Differentiation and Development of Tiller Buds in Rice Plants

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Development of tillers plays an important role for getting high yields of rice by increasing number of panicles per plant. The tiller develops from an axillary bud which differentiated on an axil of a leaf of rice plants. Number of tillers per plant depends on the differentiation of axillary buds (referred to as tiller buds hereafter) at leaf axils and the succeeding development of the tiller buds.

It was shown by Katayama[6] that the tillers develop synchronously with the development of the main stem, in other words, a leaf of a tiller develops synchronously with the development of a definite leaf of the main stem and those of other tillers.

The present author carried out a series of experiments for the purpose of finding general rules involved in the processes of differentiation and development of tiller buds, and of knowing the effects of environmental conditions and some cultural practices such as transplanting and so on[2,3,4,5,7]. The results will be presented in this paper.

Differentiation of leaves and tiller buds on a main stem[5,7]

The $(n+4)$th leaf*1) was found to be the newest leaf which had differentiated on the shoot apex at the plant-age n*2). This relationship can be applied throughout the all growth stages of rice plants except for stages earlier than plant-age 4 (Plate 1). The primordium of the $(n+5)$th leaf was found as a protuberance on the peripheral zone of the shoot apex at the plant-age n.

The tiller primordium which existed as a protuberance at the axil of the nth leaf, i.e. at the outside basal part of the $(n+1)$th leaf, at the plant-ages $(n-2)$ and $(n-1)$ (plate 2) was found to have differentiated into a tiller bud at the nth node of the main stem at the plant-age n (plate 3).

As to the length of the nth node tiller bud*3) at the plant-age n*4), that is the length of tiller buds at the time of their differentiation, it was found that the higher the node of tiller bud differentiation the longer was the length of tiller bud. Thus, the length (y) of tiller buds can be shown as a function of the node number (n) statistically. Values of y, calculated by a cubic regression equation of n were very close to the observed values (Fig. 1). As the final length of leaf sheath of upper leaves (higher node leaves) is usually longer than that of lower leaves (lower node leaves), higher node tillers must be longer than lower node tillers at the time of emergence from their subtending leaf sheath. On

*1) The $(n+4)$th leaf: Numbered in ascending order starting from the lowest leaf next to coleoptile (this leaf is refferred to as the first leaf). n is an arbitrary integer.

*2) Plant-age: Expressed by the number of leaves produced on a main stem. The leaves whose leaf blades emerged out completely were counted.

*3) The nth node tiller bud: The tiller bud which developed at the axil of the nth leaf of a main stem, sometimes called briefly the nth tiller bud.

*4) Plant age n: At this stage, the nth tiller bud was recognized as a bud for the first time. This stage will be referred to as the differentiation stage of the nth node tiller bud hereafter.

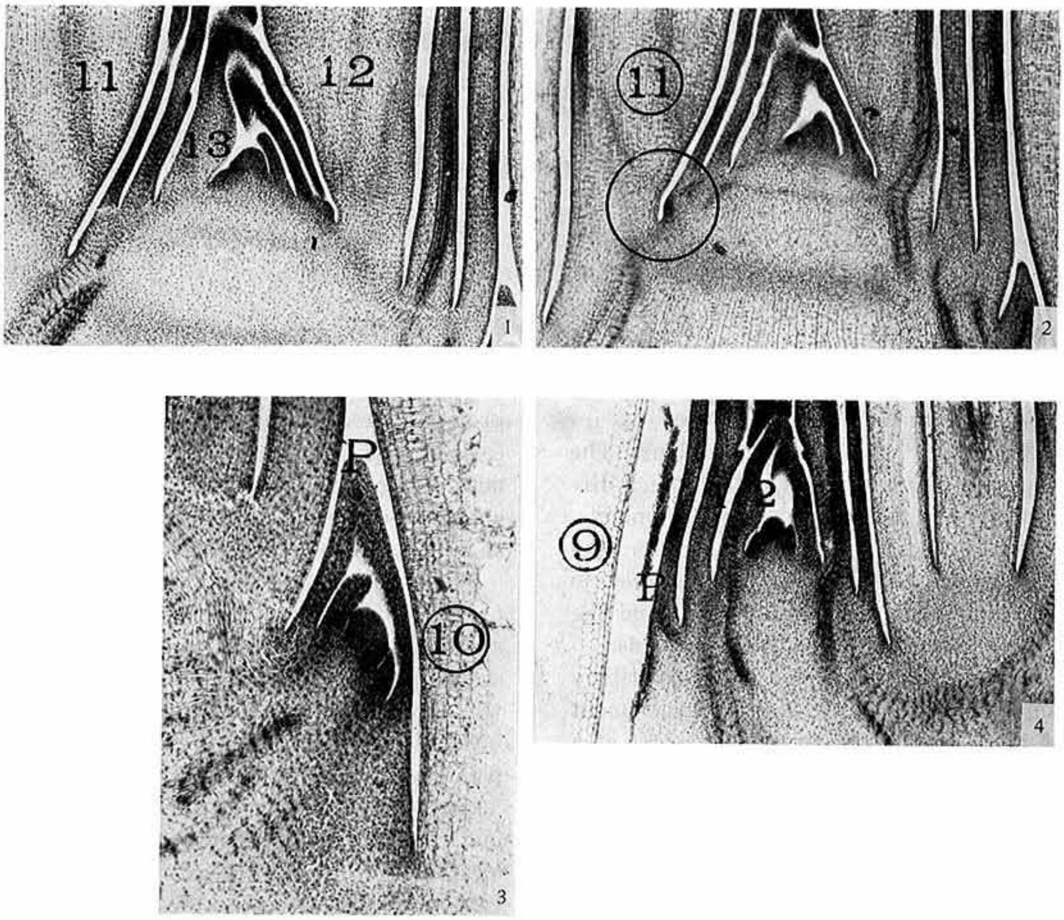

Plate 1. Differentiations of leaves and tiller buds in rice plants at plant-age 10*
1: Apical part of main stem
2: Protuberance at the leaf axil of the 11th leaf of main stem, which will differentiate into the 11th node tiller bud at plant-age 11*
3: The 10th node tiller bud at the leaf axil of the 10th leaf
4: The 9th node tiller bud at the leaf axil of the 9th leaf
Note *: See *2) in the text
Numerals without circle in Plate 1–1 and 1–4 indicate the leaf number of main stem and tiller bud respectively. Numerals in circles show the leaf number of main stem.

the other hand, the emergence of the nth tiller takes place at the plant-age $(n+3)$[6], i.e. all the tillers require three plant-age periods from their differentiation stage to the emergence from the subtending leaf sheath, irrespective of their nodal position.

The above-mentioned fact that the tiller buds differentiated at higher nodes are characterized by longer bud length seems to be responsible for attaining longer length of higher node tillers at the time of their emergence.

Developmental process of a tiller bud after its differentiation[5]

The growth in length of a tiller bud was found to proceed generally along the process of so-called growth curve, which is known to express the process of monomolecular auto-

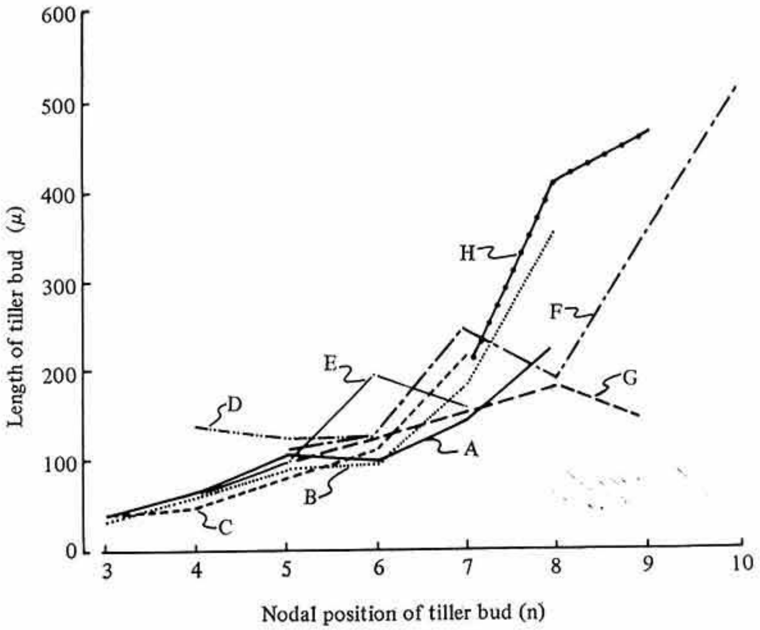

Fig. 1. Length of tiller bud on nth node of the main stem at plant-age n^*

- A: from planting density experiment (1958) 4.5 cm × 4 cm
- B: from planting density experiment (1958) 3 cm × 1.5 cm
- C: from planting density experiment (1958) 1.5 cm × 1.5 cm
- D: from shading and transplanting experiment (1958) control plot, 5 cm × 3 cm
- E: from leaf removal experiment (1958) control plot, 5 cm × 3 cm
- F: from leaf removal experiment (1959) control plot, 6 cm × 5 cm
- G: from thinning experiment (1959) control plot, 3 cm × 1.5 cm
- H: from thinning experiment (1961) control plot, 3 cm × 1.5 cm

catalytic reaction[8], that is, when the growth expressed by a logarithmic scale is plotted against the plant-age of the main stem, the initial growth shows a line during the first two or three plant-ages, and then it curved down, indicating that the growth rate is decreased gradually. As shown in Fig. 2, at a low planting density favorable for growth, the tiller buds on the fourth or higher nodes proceeded their growth linearly, namely the buds grew with a constant rate, during the first three plant-ages after the differentiation stage, whereas the second and third node tiller buds grew linearly for only the first two plant-ages. Growth of the second and third node tiller buds were found to be inhibited by inferior environmental conditions such as higher planting density more sensitively than the upper node tiller buds.

The following facts were recognized as to the differentiation of leaves on the shoot apex of a tiller bud during its development. The first leaf[*5] was recognized to have differen-

*5) The first leaf: Numbered in ascending order, excluding prophyll.

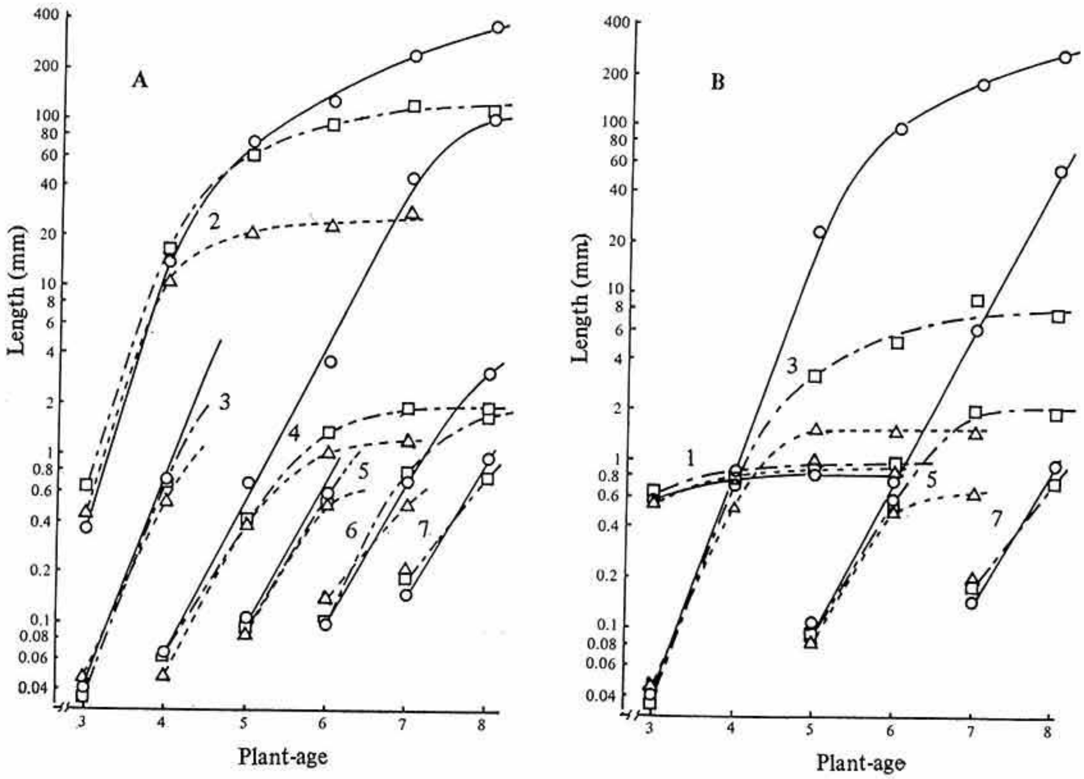

Fig. 2. Growth in length of tiller buds or tillers of rice seedlings grown at different plant spacing.
Notes Plant spacing ○: 4.5 cm × 4 cm □: 3 cm × 1.5 cm △: 1.5 cm × 1.5 cm
Numerals in the figures show nodal position of tillers or tiller buds on main stem
A: Tillers or tiller buds on even number nodes of main stem
B: Tillers or tiller buds on odd number nodes of main stem

tiated at the differentiation stage of a tiller bud in most primary and secondary tillers (Plate 1–3 and Fig. 3) except for lower node primary tillers, in which only prophyll was observed to have differentiated. During the period of one plant-age following the differentiation stage, a tiller bud formed two new leaves. At the third plant-age after the differentiation stage of a tiller bud, the fifth leaf, which had emerged slightly from the subtending leaf sheath as a tiller*6), was found to be the newest leaf at the shoot apex of the tiller bud. Since then, the tiller, similarly to the main stem, formed a new leaf at every plant-age of the tiller (Fig. 3).

Development of tillers in varieties differing in tillering ability under different light intensities and air temperatures[4,5]

The plant-age of tillers (tiller-age) increased at the rate of 1 to 1.1 against the increase of one plant-age of the mother stem*7). No varietal differences were observed either in the increasing rate of tiller-age or in the plant-age of the mother stem at the time when each tiller has reached the tiller-

*6) Tiller: Tiller buds grown to emerge from their subtending leaf sheaths are referred to as tillers.

*7) Mother stem: The stem on which the tiller concerned differentiated and developed.

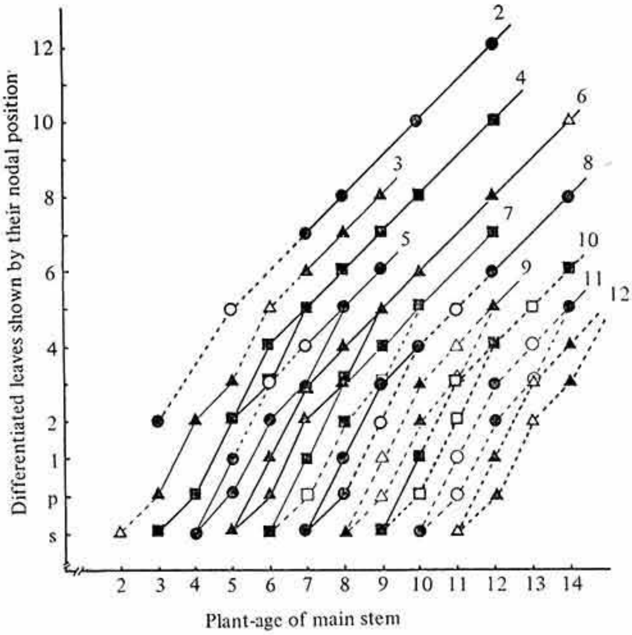

Fig. 3. Leaf differentiation on primary tiller (or tiller bud) on each node of main stem at different plant-ages after the differentiation of tiller bud.
Notes 1) Numerals in the figure show the nodal position of tillers (or tiller buds)
2) ●▲■: observed in the present study
○△□: not actually observed but assumed from observations on tillers or tiller buds on the other nodes
3) p: prophyll s: at the stage of protuberance

age one. Therefore, there is no possibility that the varietal difference in number of tillers per plant observed at a definite plant-age of a main stem is caused by difference in the preceeding rate of the age of the primary or secondary tillers, which are mother stem of the secondary or tertiary tillers, respectively.

But, the emergence percentage of tillers*8) was small under inferior environmental conditions. In this case, the emergence percentage was decreased more remarkably in tillers of lower nodes, such as the second and third nodes in primary tillers or prophyll and first nodes in secondary and tertiary tillers, and in tillers of upper nodes than in tillers of intermediate nodes. Furthermore, varietal difference in number of tillers per plant was exclusively caused by the varietal difference in emergence percentage of tillers. As mentioned above, the decrease in emergence percentage under bad conditions is more liable to occur in lower and upper node tillers than intermediate node tillers. Especially, the difference in number of primary and secondary tillers at lower nodes of mother stems is responsible for the

*8) Emergence percentage of tillers: Concerning a definite node tiller, number of plants in which the tiller emerged from the subtending leaf sheath, is expressed as percent of the number of plants examined.

varietal difference in number of tillers per plant.

It is considered that every tiller bud has an ability to grow into a tiller, so that under an extraordinarily good condition, the number of tillers of a plant increases according to the regularity of a "standard plant" proposed by Katayama[6]. In practice, however, not the all tiller buds can become tillers. The growth of tiller buds into tillers requires a better condition. This requirement is higher for higher order tiller buds than for lower order tiller buds, and lower for upper node tiller buds than intermediate node ones respectively. In addition, the tiller buds of poor-tillering varieties seem to require a better condition than those of heavy-tillering varieties.

Effects of environmental conditions on the differentiation of tiller buds[1,2,3,5,7]

The *n*th node tiller bud was always recognized to have differentiated at plant age *n* of the mother stem under any planting density examined[7] (30 to 2.2 cm^2 per plant), and also even after sudden changes of the growing condition such as shading[1], transplanting[1], leaf removal[2] or thinning[3]. It was concluded that the relationship between tiller bud differentiation stage and plant-age of main stem is not affected by any severe condition which may occur during rice cultivation[1,2,7]. The number of leaves differentiated and the length of a tiller bud at the differentiation stage were also found to be seldom affected by environmental conditions, though the latter was a little more sensitive than the former.

Effects of environmental conditions on the development of a tiller bud after differentiation[1,2,3,7]

Growth of tiller buds was inhibited under a densely-planted condition. The inhibition of growth of the *n*th tiller bud under a high planting density was remarkable in the stage later than plant-age $(n+1)$ of the mother stem. Under a very high planting density, the growth of the tiller bud was completely inhibited. Even in this case, however, the *n*th tiller bud did not cease growing before plant-age $(n+2)$ of the mother stem (Fig. 2). When a treatment such as shading, transplanting or removal of leaves was given to a plant at plant-age *n* of the mother stem, growth of every tiller bud which had already differentiated by that time was inhibited during the next one plant-age period, especially the $(n-1)$th node tiller bud was most severely affected[1,2,7]. On the contrary, when a thinning treatment which causes a decrease of planting density was given to the plants growing with a high planting density at the plant-age *n*, the tiller buds of the $(n-1)$th and several upper nodes grew without fail, but the lower node tiller buds whose growth had already ceased did not recover their growth after the thinning. Even in those tiller buds, however, the differentiation of new leaves on their shoot apex and respiration of tiller buds were promoted by the thinning[3].

It was generally noted throughout the all experiments related to planting density and various other kinds of treatments, that the effect of the treatment which was given at the plant-age *n* of the main stem on the number of differentiated leaves and the length of the $(n+1)$th tiller bud was more remarkable than on those of the *n*th tiller bud, and less remarkable than on those of the $(n+2)$th node tiller bud[5]. In addition, the number of leaves differentiated and thickness of a tiller bud of any node were less sensitively affected than the length of the bud[5,7].

Effect of removal of different leaves or addition of gibberellic acid (GA) or maleic hydrazide (MH) to different leaves of a main stem upon the growth of tiller bud on each node was also examined[2,5]. The growth of tiller buds was generally inhibited by removal of leaves and GA application and promoted by MH application. The tiller bud on which node was most strongly affected in growth was dependent upon the plant-age of the main stem when the treatment was given, but not upon the nodal position of the treated leaf.

Table 1. Different effects of various kinds of treatments on the growth of tiller buds

Plant-age at the time of treatment	Nodal position of tiller bud	Shading 2days		Shading 4days		Trans-planting		Removal of Upper-most leaf		Removal of 2nd upper-most leaf		Removal of Two upper-most leaves		GA 500ppm		MH 2,500ppm	
		E	L	E	L	E	L	E	L	E	L	E	L	E	L	E	L
4	2	△	△	△	□	△	▲	▵	—	—	—	△	△				
	3	□	□	□	□	□	▲	□	□	□	□	□	□				
	4	△	▵	△	○	△	○	△	△	△	△	△	△				
	5	—	○	△	○	∘	○	—	○	—	○	—	○				
	6		—		—		—		○		∘		○				
5	2							—	—	—	—	▵	—	∘—	▵	—	▲
	3							—	▵	—	▵	△	△	∘—	△	—	▲
	4							□	△	□	▵	□	△	□	□	◎	◎
	5							△	□	△	□	△	□	—	△	—	—
	6							—	—	—	▵	▵	○	▵	▵	▵	△
	7								○		▵		○				

Notes 1) E : early stage after the treatment, i.e. one plant-age after the treatment.
L : later stage after the treatment, i.e. 3 or 4 plant-ages after the treatment.

▲: completely inhibited □: inhibited most severely
△: inhibited severely ▵ : inhibited slightly
◎: promoted most remarkably ○: promoted remarkably
∘ : promoted slightly —: no effect

3) GA and MH: Application of gibberellic acid or maleic hydrazide.

From the results, it is not likely that there exists any direct interrelationship between the nodal position of tiller buds and a leaf of definite nodal position[2,5].

After the period of several plant-ages following the treatment such as thinning, shading, transplanting and removal of leaves, growth of tiller buds of upper nodes was found to be promoted (Table 1). This result may be due to 1) the subsequent recovery of dry matter production which was suppressed by the treatment and 2) lower density of the treated plants caused by the inhibition of growth of lower node tiller buds by the treatment. The nodal position of tiller buds whose growth was promoted was dependent on the kind of treatments: when the treatment was given at the plantage n of main stem it was the $(n-1)$th and upper nodes in case of thinning treatment, the nth and upper nodes in case of shading and transplanting, and the $(n+1)$th and upper nodes in case of removal of leaves (Table 1). The difference in the critical nodes of the tiller buds whose growth was promoted was obviously caused by the following fact. When the planting space was enlarged by thinning, the growing condition turned better immediately after the treatment, whereas the plants were recovered after one plant-age following the end of the treatment in case of shading and transplanting, and after two plant-ages following the treatment of removal of leaves. These facts offered us a general rule that the growth of tiller buds of the $(n-1)$th and upper nodes is promoted if the growing condition after the treatment was recovered at the plant-age n. This general rule corresponds very closely with the afore-mentioned rule that the $(n-1)$th node tiller bud was most sensitively inhibited by a growth-suppressing treatment given at the plant-age n during one plant-age following the treatment[5].

The results of the experiments of various kinds of treatments showed a common rule that the effect of environmental conditions on the growth of the nth node tiller buds is remarkable in the period later than the plant-age $(n+1)$ of the mother stem.

When the growth of tiller buds which are expected to grow normally into tiller from the viewpoint of nodal position and the growing condition is inhibited by some adverse conditions, the retarded growth of the tiller buds or tillers, even after emergence, may be difficult to recover, as the growth delay lasts for long.

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