Developmental Morphology and Yield Determining Process of Maize

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The growth stage concept is necessary to elucidate yield determing process of maize, because developmental progress of yield components is implicated with definite growth stages. Hanway[5] presented the growth stages concerned with Corn Belt varieties in 1963, and which have been widely used for agronomic purposes until the present.

In the present paper, the authors propose the growth stages of maize to be applied to agronomic studies and cultural practices, on the basis of the knowledges obtained by studies on developmental morphology of maize. The number of collars, a joint part between blade and sheath in a leaf, and grain development, as visual indices, have received considerable attention in our studies. Transitional changes in both of them are easily identified by field observations. The authors also introduced the phytomer concept to pursue the growth of organs and the development of axillary buds produced on the main stem in a maize plant.

Terms and criteria used for data determination are shown in Table 1 and 2. The proposed growth stages and their identifying visual indices[8] are presented in Table 1. The vegetative, reproductive and ripenning phases of maize correspond to the periods from stage 1 to 2, from stage 2 to 5 and from stage 5 to 7, respectively. The lag period[3,6] and grain filling period,[6] or EFPD (Effective Filling Period Duration)[2] coincide with the periods between stage 5 and 6, and between stage 6 and 7, respectively.

Phytomers of the main stem

A phytomer includes the sequence of structures produced by meristematic tissues contiguous to a leaf primordia. From top to bottom, a phytomer consists of blade, sheath, internode (even though not visibly elongated), axillary bud (or potential thereof), and node.[4] Applying this definition to our experimental results, the phytomers produced on the main stem can be classified into the following gruops.

1) Cotyledon-phytomer, phytomer 1 to 5

These phytomers are initiated during the process of embryogeny. The foliage leaves produced on these phytomers contribute to early growth of plant and then die successively from bottom to top until the silking stage. The internodes do not elongate. The adventitious roots develop around the nodes and increase acropetally in number. The axillary buds occasionally develop into suckers (tillers) under sparse population and high nitrogen conditions.

2) Phytomer 6 to i

Phytomer i will develop a reproductive ear on its axillary bud. Almost all axillary buds initiate young ears basipetally. The leaf area of each leaf increases with increment of leaf positions. The maximum leaf area is attained on phytomer i-1 or i-2. These leaves contribute to vegetative growth and reproductive development and then die prior to physiological

Table 1. Terminology and criteria for proposed growth stages of maize, and identifying visual indices in the field

Growth stages	Development events	Identifying visual indices
1. Emergence stage	—	Coleoptile emergence
2. Tassel differentiation stage	Differentiating branch primordia on the base of elongated shoot apex	Number of collars visible
3. Ear difierentiation stage	Differentiating spikelet primordia in the uppermost axillary bud	Number of collars visible
4. Transitional stage of leaf emergence rate	Beginning of rapid internode elongation	A turning point of increasing rate of collars
5. Silking stage	Seed setting, or fertilization	First emergence of silks from the tip of husks
6. Initial stage of starch accumulation	Beginning of starch accumulation in the endosperm of grains	External colour change, milky white to paly-yellow, on the grain surface
7. Initial stage of physiological maturity	Ceasing dry matter accumulation in the grains	Black layer visible in the upper grains of an ear

Table 2. Terminology and criteria for development of tassel and ear

Stages:	Developmental events
Tassel	
A:	Vegetative shoot apex
B:	Elongating the shoot apex prior to tassel differentiation
C:	Differentiation of the branches on central axis (Tassel differentiation stage)
D:	Beginning of the differentiation of the spikelet initials, and developing of the basal branches
E:	Differentiation of the empty glumes on the central axis
F:	Beginning of the differentiation of anthers in the upper flower
G:	Development of the silks
H:	Fully differentiated spikelet stage by indications of yellow anthers and chlorophyll accumulation in glumes
Ear	
a:	Vegetative shoot apex on axillary bud
b:	Elongating the axillary shoot apex prior to ear differentiation
c:	Differentiation of branch primordia (Ear differentiation stage)
d:	Beginning of spikelet differentiation by an unequal division of the branch primordia
e:	Differentiation of the empty glumes
f:	Beginning of the differentiation of anthers in the upper flower of a pair of spikelets
g:	Beginning of the differentiation of silks
h:	Silk elongation
i:	husk emergence
j:	silk emergence (Silking stage)

Note: Alphabets indicating the stages show the developmental events occuring in that order, and are used in Figure 1. Designation of the developmental events of tassel and ear is referred from Bonnett (1940).

maturity under favorable conditions. The internodes elongate and increase successively in length.

3) Phytomer i+1 to n

Phytomer n bears a flag leaf. Leaf area decreases toward the top leaf. The leaves contribute to grain filling exclusively. The length of each internode is more or less same when there is no extreme water stress. The axillary buds can not be observed with the naked eye.

4) Tassel-phytomer

The uppermost leaf primordium metamorphoses into the tassel by flower induction. The internode is considered to become the peduncle from the node base of tassel to the lowest branches of the tassel.

In the following sections, the detailed explanations of developmental morphology and development of yield components, in relation to the proposed growth stages will be given.

Leaf growth, and differentiation of tassel and ear

The growth of leaf length of each phytomer fitted with the Robertson's growth equation. The infection point of a growth curve and the actual growth rate were calculated by using the formula. According to the result,[7] the actual growth rates were related to final leaf length. The infection points of phytomer 1 to 5 were situated in the period between emergence and tassel differentiation stages and those of phytomer 6 to i in the period between tassel and ear differentiation stages. Phytomer i+1 to n had their infection points on and after the ear differentiation stage. The infection point of the phytomer with maximum leaf area was at the time of ear differentiation stage.

External leaf growth of a whole plant can be observed by the increase in number of visible collars which was represented by two linear equations connected at a point, the

Table 3. Relationships between the number of collars visible and tassel and ear differentiation stages

Variety	No. of collars visible at the differentiation stage of		Phytomer i*	Phytomer n**
	Tassel	ear		
Japanese varieties				
Azuma-yellow	5	9	13,14	18.0
Takanewase	5	9	14,15	19.7
Kho No. 3	6	10	14,15	19.7
Chokho B 411	6	10	14,15	20.7
Chokho No. 161	7	11	15,16	21.2
Kho No. 9	7	11	15,16	20.8
Mutsumidori	7	11	16,17	22.4
Introduced varieties				
Golden Cross Bantum	5	7	11,12	16.0
P-3715	6	9	12,13	17.9
G-4553	6	9	13,14	18.5
P-3422	6	9	13,14	18.8
P-3382	6	9	14	18.6
G-4810	6	9	14,15	20.6
XL-1214	7	11	15.16	23.1

* Either of two successive phytomers shown below produced a reproductive ear.
** Average number of phytomers grown by May-planting in Kyoto.

turning point. The increasing rate of collars was more rapid in the first half before the turning point than in the second half after the turning point. The turning point of leaf emergence occurs as a result of rapid and simultaneous elongation in the upper internodes.[9] The relationships between the number of visible collars and the differentiation stages of tassel and ear are shown in Table 3. The number of collars at the both stages were related to the total number of phytomers produced with foliage leaf. The relationship given in each variety was retained for different planting dates. This suggests that the number of visible collars can be used as an indication for identifying the tassel and ear differentiation stages, although the number itself varys with different varieties.

Development of tassel and ear, and internode elongation

Time-relationships between development of the tassel and ears and internode elongation were observed by using four varieties with different maturities. The result of a cultivar, Takanewase is shown in Fig. 1. Tassel differentiated on the shoot apex, when the collar of phytomer 5 emerged. As soon as the collar

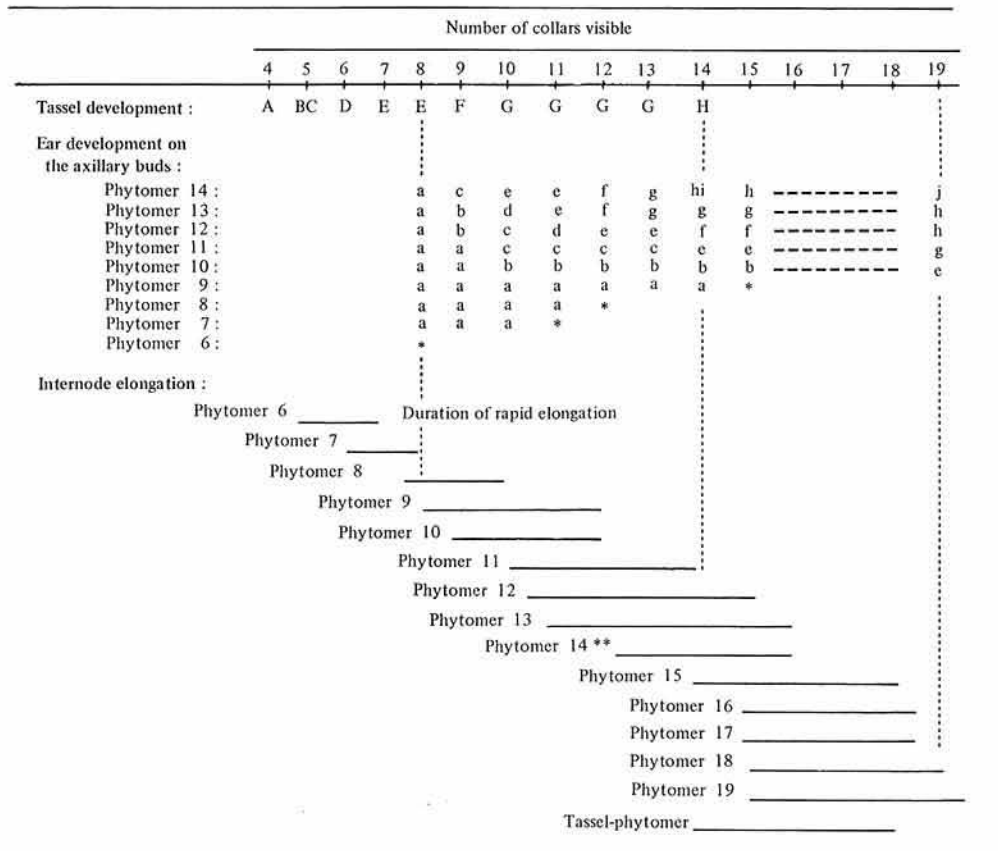

Fig. 1. Time-relationships between development of tassel and ears and internode elongation with reference to the number of collars visible. Alphabets indicate the developmental events shown in Table 2. (cultivar Takanewase, unpublished data)

Note *, the axillary bud died; **, Phytomer 14 produced a reproductive ear.

of phytomer 9 emerged, the ear differentiated on the axillary bud of phytomer 14. When the collar of phytomer 10 emerged, the empty glume initiated on the ear of phytomer 14, spikelet primordia differentiated on the ear of phytomer 13, and branch primordia on the axillary buds of phytomer 11 and 12, respectively. The ear of phytomer 14, thereafter, developed more preeminently than the others. The axillary buds of phytomer 6 to 9 continued to be vegetative and died by the silking stage. When the collar of phytomer 14 emerged, the silks began to elongate in its axillary ear. At this stage, the number of spikelet primordia ceased to increase in the uppermost ear and the tassel reached its final stage of development.

The internode elongation, commencing with tassel differentiation, occured in phytomer 6 and extended to the upper phytomers. The internodes of phytomer 6 to 14 elongated in the period during which the tassel development completed and the silks began to develop in the upper ears. The internodes of phytomer 15 to 19 elongated simultaneously in the period of silk development. There was a co-growing relationship between the peduncle of tassel-phytomer and the internode of phytomer 15.

As the results, the number of potential rows is determined at around the ear differentiation stage which might be easily identified by the number of visible collars. The number of potential spikelets is determined by the initial stage of silk elongation, in spite of indeterminate characteristics of ear development. This stage may be approximately identified by the collar of phytomer i in the field. The number of potential ears is determined in the period between the ear differentiation and silking stages. The number of reproductive ears, however, may be determined during the silk development period. The yield capacity represented by three components will be determined through the seed setting or fertilization at the silking stage.

Grain growth and a role of stem

When the silks emerged, the cob, ear shank and husks began to grow rapidly. The grains consisted of nucellus mainly. The embryo and endosperm were initiated 4–5 days after the silking. The cob, ear shank and husks ceased to grow, as the grain reached the blister stage. A couple of days after this stage, a pale-yellow color appeared on the grain surface. This color change coincided with the beginning of starch accumulation in the endosperm and the differentiation of plumule and radicle in the embryo. Thereafter, the leaf primordia of phytomer 1 to 5 were initiated successively. The black layer appeared in the upper grains of an ear. This indicated that the grain reached the initial stage of physiological maturity. Another 7 to 10 days were required to observe the black layer in entire grains.

The grains per ear indicated a linear growth in dry weight during the grain filling process between the initial stages of starch accumulation and physiological maturity. The grain growth may be affected by the rate of starch accumulation depending upon phytosynthesis of and length of grain filling period. Furthermore, contribution of stem to the grain growth must be mentioned, because carbophydrates are accumulated in the vegetative organs, particularly in the stem, during the lag period, and then are translocated into the grains.

Water contents, brix readings of phytomers and their C.V.s during the grain filling period are shown in Table 4. Some morphological characteristics observed at the silking stage are also presented in the Table. The water contents decreased rapidly from top to bottom in the lag period. There, however, was little fluctuations in water content during the grain filling period. The water contents of successive phytomers declined from bottom to top. On the contrary, the brix readings increased in every phytomers during the lag period. In particular, the brix readings of phytomer 15 to tassel-phytomer increased remarkably

Table 4. Morphological characteristics, water content and brix reading of each phytomer during the grain filling period (cultivar Takanewase)

Phytomer on main stem	Leaf area (cm^2)	Internode (cm^3)	Water content		Brix reading (%)		
			mg/cm^3	C.V.%	Range	Mean	C.V.%
6	236	—	—	—	—	—	—
7	321	30.4	889	1.5	1.5— 4.5	2.6	38.6
8	509	54.0	901	1.0	1.4— 4.2	2.4	38.7
9	590	75.7	880	1.8	1.6— 4.2	2.6	32.9
10	724	81.8	835	3.3	1.8— 4.2	2.9	28.2
11	809	87.1	782	4.1	2.7— 5.8	4.0	24.9
12	857	99.8	683	6.7	5.0— 6.7	5.6	11.1
13	853	101.1	597	4.7	6.6— 7.9	7.1	6.4
14*	811	87.3	522	4.9	8.0— 9.2	8.6	5.5
15	767	66.7	464	4.0	8.9—10.0	9.5	3.7
16	676	47.1	439	5.5	9.1—10.5	9.7	4.4
17	565	32.9	437	1.4	8.8—10.3	9.7	4.8
18	369	24.2	444	3.4	8.0—10.1	9.4	7.2
19	172	17.8	446	2.0	7.9— 9.6	8.7	5.9
Tassel	—	13.6	443	2.7	7.8— 9.8	8.5	8.3

Note: Brix readings were taken at the middle portion of each internode sampled at noon every three or four days.

from ca. 4.0% to 8.0%. The fluctuations of brix readings during the grain filling period were smaller in phytomer 13 to tassel-phytomer than in the lower phytomers. The transitional change of brix reading of each internode was confirmed by that of dry weight of each internode evaluated on cubic basis. When the ear entered into the physiological maturity, further increment of the brix readings was observed. This result[10] was obtained in a favorable condition in Kyoto. This, however, suggests that the internodes of phytomer 6 to i elongated in the period during which the number of potential spikelets is determined might play an important role to adjust the grain growth during the grain filling period, particularly under unfavorable conditions such as low light intensity and accidental frost.

Consequently, the number of grains and 1000-grain weight will be determined by three factors: the rate of starch accumulation, the length of grain filling period and the amount of carbohydrates redistributed from the stem.

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