Studies on Leaf Orientation Movements in Kidney Beans (*Phaseolus vulgaris* L.)

II. Difference among cultivars and the inheritance*

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Abstract : A study was conducted to examine the differences among cultivars and the nature of inheritance in the leaf orientation movements of kidney bean (*Phaseolus vulgaris* L.). The left leaflet of the first or second trifoliate leaf of each plant grown in a pot was exposed to the artificial light. The plant was exposed to the light at an angle of 30 degrees from the horizontal onto the pulvinule and leaf blade from the base of the leaflet. Changes of vertical (up- and down-ward) and twisting (rotative on midrib) angles of each leaflet were measured during the period of light exposure. Four cultivars examined were classified into two types : one oriented the leaflet surface more perpendicularly toward the incoming light, and the other oriented more parallel toward the light. In the former type a considerable change in the vertical angle was also observed, and such a cultivar was designated as "Vertical type"; while a great change in the twisting angle was seen in the latter, which was therefore designated as "Twisting type". These two movements were seemingly, although imperfectly, independent of each other. The leaflet orientation movements of the vertical type appeared to be controlled by two kinds of dominant genetic factors with extensive modifiers, which give the plant leaflet a large vertical and small twisting movements.

Key words : Artificial light, Cultivar, Inheritance, Leaf movement, *Phaseolus vulgaris* L., Twisting type, Vertical type.

インゲンマメの葉の調位運動に関する研究 第2報 品種間差異およびその遺伝性について：佐藤 肇
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要 旨：インゲンマメの4品種とこれらの組合せによる F₁ および F₂ 雑種を用いて、葉の調位運動における品種間の差異とその遺伝性を検討した。ポット栽培した供試個体の第1あるいは第2本葉の左側小葉に人工光を継続的に照射して、その「上下傾斜角」と「横向き傾斜角」を測定した。得られた結果の要点は、以下のとおりである。

4つの品種における小葉は、「上下傾斜角」が大きく、しかも入射光と葉面法線となす角度が、著しく小さくなる方向に傾斜するものと、「横向き傾斜角」が大きく、入射光との角度が大きくなるものの、2つのタイプに大別された。前者の品種を「上下傾斜型」、後者を「横向き傾斜型」と呼ぶことにした。

「上下傾斜型」と「横向き傾斜型」の品種を両親とする2組の F₁ 雑種は、ともに「上下傾斜型」の親と等しい葉面傾斜を示し、「上下傾斜型」の運動が「横向き傾斜型」に対して、遺伝的に優性とみられた。2組の F₂ 集団における「上下傾斜角」と「横向き傾斜角」の分布によって、これらの傾斜角の変化に関わる因子は極めて密接な関係にあるが、互いに独立的であることが示唆された。また「上下傾斜型」の小葉運動は、大きな「上下傾斜角」と小さな「横向き傾斜角」をもたらす、修正効果を伴う2種類の優性主働因子によって支配されているようにみうけられた。

キーワード：遺伝性、インゲンマメ、上下傾斜型、人工光、調位運動、品種、横向き傾斜型。

Light is necessary to induce the leaf orientation movements in leguminous plants. The pulvinule of leaflet receives the stimulus of light^{4,5,14,15)}, but there is a report stating that the leaf blade is also a receptor of light¹¹⁾. The inclination angle of the leaflet in soybean⁶⁾ and kidney bean¹¹⁾ is changed by the level of light intensity. In addition, many investigations^{1,2,3,8,9,13)} indicated that water stress causes plant leaves to move so as to

avoid light. These facts imply that the movement of leaf surface is influenced by some environmental factors.

Wien and Wallace¹⁵⁾, on the other hand, have reported that there are some variations in vertical changes of leaflets among cultivars of dry bean. A similar variation was indicated as the movement of the leaf surface in three-dimensional space^{10,16)}.

The present study was conducted to obtain farther information about the differences in the leaf orientation movements among kidney bean cultivars, and to study inheritance of the

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observed differences.

Materials and Methods

To ensure uniform development of the seedlings, seeds of kidney bean (*Phaseolus vulgaris* L.) were germinated at 30°C until the radicles were 1 cm in length. Plants were grown in pots until the first or second trifoliate leaves expanded perfectly. Two experiments were conducted.

In the first experiment, four kidney bean cultivars, Taisho-kintoki, Hime-tebo, Mexico 489 and Dneprovskaja Bomba, were used to make the difference in the leaf orientation movements among cultivars apparent. Each plant was grown in a plastic pot of 3.7-liter capacity containing the soil. Fertilizers of N, P₂O₅, K₂O and lime were applied at 0.1, 0.28, 0.2 and 0.2 g/pot, respectively. The leaf movements of five plants of each cultivar were measured under 30 and 80 klx of artificial light at a temperature of about 25°C.

The second experiment was conducted to investigate the inheritance of leaf orientation movements among kidney bean cultivars. The F₁ and F₂ progenies of two crosses, Taisho-kintoki × Mexico 489 and Hime-tebo × Dneprovskaja Bomba, were tested. Each plant was grown in a pot of 1.4-liter capacity containing a mixture of soil and barnyard manure (4:1). Fertilizers were added to the soil mixture at 0.24, 0.72, 0.30 and 0.24 g/pot of N, P₂O₅, K₂O and lime, respectively. Ten plants of each parent, 10 plants of F₁ population, and 60 plants of F₂ population were examined under the illumination of 40 klx at 25 to 30°C of air temperature.

The apparatus and methods used to determine the leaf orientation movements were similar to those described in the previous paper¹¹⁾. Left leaflets in the first or second trifoliate leaves were used in this study. The artificial light was directed at an angle of 30 degrees from the horizontal onto the pulvinule and leaf blade from the base of the left leaflet. The vertical (up- and downward) and twisting (rotative on the midrib) angles were measured for each left leaflet of the trifoliate leaves. The angles of the leaflets were recorded at 10 minutes intervals during 90 minutes of continuous light exposure in the first experiment and 60 minutes in the second one, in which case the horizontal level was expressed

as zero degree.

In the first experiment, the angles between the leaflet normal and incoming light were calculated from the vertical, twisting and direction angles of the leaflet. Although it was not measured, the direction angle was assumed to be opposite to the incoming light and not to change throughout the lighting period.

Results and Discussion

Response curves defined by the vertical and twisting angles of the left leaflets are presented graphically in Fig. 1. There were, obviously with time, differences in both vertical and twisting angles among cultivars. The vertical angle changed more largely in Hime-tebo and Mexico 489 than in Taisho-kintoki and Dneprovskaja Bomba. The twisting angle of the latter cultivars, however, changed more largely than those of the formers. The characters of Taisho-kintoki and Hime-tebo agreed with the result reported in the previous paper¹¹⁾. These differences were recognized at each level of light intensity, indicating that the different movement of the leaflet characterized by the vertical and twisting angles is a property of each cultivar. It should be noted, however, that the cultivars of kidney bean can not always be classified into the two groups, because in some cultivars the horizontal inclination of their leaflets still remained¹²⁾.

Changes in the angle between the leaf normal and incoming light in kidney bean cultivars are shown in Fig. 2. There were evident differences among cultivars in the changes of this angle. The angles of Hime-tebo and Mexico 489 were much smaller than those of Taisho-kintoki and Dneprovskaja Bomba, indicating that the leaflet of the former cultivars moved more vertically to track the light, while that of the others oriented more twistingly to avoid it.

Wien and Wallace¹⁵⁾ observed variations of the changes in the vertical angle of the leaflet in dry bean (*Phaseolus vulgaris* L.) cultivars. In soybean, the variation of cultivars was also recognized in the degree of orientation of their trifoliate leaves¹⁶⁾. The result of this experiment indicates that those cultivars examined can be classified into two types. Hime-tebo and Mexico 489 oriented the leaflet surface more perpendicularly to the incoming light.

Fig. 1. Time courses of the vertical and twisting angles of left leaflet in the first or second trifoliate leaf of four kidney bean cultivars. —; 30 klx, - - -; 80 klx, ▲; Hime-tebo, △; Mexico 489, ●; Taisho-kintoki, ○; Dneprovskaja Bomba.

Such cultivars were designated as **Vertical type** because of the considerable vertical movement of the leaflet. On the other hand, Taisho-kintoki and Dneprovskaja Bomba oriented the surface more parallel to the incoming light. Such cultivars were designated as **Twisting type** because of the considerable twisting movement. Photographs in Fig. 3 show typical movements of the left leaflet of the two types. Hime-tebo (A), the vertical type, lifts up the leaflet as soon as lighting started, and shows only the margin of the leaflet throughout the period of light exposure because that the twisting movement is not so active. In contrast, the leaflet of Taisho-kintoki (B), the twisting type, orients the adaxial surface toward the direction of the terminal leaflet because of an active twisting movement, although it did not raise much.

Fig. 4 illustrates the time courses of the vertical and twisting angles in the parents of the two types, and their F_1 generations in two crosses. The patterns of the leaflet movements were different between the parents, Hime-tebo and Dneprovskaja Bomba. Hime-tebo was significantly greater in the vertical angle, but smaller in the twisting angle than Dneprovskaja Bomba at 60 minutes after the start of lighting (the uppermost point of each curve in

Fig. 2. Time courses of the angle between leaflet normal and incoming light for four kidney bean cultivars. Symbols are the same as those in Fig. 1.

the figure). In comparison between Mexico 489 and Taisho-kintoki, the difference was significant in the vertical angle, but not significant in the twisting angle. T-tests showed that F_1 progenies of both crosses were not significantly different from each parent of the vertical type, implying that the leaflet movement of Mexico 489 and Hime-tebo of

Fig. 3. Typical movements (from right to left) of left leaflets in kidney bean cultivars, Hime-tebo (A) and Taisho-kintoki (B). Each leaf was multiplex-exposed at 10 minutes intervals. Artificial light was directed at an angle of 30 degrees from the horizontal onto the pulvinule and leaf blade from the base of the left leaflet.

the vertical type is dominant over that of Taisho-kintoki and Dneprovskaja Bomba of the twisting type, respectively. The difference in response curves of F_1 progenies to each parent of the vertical type, however, suggests that the action of the dominant factor is not simple. Kemp⁷⁾ investigated the photonastic response of unifoliate leaves of common bean (*Phaseolus vulgaris* L.) at low temperatures and reported that this trait is controlled by two recessive genes. Disagreement with the result of this experiment may be due to some different mechanisms between the photonastic movement and the phototracking movement observed in this experiment.

Two-dimensional distributions for the vertical and twisting angles of individual plants in two F_2 populations are shown in Fig. 5. Correlation coefficients between the vertical and twisting angles were significantly negative in both F_2 populations. But plants showing greater vertical angle did not always exhibit smaller twisting, and *vice versa*. For example, in the cross Taisho-kintoki $\times$ Mexico 489, some plants which showed a vertical angle of approximately zero degree had a wide distribution of the twisting angle from 10 to 75 degrees. In the cross Hime-tebo $\times$ Dneprovskaja Bomba also, some plants which showed a twisting angle of approximately 15 degrees had a distribution of the vertical angle from 25 to 75 degrees. These facts suggest that the vertical and twisting movements of the leaflet are separately controlled, although related to each other.

Fig. 4. Time courses (from the left corner to right-above) of the vertical and twisting angles of the parents and their F_1 generations in the crosses Taisho-kintoki $\times$ Mexico 489 and Hime-tebo $\times$ Dneprovskaja Bomba. Marks show the angles of 10 minutes intervals during 60 minutes from the start of lighting.

Two-dimensional distribution in the cross Taisho-kintoki $\times$ Mexico 489 showed an extensive transgressive segregation for large and small angles. A similar result was also seen in the cross Hime-tebo $\times$ Dneprovskaja Bomba, indicating that more than one genetic factors were involved in each cross. However, the frequency distributions of the vertical and twisting angles in F_2 populations were discontinuous in both crosses. These suggest the presence of a few genetic factors of major effect with genes of minor effect and/or environmental factors which modify the inclination angle of the leaflet. Thus, the vertical type

Fig. 5. Distributions of the vertical and twisting angles at 60 minutes after the start of lighting for the plants in F_2 populations of crosses Taisho-kintoki × Mexico 489 and Hime-tebo × Dneprovskaja Bomba. P_1 ; Taisho-kintoki, P_2 ; Mexico 489, P_3 ; Hime-tebo, P_4 ; Dneprovskaja Bomba, ** ; significant at 1% level.

in the leaf orientation movements in kidney bean may be controlled by two kinds of dominant genetic factors with extensive modifiers, which independently give the plant leaflet large vertical and small twisting movements.

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