A Developmental Analysis of Yielding Ability in Varieties of Field Crops

IV. Quantitative and spatial development of the stem-system¹⁾

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In order to clarify the situation of a stem-system as a component of the productive system of plants, it would be necessary at least to deal with quantitative and spatial development of the stem-system, bearing in mind the various characters of the leaf-system which have been reported in the previous papers of this series (TSUNODA, 1959ab and 1960).

The term *stem-system* is to be taken in this paper as involving not only stems but also stem-like organs such as petioles in the case of sweet potato as well as leaf sheaths and midribs in the case of rice.

The main materials used were the same as reported in the first paper (TSUNODA, 1959a).

Relative weight of the stem-system to leaves

The weight ratio of stem to leaf is obviously one of the main factors determining the leaf area plant weight ratio. On this account, it may be reasonable to assume that varieties adapted to light manuring tend to have a lower weight ratio of stem to leaf than those adapted to heavy manuring, because a higher leaf area plant weight ratio seems to be essential for rapid growth and high yield under light manuring as has already been pointed out by the author (1959a).

The actual values of the weight ratio of the stem-system to leaves measured in rice and in sweet potato are shown in Figs. 1~2 and Table 1, respectively. At first sight, it seems that there is no difference in this character between varieties adapted to light manuring and those adapted to heavy manuring. However, taking into account the longitudinal growth of the stems or stem-like organs, we can point out the following facts.

(1) The varieties adapted to light manuring tend to promote the longitudinal growth of stems or stem-like organs (Figs. 1~2 and Table 1).

(2) The varieties adapted to light manuring tend to restrict the relative quantitative development of stems or stem-like organs to leaves in proportion to their longitudinal growth (Figs. 1~2).

The amount of solar radiation received by leaves may often become a limiting factor for high yield under light manuring, because in the case of light manuring the production of leaves tends to be restricted and consequently a larger part of the incident solar radiation cannot be intercepted by leaves but must fall on bare soil. In order that the leaves receive as much light as possible in such a case, their overlapping should be

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Fig. 1. Rice. Relations between leaf sheath : leaf blade weight ratio and plant height. In the figure, white symbols and thin lines are used for varieties adapted to light manuring; black symbols and heavy lines are used for varieties adapted to heavy manuring. Observed on July 4-9, 1958 (cf. Table 3 of Part I). The first of ten repeated observations was omitted in every variety on account of mistakes in weighing.

Fig. 2. Rice. Relations between mid-rib proportion and leaf length. Observed on Aug. 5, 1957 (cf. Fig. 1 of Part II).

avoided, keeping leaves with large area per unit weight horizontally (cf. TSUNODA, 1959 b). This may be the reason for the first fact, i. e., the varieties adapted to light manuring tend to promote the longitudinal growth of stem-like organs. Further, in order to receive as much light as possible, it is also essential to have a higher leaf area plant weight ratio as has already been mentioned, and this may be the reason for the second fact, i. e., the varieties adapted to light manuring tend to restrict the quantitative development of stems or stem-like organs relative to leaves.

Table 1. Sweet potato. Quantitative and expansive development of stem-system

Variety name	Optimum levels of fertilization	Stem* weight (g)	Leaf** weight (g)	Stem : leaf weight ratio	Stem length (cm)	Stem weight : stem length (mg/cm)
1 Genji	low	1.48	1.54	0.96	33.0	22.4
2 Kenroku	high	1.23	1.33	0.92	17.4	35.1
3 Aichi-beniaka	low	1.68	1.83	0.92	27.9	30.0
4 Norin-4	high	1.39	1.43	0.97	15.5	44.7
5 Gokoku	low	1.48	1.61	0.91	27.6	26.8
6 Okinawa-100	high	1.20	1.36	0.88	19.9	30.2
7 Norin-3	medium	1.36	1.29	1.06	20.6	33.1
8 Norin-6	high	1.09	1.13	0.97	20.8	26.1
9 Norin-5	low	1.18	1.26	0.93	35.8	16.8
10 Tachi-1	—	0.73	0.98	0.74	5.8	50.5

* Dry weight, inclusive of petioles

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Seed potatoes were planted on April 13, 1953. Materials observed were the medium size sprouts cut off from the seed potatoes on June 6 with 6 open leaves. Figures show the average of 12 detached sprouts.

(3) As an inevitable consequence, the varieties adapted to light manuring tend to have thinly elongated stem or stem-like organs (cf. Table 1), which are apt to bend or to lie horizontally.

In fact, in the case of rice varieties adapted to light manuring, the leaf blade, strictly speaking, the midrib of the leaf blade, was markedly inclined horizontally (cf. Fig. 5 of Part II), and the plant, strictly speaking, the culm and leaf sheath of the plant, was liable to lodge at the ripening stage. For instance, in an experiment, the mean inclination of the plants from the upright position observed five weeks after the heading time was about 60° for Mao zu tao, 40° for Tamanishiki, 10° for Kanto-9 and in the case of Ginbozu-midashi the plants were keeping the upright position approximately.

Further, it was observed in sweet potato that the stems of the varieties adapted to light manuring tended to lie horizontally even at earlier stages of the growth, i. e., the mean inclination of the main stems to the horizontal plane observed one month after transplanting was about 20° or 30° in the case of varieties adapted to light manuring (Genji, Aichi-beniaka, Gokoku and Norin-5), while it was about 60° in the case of varieties adapted to heavy manuring (Kenroku, Norin-4, Okinawa-100 and Norin-6). This difference was observed in 1957 as well as in 1958.

Evidently, (1) the promotion of the longitudinal growth of stems and stem-like organs combined with (2) their restricted quantitative development may be a major factor being liable for (3) bending of leaves and lodging of plants in the case of rice, as well as for the prostrate habit of the sweet potato varieties adapted to light manuring.

Now, if the crops were cultured under heavy manuring, bending of leaves and lodging of plants in rice, or an extremely prostrate habit in sweet potato might be unfavorable, or even fatal, to the crops, through destroying a well organized ideal disposition of leaves as shown in Fig. 9a of Part II (TSUNODA, 1959b). However, in the case of light manuring, the problem of lodging of rice is not so serious as in the case of heavy manuring ; moreover the inclination of leaves towards the horizontal in rice as well as the prostrate

habit of plant in sweets potato are rather advantageous for growth and yield of the crops in the case of light manuring (cf. Fig 3).

This may be the final reason, and by combining this with the above mentioned two reasons, we can fully understand why (1) varieties adapted to light manuring tend to promote the longitudinal growth of stems or stem-like organs, (2) restricting their quantitative development and (3) consequently tend to have thinly elongated stems or stem-like organs which are apt to bend or to lie horizontally.

While, on the contrary, varieties adapted to heavy manuring should have shorter stiff stems or stem-like organs in order to maintain a well organized ideal disposition of crowded leaves as shown in Fig 9a of Part II (TSUNODA, 1959b), and in this case the relative quantitative development of stems or stem-like organs to leaves can be promoted to some extent without accompanying any adverse effect on dry matter production of plants, because even a surplus production of leaves is apt to occur in the case of heavy manuring (cf. also Fig. 8 of Part I).

It may be suggested here that, in the course of evolution of cultivated plants in future, the relative quantitative development of the stem-system to leaves should be promoted further at least in the case of field crops, in accordance with further progress of intensive cultivation, provided that any artificial framework is not adaptable.

Spatial development of the stem-system

The length and the inclination of stems and stem-like organs have already been mentioned in the previous section. However, to clarify the spatial development of a stem-system, it is necessary further to deal with the number of stems or stem-like organs, the position of branching nodes and so forth.

It is widely known among rice breeders of Japan, that varieties suitable for heavy manuring generally belong to the type which has shorter culms and higher ability to tiller (the so-called *short culm-much tillering type*) and varieties suitable for light manuring generally belong to the type which has longer culms and lower ability to tiller (the *long culm-less tillering type*).

Further, in the case of sweet potato, it is known just as in the case of rice that varieties suitable for heavy manuring generally belong to the type which has shorter stems and higher ability to branch (the *branching type*) and varieties suitable for light manuring generally belong to the type which has longer stems and lower ability to branch (the *elongating type*).

It seems, however, that any sufficient explanation of the relationship between these plant types and their adaptability to soil fertility and to manuring has not yet been made (BABA, 1954). At first it may be noticed that, though these type classifications are based on varietal difference in stem-system, only two characters, i.e., the length and the number of stems, are actually dealt with, presumably following the method of so-called developmental study founded by ENGLENDOW (1923) and others. And it is evident that the aspect of a stem-system can not be clarified unless other characters such as the position of branching nodes, the direction and the inclination of stems and stem-like organs and

so forth are observed further.

From this point of view, taking into account not only the length and the number of stems but also other characters as mentioned above, the author observed the stem-system of varieties belonging to the different plant types. Fig. 3 shows diagrammatically the author's observations on the spatial development of the stem-system, together with the author's presumption of the relationship between types of stem-system and their adaptability to fertilization.

Fig. 3 Scheme to illustrate the relationship between types of stem-system and their adaptability to fertilization

As illustrated in Fig. 3, the stem-system of rice varieties belonging to the short culm-much tillering type as well as that of sweet potato varieties belonging to the branching type bring about a well organized "gathering type" leaf arrangement (cf. TSUNODA, 1959b) favorable for uniform illumination of many leaves and consequently favorable for high yield under heavy manuring.

Whereas, the stem-system of rice varieties belonging to the long culm-less tillering type as well as that of sweet potato varieties belonging to the elongating type bring about a well expanded "dispersing type" leaf arrangement (cf. TSUNODA, 1959b) which is favorable for an increased utilization of solar energy with a limited quantity of leaves and, consequently, favorable for high yield under light manuring.

Additional remarks must be noted here. (1) Generally speaking, in rice, high ability to tiller tends to be combined with short culms as in the case of Kanto-9, and low ability to tiller tends to be combined with long culms as in the case of Tamanishiki. However, this tendency is not so strict. In the case of Mao zu tao, high ability to tiller is combined

with long culms. When high ability to tiller is combined with promoted longitudinal growth, the stems, leaf sheaths and midribs become generally extremely thin and, consequently, they are apt to bend or to lie horizontally. And, in this case, the stem-system brings about a rather "dispersing type" leaf arrangement, in spite of the high ability to tiller. (2) An appropriate thickness of stems and stem-like organs for their length is obviously a prerequisite for their erectness, but thick stems or stem-like organs are not necessarily always erect. It was observed in rice as well as in sweet potato that a few strains, which were not included in the main materials, showed a prostrate habit having thick stems and stem-like organs.

Relation between type of the stem-system and the area weight ratio of leaf blade

As pointed out in the previous section, the type of stem-system influences the growth and yield of the crop plant directly through determining the type of leaf disposition. However, it seems that it is also related to the growth and yield of the crop plant, through correlations with other important growth characters. One of the remarkable correlations was observed between the expansive development of stem-system and the area weight ratio of leaf blade, the latter being a very important plant character with respect to fertilizer response as pointed out in Part II of this series (TSUNODA, 1959b).

As seen in Fig. 4, in sweet potato as well as in soyabean, varieties showing a longer stem length are inclined to have leaves with a higher area weight ratio, in other words, to have "thinner" leaves.

Fig. 4. Varietal correlations between leaf area : leaf weight ratio and stem length
* Significant between 1% and 5% levels ** Beyond 1% level

These fairly high correlations observed among cultivated varieties may be partly attributable to the result of selection for yield, because the combination of "thinner" leaves with elongated stems is favorable for high yield under light manuring and the combination of "thicker" leaves with stiff stems is favorable for high yield under heavy manuring (cf. TSUNODA, 1959b and the previous sections of this paper). Another possible interpretation of these correlations is that an internal factor, presumably a plant hormone,

may stimulate both the elongation of the stem and the expansion of the leaf surface, as has been suggested by WENT (1951), i. e., a pleiotropy is involved. It is probable that, in fact, both pleiotropy and selection are playing roles in these correlations, the former being supported by the latter.

The same correlation was also observed in rice among fifteen strains which came into ear on the same date in 1948 belonging to the world-wide living specimens maintained by the National Institute of Agricultural Sciences, the value of the correlation coefficient between the mean length of culms and the mean area weight ratio of flag leaves being +0.659 (significant beyond 1% level).

In rice, it was also observed that high ability to tiller tended to be associated with lightness in weight of single leaf, and, further, the lightness in weight of single leaf tended to be associated with a higher area weight ratio of the leaves (cf. Fig. 1 of Part II); thus, in other words, much-tillering varieties of rice tended to have "thinner" leaves.

Therefore, when varieties of rice are classified into following four types; *long culm-much tillering*, *long culm-less tillering*, *short culm-much tillering* and *short culm-less tillering*, the type expected to have "thinnest" leaves is the long culm-much tillering type. Mao zu tao belongs to this type, having very "thin" leaves. On the contrary, the type expected to have "thickest" leaves is the short culm-less tillering type. Ginbozu-midashi and Norin-22, which are not typically short culm-less tillering type but mostly resemble this type among the varieties tested, have, in fact, "thick" leaves.

In Japan, rice varieties belonging to the long culm-much tillering type went out of existence long before, and varieties belonging to the long culm-less tillering type also lost their leading position, being replaced by varieties belonging to the short culm-much tillering type. But, further, some of the latest improved varieties seem to belong to the short culm-less tillering type, and it may be reasonable to assume that the short culm-less tillering type is more suitable for heavy manuring than the short culm-much tillering type partly because of their "thick" leaves (cf. TSUNODA, 1959b), as well as on account of their stiff stems.

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作物品種の多収性の生育解析的研究

IV 茎系の量的ならびに空間的発達

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前報までにとりあつた葉系の諸特性と密接に対応づけながら、茎系の量的ならびに空間的発達と作物品種の多収性との関係を追究した。

(1) 茎系の量的発達 甘藷でも稲でも「少肥向品種は茎あるいは茎的器官(葉鞘・中骨)を長く発達させながら、その割にその量的発達を抑制している」という一般的傾向が見られた。このことは次の3つかその裏付けとなつてゐる。(a) 第II報で論じたように少肥条件下で多収をあげるためには疎散型の葉配置をとることか望ましいか、そのためには茎または茎的器官を伸長しなくてはならない。これは一般的には茎系の量的発達を伴う。(b) 第I報で論じたように少肥条件下で多収をあげるためには葉面積 植物体重比率を大にして旺盛な生育をはかることか望ましいか、このためには非同化部である茎系の量的発達を可及的抑制する必要がある。(c) 茎、葉鞘、中骨などの伸長をはかりつつそれらの量的発達を抑制することは、茎、葉鞘、中骨などを細くまたは薄くして長く引伸はすことであり、少肥向甘藷の極端な匍伏的草型、少肥向稲の易倒伏性や葉のなひき易いことと密接な関係を持つか、これらは少肥条件下では多肥条件下ほど生育収量をそこなわない。多肥向品種の茎、葉鞘、中骨などが比較的短かい割に量的に発達しているのは(a)、(b)、(c)とも逆か成立しているためである。

(2) 茎系の空間的発達 稲の長稈少けつ型は一般に

少肥向、短稈多けつ型は多肥向、甘藷でも伸長型は少肥向、分枝型は多肥向とされているか、何故そうか明確にされていない。茎の伸びと茎の数とに注目するのは developmental study の流儀であるか、更に分枝位置や分枝の方角、傾斜(すへて茎たけてなく、葉柄、葉鞘、中骨を含む)をも観察することによつて、稲の長稈少けつ型、甘藷の伸長型の茎系は疎散型の葉配置をもたらすことを通し少肥多収性と直接結びついており、一方稲の短稈多けつ型、甘藷の分枝型の茎系はよく規整された密集型の葉配置をもたらすことを通し多肥多収性と直接結びついていることを指摘できる。すなわち茎系全体の空間的発達の様相か問題なのである。

(3) 茎系の様相と葉の面積重量比率との相関 葉の面積重量比率は第II報で論じたように生育収量を支配する重要な形質であるか、甘藷、大豆、稲とも茎の伸び易い品種ほど葉が“薄く”、稲で茎数の多い品種ほど葉が“薄い”傾向が見られた。我が国の水稻は(a)長稈多けつ型か絶滅し(b)長稈少けつ型か激減し(c)短稈多けつ型か増え(d)短稈少けつ型か出現し始めたか、(a)は葉か最も薄い点においても最も少肥向であり、(d)は茎か丈夫なたけてなく葉か最も厚い点においても多肥適応性を一歩進めたものと言えよう。尚これらの品種相関には pleiotropy および selection の両者とも関係しているものと推定される。(摘要)