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Cleistogamy in wheat: genetic control and the effect of environmental conditions

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Summary

Wheat flowers are generally observed first in the middle of the spike. After pollination, the anthers grow out of the floret. In general, wheat flowers are open (chasmogamy). However, in several varieties the flowers remain closed (cleistogamy). In this study, we surveyed the genetic control of and influence of environmental conditions on cleistogamy.

It appeared that cleistogamy was controlled by three recessive genes and cleistogamous plants tended to have short spikes. Although scarcely any extruded anthers were on field-grown cleistogamous plants, culture of spikes at 10 ℃ or 20 ℃ yielded an increased number of extruded anthers. The number of extruded anthers tended to be higher under illumination than in darkness, but the difference was not significant.

Key words: cleistogamy, culture, flowering trait, genetic control, wheat

Introduction

Several plant species have mixed reproductive strategies. The proportion of cleistogamous and chasmogamous flowers has been reported to be modified by soil moisture, light intensity, fertilization of soil and plant density (Le Corff 1993, Mattila and Salonen 1995). Less attention has been paid to cleistogamy of crop plants, but Frederickson et al. (1994) emphasized that cleistogamy is a desirable characteristic for avoidance of ergot infection in sorghum.

Wheat plants are self-reproducing and flower about one week after heading. The first spikelet that flowers is generally in the middle of the spike. During the opening of the flowers, the filaments of the stamens elongate and, after the pollination, the anthers extend from the floret. It has been reported that low temperatures, rain and protracted dry heat influence the opening of wheat flowers. Moreover, the effects of weather on the opening of flowers depend on the genotypes. The opening of flowers is closely related to production of hybrid seeds and the floral biology of wheat has been clearly summarized (DeVries 1971). However, the available data on cleistogamy of wheat flowers are rather limited.

In this study, we identified varieties of wheat that exhibit cleistogamy and then we examined its genetic control, its relationship to agronomic characteristics, and effects of environmental conditions on the opening of flowers.

Material and Methods

Field experiment: The Haruyutaka (Japan) and Corringin (Australia) varieties and the F_1 and F_2

progeny of crosses between them were planted in the field at the Faculty of Bioindustry, Tokyo University of Agriculture, Hokkaido, in 1994. Seeds were sown on April 28, with 50 cm between rows and 10 cm spacing between plants. Before planting, a compound fertilizer (6-22.5-17.5%, N- P_2O_5 -K_2O) was applied at a rate of 100 g m^{-2}. After heading, plants were checked daily for cleistogamy until we were able to recognize flowers developed to seeds. Culm length, spike length and spikelet number were measured for all the matured materials.

On May 1, 1996, seeds from a total of 487 varieties of wheat, collected from various countries, were planted in the same manner as described above, with the exception of the formulation of the compound fertilizer (8-30-17%, N- P_2O_5 -K_2O). Ten seeds of each variety were planted. After heading, cleistogamous varieties were identified.

Environmental effects on cleistogamy: The effects of environmental conditions on cleistogamy were analyzed in 1996, using spikes of the Corringin variety. When a terminal spikelet of a field-grown plant had emerged from the flag leaf sheath, the stem was cut in the middle of the second internode. The basal part of the detached spike was placed in a conical beaker with 150 ml of a culture solution that contained 100 g l^{-1} sucrose, inorganic salts of Murashige and Skoog's medium and 0.075% sulfurous acid as an antiseptic (Kato et al. 1996). Spikes were cultured at 10 ℃, 20 ℃ and 30 ℃ under illumination (12,700 lux at plant level). In the case of culture at 20 ℃, detached spikes were also incubated in continuous darkness. Five spikes were placed in a conical beaker for each treatment, and kept in an incubator for 3 days. A 7-day culture was also performed at 10℃. To evaluate the effects of the various treatments on cleistogamy, the number of extruded anthers was counted. At anthesis, five field-grown plants were also checked for the numbers of extruded anthers. All experiments were performed with two replicates.

Results and Discussion

Table 1 shows the agronomic characteristics of the cleistogamous varieties of wheat. Cleistogamy were found in varieties from the Xinjiang Uygur district of China, from Greece and from Australia. Compared with Haruyutaka, the spikes of U56, IL416 and Corringin were shorter, but spikes of U24 were about the same length as those of Haruyutaka.

Table 1. Agronomic characteristics of cleistogamous varieties.

Variety	Culm length(cm)	Spike length(mm)	Spikelet number	Heading date*
U24 (China)	66.2	97.0	15.8	78
U56 (China)	103.0	58.0	15.8	85
IL416 (Greece)	81.2	48.2	12.4	78
Corringin (Australia)	74.0	37.4	15.2	78
H** (Japan)	66.8	86.8	13.2	76

* ..... Days after sowing

** ..... Haruyutaka is a chasmogamous variety. Data are presented for comparison.

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Table 2.

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Table 2. Effects of environmental conditions on cleistogamy.

Treatment	Number of anthers/spike	Number of spikelets/spike
10℃, illuminated*	0.1	16.6
10℃, illuminated**	4.6	16.6
20℃, illuminated*	6.9	17.1
20℃, darkness*	4.0	16.4
30℃, illuminated*	0.2	16.3
Field	0.9	16.8

* ····· Cultured for 3 days

** ····· Cultured for 7 days

daily maximum, average and minimum temperatures in July 1996, in Abashiri, were 19.7, 16.2 and 13.4℃, respectively. Since Corringin headed on July 18, absence of extrusion of anthers on field-grown plants cannot be ascribed to higher temperatures. Some factor other than temperature might effect anther extrusion in Corringin. Drought and rain are known to increase the numbers of cleistogamous flowers in wheat (DeVries 1971). The relative humidity of cultures at 30℃ was lower than at other temperatures. Although the numbers of extruded anthers were lowest at 30℃ in culture, the effects of the low humidity at 30℃ cannot be ruled out. Since seeds were formed during culture at 30 ℃, fertilization and pollination should be accomplished normally in culture of 30℃.

Leighty and Hutcheson (1919) monitored the timing of flowering of wheat during entire 24-h periods. They found two periods of extensive flowering during the daytime. The number of extruded anthers tended to be higher under illumination than in the darkness (Table 2). However, the difference was not significant. These observations suggest that, although light does not affect flowering of wheat, some autonomous factor such as periodism might exist.

Acknowledgements

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Figure 1 shows the frequency distribution of spike lengths and flowering traits for the F_2 generation of Corringin x Haruyutaka. Spike length showed a bimodal distribution, with a minimum frequency around 70 mm. The distribution corresponded segregation ratio that was controlled by a major gene (< 70 mm : >70 mm = 347:112, χ^2=0.088). F_1 hybrids between a cleistogamous variety (Corringin) and a chasmogamous variety (Haruyutaka) exhibited chasmogamy. Since nine of the 459 F_2 plants exhibited cleistogamy (Figure 1), the distribution fitted a segregation ratio of 63:1 (χ^2=0.475). Thus, cleistogamy seemed to be controlled by three recessive genes. All of the cleistogamous plants had spikes shorter than 70 mm in length. Three of the four cleistogamous varieties had short spikes. These observations suggest a relationship between cleistogamy and spike length. However, since short spike varieties are not always cleistogamy and a cleistogamous variety with longer spike length was found (U24), it remains unclear how cleistogamy is related to spike length. Experiments using several combinations of crosses between cleistogamous and chasmogamous varieties might shed some light on this issue.

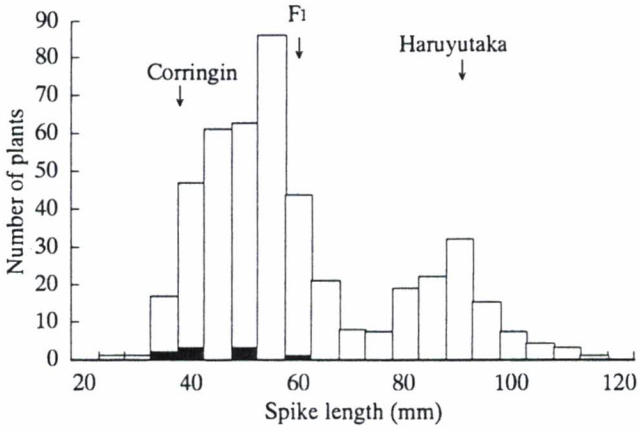

Figure 1. Frequency distributions of spike lengths and flowering traits in the F_2 generation of Corringin x Haruyutaka.

□: Chasmogamous plants
■: Cleistogamous plants

Table 2 shows the effects of environmental conditions on cleistogamy. There were scarcely any anthers on field-grown plants. By contrast, spikes cultured at 20 ℃ had numerous extruded anthers. Although a three-day culture at 10℃ caused extrusion of only small numbers of anther, seven days in culture yielded as many anthers as culture of 20 ℃ for three days. Low temperature might merely decrease the rate of development of flowers. Numbers of

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