Physio-ecological Studies on Prolificacy in Maize

I. Differences in dry matter accumulation among one-, two- and three-eared plants*

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Although the corn plant, *Zea mays*, L., develops several potential ear buds at an early growth stage, the recent corn hybrids grown in Japan produce generally only one harvestable ear. Collins *et al.* (1965)⁴⁾ pointed out that corn plants in Corn Belt have been selected for many years to produce only one harvestable ear, and that there were no information on the agronomic performance of two eared corn hybrids adapted to the Corn Belt.

However, it is known that prolific hybrids and varieties are widely used throughout the southern United States, and some available information have been obtained. Josephson (1957)⁶⁾ in Tennessee reported that hybrids capable of producing more than one ear per plant could better adjust to fertility and available moisture. Bauman (1960)²⁾ pointed out that the primary advantage of prolific hybrids was flexibility in adapting their production with a minimum plant population to the wide range of yield levels in the South. Zuber *et al.* (1960)¹⁴⁾ found in Missouri that prolific type corn had more consistent yields than single-ear types regardless of planting rate. Furthermore, in Corn Belt, the prolific hybrids were emphasized by Collins *et al.* (1965)⁴⁾ to have more consistent in yield than single ear hybrids across different plant densities.

Summing up the above studies, it can be characterized that prolific type corn may well adapt to various environmental conditions. However, there are little information at present, to well explain the reason why prolific types are better in adaptation to environmental factors than single

types. To solve this problem, more detailed experimental research is required. The purpose of this study is to obtain some information on physio-ecological characteristics of prolific type corn for better understanding prolific characters.

For the first trial in this study, the differences in dry matter accumulation among one-, two- and three-eared plants of prolific hybrid were compared with single ear hybrid. In this paper we report the results of some measurements and discuss them from the viewpoint of growth analysis.

MATERIALS AND METHODS

The study was conducted at the Experimental Farm, Faculty of Agriculture, Hokkaido University, in 1971. Hokko 22 (double-cross hybrid) and Koh 4 (three-way-cross hybrid) were used as prolific and single ear types, respectively. Hokko 22 produced about 1.5 harvestable ears on the average from 1967 to 1970 in the pre-testing field with the recommended rate of planting at Hokkaido National Agricultural Experiment Station.

Corn seeds were dibbled by hand on May 14, with 30 cm spaced hills and 75 cm wide rows, as main plots replicated two times. Nearly perfect stands were obtained by seedling 2 to 3 kernels per hill and thinned to single plant/hill at 3 weeks after emergence. Tillers of each plant were removed entirely on July 13. Fertilizer was applied at the rate of 63 kg N/ha, 63 kg P/ha and 113 kg K/ha, as basal dressing.

Dry weight and leaf area of plants were measured at 5 stages, taking the half silking date as the central sampling stage, with 3 weeks interval. The half silking date of Koh 4 and Hokko 22 were at 4th and 14th of August, respectively. At the half

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silking stage, one-, two- and three-eared plants were distributed at random in Hokko 22 population, whereas all plants in Koh 4 were one ear type only.

After determination of plant height and leaf number of 20 plants from each subplot with adequate borders of 3 rows between successive sampling area, 10 plants were cut at ground level and recorded their top fresh weight. After the half silking date, one-, two- and three-eared plants in Hokko 22 population were sampled separately from each subplot. Sampled materials were divided into leaf blade, culm including leaf sheath and ear parts after the half silking date, respectively, dried in a forced-air circulation oven set at 80°C for two days and weighed their dry weight. Root system within the area with 30 cm square occupied by hill was dug out to a depth of 30 cm, washed by water in a wire basket and collected to be dried and weighed. Leaf area measurement was done by an automatic leaf area meter. Leaf area data were determined from the mean leaf dry weight of samples and the mean specific leaf area (leaf area, cm²/leaf dry weight, g) of 2 plants judged as representative from each subplot.

RESULTS AND DISCUSSION

Silking ear number, Plant height and Leaf number

Percentage of one-, two- and three-eared plants in the populations, plant height and leaf number at one week after the half silking date are presented

Table 1 Frequency distribution of one-, two- and three-eared plants, plant height and leaf number at one week after the half silking date

Variety	Ear number per stalk	% of plants	Plant height (cm)	Leaf number
Koh 4	1	100.0	206	15.9
Hokko 22	1	26.5	227	17.8
	2	50.2	235	17.9
	3	23.3	229	17.2
LSD at 5% level.		—	12	1.2

Note. Half silking date, Koh 4: 4th Aug
Hokko 22: 14th Aug

in table 1. Koh 4, one ear type hybrid, had no silking second ears, but 74% of Hokko 22, semi-prolific type hybrid, produced more than two silked ears. Silks of the first (apical) ear of two- and three-eared plants emerged mostly 2 to 3 days earlier than those of the second ear. But some of them, the initiation of silking of the second ear was at the same time or slightly prior to that of the first ear.

Fig. 1 Changes of top fresh weight (A) and total dry matter weight (B)

Note. ×: Koh 4

○: One-eared plant, in Hokko 22

◐: Two-eared plant, in Hokko 22

●: Three-eared plant in Hokko 22

Vertical bars presented in A are the least significant interval at 5% level

Plant height and leaf number differed significantly between hybrids, but not significantly among plants which differed in ear number per plant, of Hokko 22.

Crop growth

Time trends of top fresh weight and total dry matter weight are shown in fig. 1 (A and B). Top fresh weight of Koh 4 increased until 3 weeks after the half silking date, then decreased. On the other hand, one-eared plants of Hokko 22 attained to the maximum top fresh weight at the half silking date and maintained this until maturity. But amount of top fresh weight of two- and three-eared plants were increasing during reproductive period, resulted in the drastic differences among plants which differed in ear number at final sampling date near maturity.

Total dry matter weight of each plant increased steadily throughout reproductive stage. In Hokko 22, the differences in total dry matter weight, which were higher in plants with larger number of ears at each sampling date, were recognized at the half silking date and magnified as season progressed. Total dry matter weight of Koh 4 was approximate-

ly similar to that of one-eared plants of Hokko 22 during reproductive stage.

Presented in fig. 2 are trends in dry matter accumulation of various plant parts. In Hokko 22, two- and three-eared plants had slightly higher dry matter weight of leaf blade and culm plus leaf sheath than one-eared plants, attained the maximum at the half silking date and continued these until maturity. But, in Koh 4, dry matter weight of those parts increased until 3 weeks after the half silking date and were lower considerably than those of Hokko 22. Root dry weight of Hokko 22 was similar to the growth pattern of leaf blade, but showed remarkable differences among plants with different ear numbers. The root dry weight of two- and three-eared plants were 3 and 1.4 times than that of Koh 4 and one-eared plants of Hokko 22, respectively.

Ear dry weight of Hokko 22 (summation of each ear in two- and three-eared plants) was heavier in plants with larger number of ears, being associated with higher dry matter accumulation rate throughout reproductive stage. On the other hand, ear dry matter accumulation rate of Koh 4 was similar to that of one-eared plants of Hokko 22, but ear growth of Koh 4 started earlier than that of Hokko 22 and this time lag continued during reproductive period.

As described above, in Hokko 22, number and dry weight of ear during reproductive stage were associated positively with other plant parts. These results may indicate that number and amount of ear at silking stage may have been decided by the extent of growth before silking stage and furthermore, the high dry matter accumulation rate of ear during reproductive period may also be supported by larger vegetative organs, especially by profuse root system.

Grain yield and Yield components

The yield data based on the average performance of plants with different number of ears are given in table 2. Total grain yield per plant was the highest in two-eared plants, although total ear dry matter weight was maximum in three-eared plants. This was because the first and the second

Fig. 2 Changes of dry matter weight in various plant parts

Note. Lb: Leaf blade. Ls+C: Leaf sheath + culm. R: Root. E: Ear

Symbols are the same with Fig. 1

Table 2 Grain yield and yield components

Variety	Ear number per stalk	Position of ear	Grain yield* (g/pl.)	Ear length (cm)	Ear diameter (cm)	Number of row per ear	Number of grain per row	Thousand kernel weight(g)*
Koh 4	1	1st	154.7	20.5	4.9	12.7	37.6	356.8
	1	1st	115.4	21.3	4.4	12.0	37.7	269.3
	2	1st	137.5	21.9	4.4	12.0	41.6	281.1
		2nd	98.2	17.5	4.0	12.0	33.7	239.2
		Total	235.7					
Hokko 22	3	1st	109.8	22.7	3.9	9.5	43.9	264.1
		2nd	88.2	20.6	3.8	10.2	35.2	248.7
		3rd**	12.2	12.2	3.1	10.7	20.7	162.7
		Total	210.2					
LSD at 5% level.			26.8	2.4	0.5	2.2	5.0	53.1

Note. *: 15% water contained. **: 70% of 3rd ear of three-eared plants were barren

ear yields of three-eared plants were lower than those of two-eared plants, and because 70% of the third ear were barren. This may also be explained physiologically as the photosynthetic substances may have been dispersed to three ears, resulting in small ears and furthermore, photosynthates distributed to the third ear may not have been enough to produce normal size of ear. Yield of one-eared plants was lower than that of the first ear in two-eared plants, but higher than that in three-eared plants.

Ear length, ear diameter, number of grain per

Fig. 3 Changes of dry matter weight of each ear on one-, two- and three-eared plants

Note. Symbols are the same with Fig. 1

—: 1st ear. - - - : 2nd ear
 : 3rd ear

row and thousand kernel weight were respectively lower in the second and the third ears. These characteristics also indicated significant positive relations with grain yield of all individual ears in Hokko 22, including that of Koh 4. In contrast to this, number of row per ear was slightly, but not significantly, higher in the second and the third ears. So due to the seed size, grain yield in Koh 4 was superior to that of every individual ears in Hokko 22.

Bauman (1960)²⁾ pointed out that the first ear

Fig. 4 Time trends in leaf area per plant, CGR per plant, NAR and Er

Note. Symbols are the same with Fig. 1

$$ER = \frac{1}{\text{Root d, wt.}} \frac{dw}{dt}$$

showed apical dominance and also the ability to grow larger than the second ear. It was confirmed in our experiment, as shown in fig. 3. Ear dry matter accumulation rate in the first ear was higher than that in the second or the third ears throughout reproductive stage.

Growth analysis

From growth analysis data, time trends in leaf area per plant (LA), crop growth rate per plant (CGR), net assimilation rate (NAR) and efficiency of root to dry matter accumulation (ER) are shown in fig. 4. Trends in each growth parameter differed considerably between hybrids. Koh 4 had lower values in LA, CGR and NAR than Hokko 22 during reproductive period. In Hokko 22, LA values of plants with different ear numbers are almost same at each sampling date, though leaf dry matter weight was different among them. This is due to lower specific leaf area in plants with more ear numbers. On the other hand, value of CGR was higher in plants with larger number of ears throughout reproductive stage. The differences in CGR value between more than two-eared and one-eared plants were very large. The same pattern was found also in NAR, showing high positive correlation ($r=0.950$, significant at 0.1% level) with CGR. These results indicate that higher dry matter accumulation rate in plants with larger number of ears are supported not by LA but by NAR, probably due to some inner factors concerning photosynthetic activity, since all individual plants were grown under the same environmental conditions.

Generally speaking, the potential activity of photosynthetic apparatus might be genetically less variable among plants within intra-hybrids. Photosynthetic activity and/or NAR were suggested by many workers to be affected by sink size⁹⁾¹⁰⁾¹²⁾¹³⁾. Another factor, influencing photosynthesis, may be activity and/or amount of root system. Reductions of photosynthesis under soil moisture stress conditions have been observed by many workers¹³⁾⁷⁾⁸⁾. Also, Runge (1968)¹¹⁾ reported that corn was most sensitive to soil moisture stress during a period surrounding pollen shedding. Fulton (1970)⁵⁾

found in corn that moisture stress at later stage of development also caused substantial reduction in yield. Plants with profuse root system may have an advantage in absorbing fertilizer and available moisture under soil moisture stress condition due to insufficient rainfall and competition within high population density. This seems also to guarantee indirectly high photosynthetic activity and/or NAR during growing season.

If sink size is the main factor to affect NAR, distribution ratio of dry matter to ear part ($\Delta E/\Delta W$) may be higher in plants with larger number of ears and indicate high positive correlation with NAR. As for effect of root system to NAR, it must be tested distinctively in two points, namely, qualitatively and quantitatively. For estimation of the qualitative effect, the efficiency of root to total dry matter accumulation (ER) was calculated from the formula of NAR, using root dry weight instead of leaf area. As indicated in fig. 4-D, there were little differences in ER among plants which differed in ear numbers. This fact indicates that qualitative effect is independent of factors changing NAR. In order to evaluate the quantitative effect on NAR, we made an index, $\bar{R}/\bar{L}$, the ratio of mean root dry weight per unit leaf area. When this ratio is high, photosynthetic activity per unit leaf area may be supported highly by sufficient nutrients and moisture uptake, if nutrients and/or moisture are limiting factors.

Then, correlation coefficients between NAR and $\Delta E/\Delta W$, $\bar{R}/\bar{L}$ and dry matter accumulation

Table 3 Correlation coefficients between NAR and three other growth parameters

Simple correlation coefficient.			
NAR- $\bar{R}/\bar{L}$	0.990**	$\bar{R}/\bar{L}-\Delta E/\Delta W$	0.129
NAR- $\Delta E/\Delta W$	0.160	$\bar{R}/\bar{L}-\Delta E/\text{day}$	0.933**
NAR- $\Delta E/\text{day}$	0.923**	$\Delta E/\Delta W-E/\text{day}$	0.089
Partial correlation coefficient			
NAR- $\bar{R}/\bar{L}$. $\Delta E/\text{day}$		0.927*	
NAR- $\Delta E/\text{day}$. $\bar{R}/\bar{L}$		-0.013	
$\bar{R}/\bar{L}-\Delta E/\text{day}$. NAR		0.354	

*: Significant at 5% level

**: Significant at 1% level

rate of ear ($\Delta E/\text{day}$) were calculated with the data pooled for 3 different ear number types of Hokko 22 at 2 reproductive stages, and presented in table 3.

NAR indicated high positive correlation with both $\bar{R}/\bar{L}$ and $\Delta E/\text{day}$. Also high positive correlation was obtained between $\bar{R}/\bar{L}$ and $\Delta E/\text{day}$. But $\Delta E/\Delta W$ was not correlated to NAR and the values were lower in plants with larger number of ears (Average value of $\Delta E/\Delta W$ for 2 stages was 99.5, 95.6 and 92.2% in one-, two- and three-eared plants, respectively). Furthermore, a high significant partial correlation was recognized only between NAR and $\bar{R}/\bar{L}$, indicating all the other correlations non-significant.

From the facts described above, it may be concluded that plants with profuse root system may permit not only to develop more than two potential ears at silking stage, but also to maintain high NAR during reproductive period, which resulted in producing more than two harvestable ears. Also, it may be suggested that prolific character may express its full capacity, only if accompanied with profuse root system. This hypothesis may well explain prolific character to well adapt to various environmental conditions at least in intra-hybrids. Next problem in this study is to examine whether this facts exist in interhybrids.

SUMMARY

For better understanding prolific characters, differences in dry matter accumulation among one-, two- and three-eared plants, of semi-prolific hybrid, were measured under the field condition, giving the following results.

1. More than two-eared plants had higher dry matter weight in each organ than one-eared plants, especially in ear and root system.
2. Total grain yield per plant was the highest in two-eared plants. The first and the second ear yields of three-eared plants were lower than those of two-eared plants and also 70% of the third ear were barren.
3. CGR per plant during reproductive period was higher in plants with larger number of ears,

being supported not by leaf area, but by NAR.

4. NAR indicated high positive correlation with $\bar{R}/\bar{L}$, the ratio of mean root dry weight per unit leaf area, and dry matter accumulation rate of ear. Moreover, a high significant partial correlation was recognized between NAR and $\bar{R}/\bar{L}$.

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〔和 文 摘 要〕

トウモロコシの多穂性に関する生理・生態学的研究

第1報 着雌穂数を異にする個体における乾物生産特性の差異について

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多穂型トウモロコシ (prolific type corn) は、これまで一般的に栽培されてきた1穂型系統 (single ear type corn) に比べ、環境に対する適応性に優れていることが報告されている。本研究は、この原因を解明する目的で、比較的2穂を着生する頻度の高い北交22号を用い、着雌穂数を異にする個体の乾物生産特性の差異について比較、検討を行なった。

1) 絹糸抽出期において、草丈、葉数は着雌穂数を異にする個体間で有意差は認められなかったが、乾物重はいずれの部位においても着雌穂数の多い個体ほど大きく、特に根部における差異が顕著であった。絹糸抽出期におけるこれらの差異は登熟期間中も継続した。

2) 個体当雌穂乾物重は3穂着生個体で最も大きかったが、子実重は2穂着生個体が最大であった。3穂着生個体における1段目(最上位)および2段目雌穂の子実重は、2穂着生個体におけるものよりやや小さく、また3段目雌穂の70%は不稔であった。2穂および3穂着生個体において、子実重、穂長、穂径、1列当子実数、千粒重の各形質はいずれも1段目雌穂ほど大きかったが、粒列数は下位雌穂ほど多くなる傾向が認められた。

3) 個体当葉面積は、葉乾物におけると異なり、着雌穂数の異なる個体間に差異が認められなかった。これは着雌穂数の多い個体ほど比葉面積が低く経過したことによる。これに反し、個体当乾物増加速度および純同化率は着雌穂数の多い個体ほど高く推移し、両者の間には生育期間を込みにして正の有意な相関が認められ、乾物重の差異は葉面積ではなく、純同化率の差異によってもたらされたことが明らかとなった。

4) 登熟期間中における純同化率と各生長パラメーターとの関係を検討したところ、純同化率は雌穂乾物増加速度および $\bar{R}/\bar{L}$ 比(根の平均乾物重/平均葉面積)と強い正の相関を示した。また、3者の偏相関係数について検討した結果、純同化率は $\bar{R}/\bar{L}$ とのみ有意な相関を示すことが明らかとなった。

以上の結果から、2穂および3穂着生個体は、単位葉面積当りの根の割合が高く、根からの養水分吸収が充分に行なわれ、この結果同化能力がフルに発揮され、純同化率が高まり、子実収量が増大したものと解される。