Morphogenesis of Spikelets, especially the Proliferative Spikelets in Rice

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Malformity in spikelets is one of the causes for sterility in rice. Floral malformities are induced by environmental disorders, for example, cold weather[5,12,20], over flooding[4], high salt concentration[2], and dry weather[1]. Genetical factor[3] is also responsible for floral abnormalities but in a very rare case. Thus, floral abnormalties as the cause for sterility in rice have a great significance in rice production.

Before taking up the problem of vegetative proliferation in rice, the present authors have investigated the morphogenesis of rice spikelets under normal and abnormal environmental conditions. The study has revealed the following facts:

1. The shoot apex of rice spikelets is not static, but it is dynamic; it changes in form and size; it becomes gradually smaller and flatter, and its organization becomes more indefinite with the lapse of time after initiation: the primordia it gives forth are also indefinite as to their mode of initiation whether they are homologous with leaf or branch[11].

2. Rice plants, if cultured under a low temperature, tend to degenerate stamens, and instead, generate pistil-like organs or vegetative ones[8].

3. Sterility caused by gibberellin is due to floral abnormalities in the spikelet which are more or less similar to those caused by environmental disorders and also by treatment with auxin[9,10].

4. TIBA[7], an antiauxin, and X-ray irradiation[6] tend to suppress the occurrence of floral abnormalities in rice cultivars which develop floral abnormalities genetically.

Therefore, it is considered that there might exist a common physiological back-ground behind the spikelet malformities caused by different external influences.

The present report dealt with the morphogenesis of proliferative spikelets, and the observations stated are the ones which were experienced during several years of our study on this problem.

The observations were based on two mutant strains of Japonica rice cultivars, Reimei and Akibare.

Gross morphology of poliferative spikelets[13,14,15]

The proliferative spikelet is the one which can not generate reproductive organs normally and instead produces one or more florets lacking usual number of stamens but with more than one pistil, a pedicel bearing one or more spikelets, or one or more leafy shoots (propagule).

Proliferation of spikelets should not be confused with the vivipary, which is simply a phenomenon of germination of seeds occurring on standing plants.

There are three forms of proliferative spikelets;

a) S-type proliferation: a spikelet having one or more spikelets in it (Plate 1).

b) P-type proliferation: a spikelet having more than one pistil, or a pistil(s) having abnormally swollen ovary (Plate 2).

c) L-type proliferation: a spikelet having one or more leafy shoots in it (Plate 3 and Plate 4).

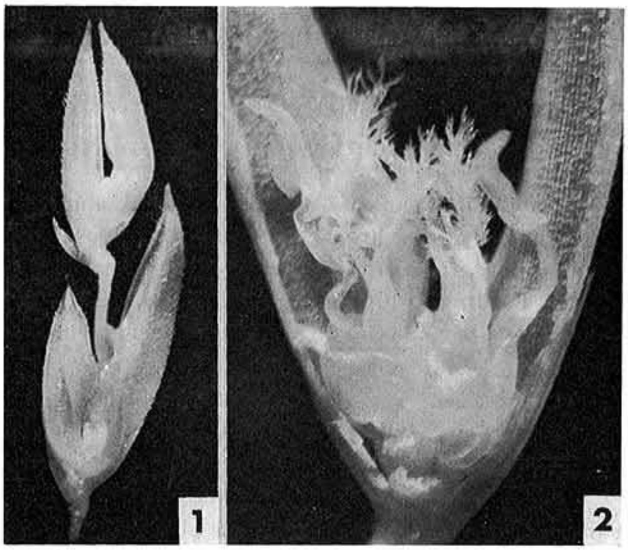


Plate 1. A spikelet having a pedicel-like internode on the tip of which a spikelet-like organ developed (S-type proliferation).

Plate 2. A spikelet having two pistils and three stigma-like tissues in it. Stamens decreased in number (P-type proliferation).

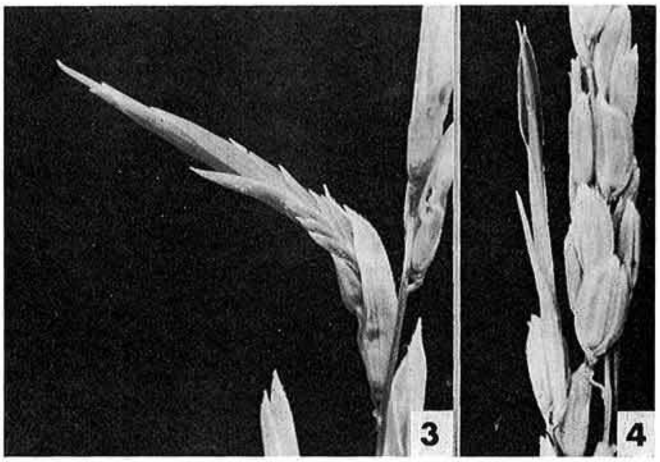


Plate 3. A leafy shoot composed of many leaf-like glumes (L-type proliferation).

Plate 4. A seedling-like leafy shoot (propagule) (L-type proliferation).

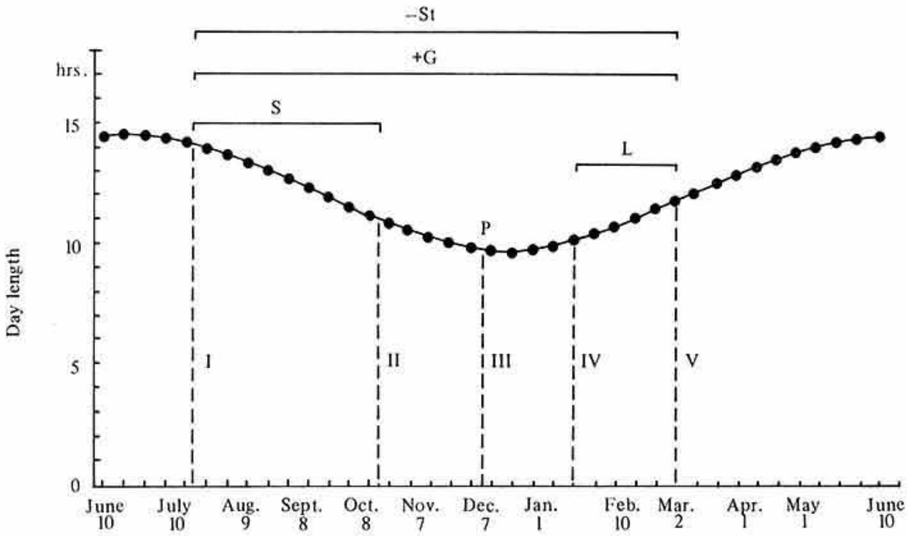


Fig. 1. Relation between the seasonal daylength in Nagoya and the change of the type of proliferations
+G : Increase in number of glumes
−St : Decrease in number of stamens
L : Leafy-shoot type proliferation
P : Pistil type proliferation S : Spikelet type proliferation

Seasonal change in form of proliferation[16]

When the stumps of the mutant strains used were transplanted in the spring in a green house and were observed throughout the year, the sequence of occurrence of proliferation in the panicles headed at different times was as follows (Fig. 1):

1. S-type proliferation in panicles headed during July to October.
2. P-type proliferation in panicles headed during December.
3. L-type proliferation in panicles headed during January to March.

Thus it is obvious that the form of proliferation changes with the transition of season.

A hypothesis as to these changes is proposed as follows;

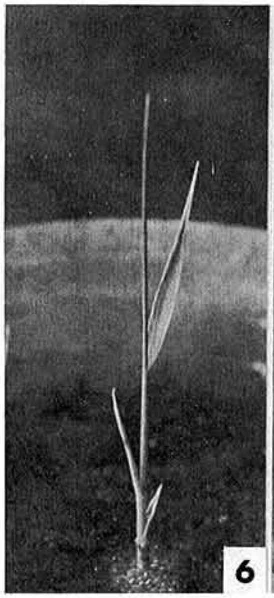
1) Moderate (or high) temperature + daylength inclining to short day → S-type proliferation
2) Low temperature + short day → P-type proliferation
3) Low temperature + daylength inclining to long day → L-type proliferation

Experimental regulation of proliferation

1) Development of propagule to plantlet through soil culture[17]

A leafy shoot produced in a proliferative spikelet if transplanted in a paddy soil (Plate 5) could grow into a healthy plant producing panicles with spikelets (Plate 6), most of which, though not all, showed the same kind of abnormalities as those in the mother plant.

Some of the spikelets in such panicles, however, were able to fertilize normally and developed into seeds. Plants grown from such seeds, in turn, also produced the same kind of proliferation in their spikelets. Therefore, it is considered that the propagule can be



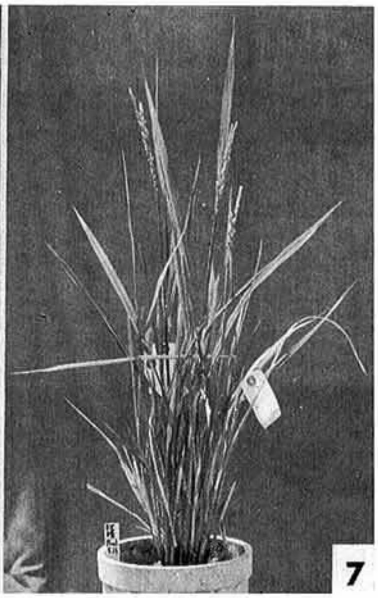


Plate 5. A propagule just after transplanted in flooded soil.
Plate 6. A plant developed from the propagule transplanted in flooded soil.

used as a means of propagation and that the proliferative character is inheritable through both propagules and seeds.

2) Influence of temperature on the proliferation of spikelet[19]

When the mutants were cultivated in the summer but at low temperature, with a small diurnal range of temperature, most of the spiklets differentiated into the P-type proliferation, whereas under a large diurnal range, most of the spikelets differentiated into the S-type proliferation. On the other hand, if the mutants were cultivated in the winter at low temperature, a small number of spikelets gave forth to the L-type proliferation only under a small diurnal range, and most of the spikelets gave forth to the P-type proliferation not only under a large diurnal range but also at high temperature with a small diurnal range.

It is therefore, suggested that a proliferative spikelet has a tendency to change the form of proliferation, from floral to vegetative, if placed under a small diurnal range at low temperature in short day for a certain period of the year.

3) Effect of gibberellin and naphthalene acetic acid on the type of proliferation[18]

In the summer, the general trend in the proliferative spikelets, as stated above, is the production of the S-type. But if the mutants were treated with GA and/or NAA it was observed that these plants produced more P-type (Fig. 3) or L-type (Fig. 4) than the untreated plants did. As a result, the number of S-type was decreased to a large extent in treated plants.

This means that the treatment with GA and/or NAA was effective to induce the P-type or L-type in the summer. From this fact, it is obvious that GA and/or NAA, by increasing the auxin contents in the treated mutant, may counteract the influence of summer environment which is responsible for the production of S-type proliferation and can produce favorable environment within the treated mutants for the production of P-type and L-type proliferations which are naturally

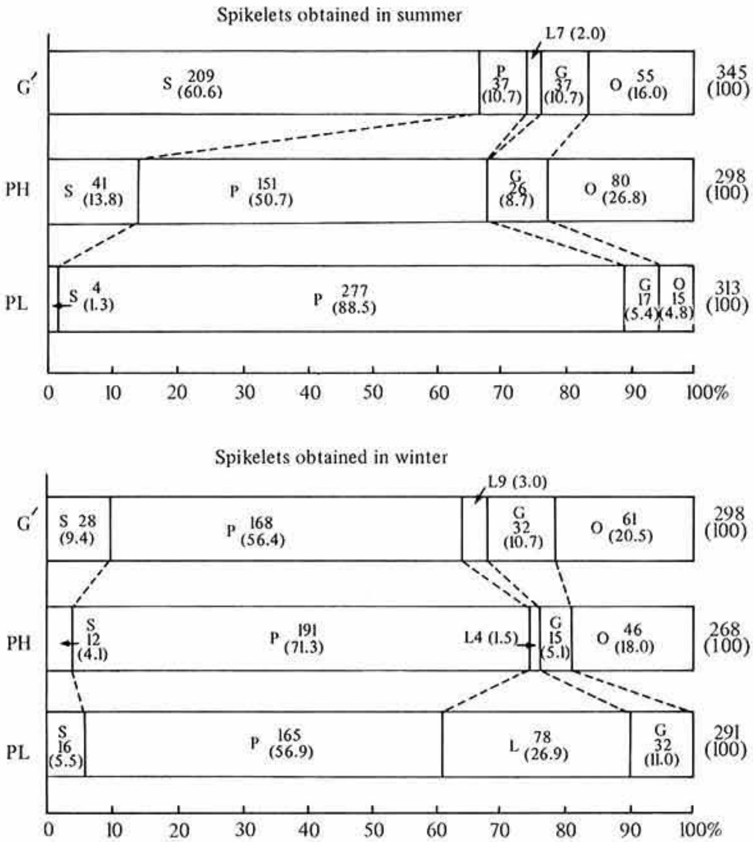


Fig. 2. Effect of temperature on the type of proliferations of spikelets under natural daylength.
G : spikelet having increased number of glumes in it,
L : leafy-shoot type proliferation, P : pistil type proliferation, S : Spikelet type proliferation, O : spikelet having other malformities than above, G′ : Green house, PH : Phytotron at high temperature, PL : Phytotron at low temperature.

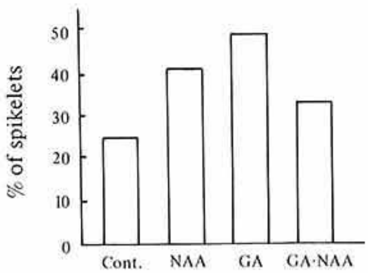


Fig. 3. Effect of GA and NAA on the development of pistil type proliferation

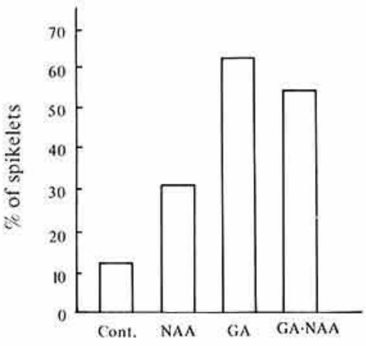


Fig. 4. Effect of GA and NAA on the development of leafy shoot type proliferation

induced by winter and early spring environment.

Conclusion

The three types of proliferation, spikelet type, pistil type and leaf-shoot type, are not independent, but represent the three successive stages of the proliferation, the final stage being the leafy-shoot type.

The ultimate objective of proliferative spikelets is to produce a leafy-shoot type of proliferation through which the plant can perpetuate its generation under abnormal conditions hampering the formation of reproductive organs for the normal propagation.

However, the production of leafy-shoot type of proliferation is not always possible as it depends on the integration of daylength and temperature, so that two early stages of proliferation occur. It was proved however that the leafy-shoot type proliferation can be produced at any season of the year by regulating the environmental condition.

If the various spikelet abnormalities in rice are considered from the view-point of vegetative proliferation, it may be noted that the basic abnormalities are the deformation of glumes in shape and structure, as well as increment in number. These basic abnormalities are shown in Fig. 1 with the initial of +G. They are always accompanied with one or more of the following four stages of incompleteness in floral organs;

Stage I: The floral organs can not develop; the floral apex grows upward and produces a spikelet on its head.

Stage II: Stamen degenerates completely or partially while the pistil remains in normal condition.

Stage III: Pistil-like organs increase in number.

Stage IV: Stamen and pistil degenerate and the spikelet develops into a leafy shoot.

We consider the Stage I as S-type, the Stage II and III as P-type and the Stage IV as L-type.

Many researchers in the world have reported various morphological causes for sterility in rice. If one analyses those causes, one will find that most of them come under the four types of spikelet abnormalities including the basic type of them. One will therefore, be able to assess the morphogenetic aspect of sterility in rice by referring the above classification.

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