the mutation with a high self-fertilization rate is advantageous (Lande and Schemske, 1985; Schemske and Lande, 1985) especially in anemophilous species (Aide, 1986). The response of the anther to floret opening, therefore, may have evolved to hasten the perfect self-fertilization. However, there are few reports on the rapid action of the stamen in such gravity-pollination systems. The rapid response may not be essential for the high self-pollination rate because it can be maintained by another system, for example, anther dehiscence before floret opening or cleistogamy. On the other hand, floral organs sensitive to mechanical stimuli are observed in entomophilous genera, such as *Portulaca* (Jaffe *et al.*, 1977), *Berberis* and *Mahonia* (Percival, 1965). The rapid response of the stamen to the mechanical stimulus seems to help the vector, such as wind and insects, to carry the pollen

efficiently. The poaceous autogamous crops may have inherited these functions from an ancestor with a cross-pollination system.

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