Morphological Bases of Shoot Growth to Estimate Tuber Yields with Special Reference to Phytomer Concept in Potato Plant*

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Received April 30, 1978

There have been many studies on the developmental morphology of various organs in potato plant, but few have been made on the gross morphological characteristics as a whole plant in relation to the establishment of final tuber yields.

Observation of a plant with stem-leaf relationship was made for the first time more than a hundred years ago. OGURA¹²⁾ outlined this point in his writing (Plant Morphology) as follows. "GOETHE (1790) considered stem and leaf as different parts arisen from the same primordia. Extending this opinion, GAUDHAUD (1841) concluded that a crop plant was composed of segmental unit called phyton or phytomer and each phytomer was a part of stem or leaf."

EVANS and GROVER²⁾, SCHARMAN¹⁵⁾ supported this phytomer unit concept. EVANS³⁾ revealed some details of a phytomer in grasses as defined following. "A phytomer includes the sequence of structures produced by the meristematic tissue contiguous to a leaf primordium. From top to bottom, a phytomer consisted of blade, sheath, internode, axillary bud and node."

There are several works accepted the phytomer concept in Japan. SEKO *et al.*¹⁴⁾ found systematic changes in elongation and dry weight of organs at each node in rice paddy. TANAKA¹⁷⁾ insisted upon a functional unit in rice plant and demonstrated that the development of the crop should be considered as an assembled body containing many units of different ages. Under such a consideration, nutro-physiological invest-

igations were carried out. KAWATA *et al.*⁷⁾ introduced the phytomer concept into the root investigation in rice plant and found many interesting informations.

Thus, the phytomer concept was applied by some researchers for the study of Gramineae plant, but works to apply for the establishment of crop yields were few. In this paper, shoot growth with special reference to phytomer unit was observed in potato plant to predict final tuber yields.

Materials and Methods

Experiment 1. Some observations of gross morphological regularity as a whole plant (1975)

1. Structures of a phytomer

Seed tubers of two main crop varieties, Danshakuimo (early) and Norin No. 1 (medium-late) were selected from each weight grade 60-70 g per tuber. Ten tubers per variety were put in a locker under a dark condition immediately after harvesting on late of October in 1974. On 18 May in 1975, tubers having emerged sprouts were took out from the locker and observed the organs of which a phytomer was composed.

2. Relation between flower stalks and branches in node position

Danshakuimo and Norin No. 1 were planted on 25 March in 1975. Fertilizers were applied 10.6 kg per 10a in N, P₂O₅, and K₂O respectively. Seed tubers were planted 70 cm apart in row width and 35 cm within row (4,082 hills per 10 a). Single stem was remained per hill detaching the others in early stages of growth. The experiment was performed at the Tottori University Farm on a sandy loam. Morphological observation was conducted during

* The outline of this paper was presented at the 160th meeting of the Crop Science Society of Japan, October 16, 1975.

the course of growing periods on the node positions between flower stalks and branches in various parts of the shoot.

Experiment 2. Morphological variations of shoot growth in various parts of a crop plant as affected by varieties and planting dates (1976)

The experiment was made to determine whether morphological regularities could be found in various parts of an individual plant or morphological variations of the shoot would be useful indices to predict the tuber growth.

Danshakuimo and Norin No. 1 were planted at different dates (optimum planting: 25 March and late planting: 30 June) in 1976. For the purpose of inhibiting the senescence of seed tubers, they kept in a cool storage house (mean temperature 1–3°C). Fertilizers, planting pattern, miscellaneous cultural practices and the experimental field were similar to those of experiment 1. Quantitative characters such as leaf length, stem thickness, length of internode, length of branch in each node were measured immediately after their growth stopped so as to be able to trace back the growth type of a test plant after harvesting.

Results

Experiment 1. Some observations of gross morphological regularity as a whole plant

1. Structures of a phytomer

Because the seed tubers were stored under a dark indoor condition till late Spring, the sprouts elongated 30–50 cm and the length of their internode reached more than 10 cm showing remarkable spindly growth. Therefore, systematic arrangement of the component organs of a phytomer was clearly observed as shown in Fig. 1 which was reproduced from the writings^{9,10)} to deepen a better understanding for the results.

In the underground main stem, each phytomer consisted of, from top to bottom, leaf (degenerated), upper root, internode, lower root, axillary bud (stolon), and node, but in the aboveground main stem, it consisted of leaf blade, petiole, internode, axillary bud (branch) and node. In consequence, phytomer concept can be applicable in

potato plant as well as Gramineae plant. However, on account of the phyllotaxis of the plant, which is different with gramineous plant, observation with node unit may be convenient when occasion demands.

2. Relation between flower stalks and branches in node position

A question occurred to the node position of flower stalk when the main stem was observed from base to top. On the other hand, it has been noticed by experience that a vigorous branching appeared near a flower stalk. The present observation was carried out to ascertain the relation between these two organs with a view point of phytomer unit. Observations were summarized to:

- 1) Flower bud appeared on the top of the main stem about 25–30 days after planting, so called at “flower-bud-appearing stage”.
- 2) Branches arose from an axillary bud of a phytomer on the main stem, but flower stalks seemed to grow directly out of the main stem.
- 3) Phyllotaxis generally fell into disorder at the leaf which arose from one or two

Fig. 1. Systematic arrangement in component organs of which a phytomer is composed (A), and schematic patterns in sprouting stem as an accumulation of several phytomers (B).

L-leaf, Ur-upper root, In-internode, Lr-lower root, Ab-axillary bud (stolon), N-node. On the aboveground main stem, Ab is branch.

lower node than that of a flower stalk.

Because a flower bud was considered to initiate on the shoot apex, the flower stalk must be a final organ on the main stem. Accordingly, the shoot so far known as a main stem (shoot) should be understood as consisted of the main stem and sympodial branch. It was found that sympodial branch usually arose from the phytomer one or two unit lower than that of flower stalk and was vigorous compared with those arisen from adjacent several phytomers but for immediately below one (Fig. 2-A). Regular patterns between flower stalks and sympodial branches in node position mentioned above were found not only on the main stem but also on any branches which borne flower stalks as shown in Fig. 2-B, which was reproduced from the writings^{9,10)}. There was varietal difference in the growth of sympodial branch, being small and weak in Danshakuimo and great and vigorous in Norin No. 1.

From these observations, the results can be concluded as follows.

1) In the main stem, primary sympodial branch arose out of the phytomer immediately below the first flower stalk. When this sympodial branch grew to have a flower stalk which so far called as secondary one, secondary sympodial branch appeared at the same manner. Therefore, the shoot which has been believed as the main stem consisted of "the main stem" and subsequent some sympodial branches.

Consequently, "the main stem in appearance" should be more suitable expression for the main stem (shoot). In this paper, the writer intended to distinguish "the main stem" with "the main stem in appearance" hereafter.

2) Branches grew at lower portion of the main stem were monopodial branches, and when they grew to have a flower stalk, they also differentiated sympodial branches as the same pattern.

3) In any shoots, monopodial branches always arose from a node immediately below the sympodial branches and these branches grew together as looked like a dichotomous branching.

Such structural regularity as the arrangement of component organs in a phytomer, the constant relations between flower stalks and sympodial branches in phytomer position, and dichotomous-like branching should be useful index to diagnose the shoot growth with special reference to tuber growth in potato plant.

Experiment 2. Morphological variations of shoot growth in various parts of a crop plant as affected by varieties and planting dates

1. Constitution in number of phytomers

Constitution in number of phytomers was shown in Table 1. On the underground main stem, both varieties had 5–6 phytomers, but on the aboveground main stem, *i.e.* on the main stem, Danshakuimo and Norin No. 1 had 13–14 and 15–17 phytomers respectively in optimum planting. Namely there were found some differences. Table 2 showed characters of primary stolons at each node and an example of tuber bearing patterns was reproduced from the writings^{9,10)} in Fig. 3. A stolon was found to have several phytomers from the observation of root initiation at each node. In spite of the length of stolon, number of phytomers was almost constant in optimum

Fig. 2. Constant relations in node position among flower stalks, sympodial branches and monopodial ones.

A-the primary flower stalk (cluster) and primary sympodial branch on the main stem. B-all shoots of individual crop in Norin No. 1. MS; main stem, SB; sympodial branch, MB; monopodial branch. Figure shows a rank, *i.e.* 1; primary, 2; secondary and so on.

planting. Primary sympodial branch of Norin No. 1 had 5–7 phytomers and differentiated secondary one from the node immediately below the second flower stalk (Fig. 2-B). Secondary sympodial branch also had 5–7 phytomers and differentiated thirdly one as the same pattern.

Monopodial branches which arisen from the lower nodes on the main stem generally had 11–12 phytomers irrespective of their node position initiated. In other words, their flower bud appeared at a constant node position.

As mentioned above, there was gross morphological regularity in number of phytomers in normal grown potato plant, but it fell into disorder under unfavorable conditions such as late planting. In general, missing of flower stalk or sympodial branches occurred. Moreover, Danshakuimo which has a weak branching habit grew vigorous main stem in appearance to have few sympodial branches. Contrarily, Norin No. 1, a vigorous branching variety, grew almost similar to that in optimum planting.

2. Changes of morphological variations in each organ with node positions

Regarding potato plant as an accumulation of segmental unit of phytomer, the growth must be considered to start from lower phytomer to upwards subsequently. Then, it was deduced that morphological changes of each organ of which a phytomer was composed should have a different function for tuber growth. Leaf length and stem thickness at each node on the main stem in appearance were shown in Fig. 4. In optimum planting, leaf length increased at the lower phytomers and reached a maximum at about 10th node, then declined subsequently. But such a tendency was not so remarkable in late planting.

Changes of stem thickness with node positions showed a similar trend to those of leaf length. In optimum planting, it reached a maximum at 2nd or 3rd node and declined subsequently.

Fig. 5 indicated a plant type with branch length in abscissa and stem length in ordinate. In optimum planting, monopodial

Table 1. Number of phytomers in various parts of the shoots in potato plant.

	Under-ground main stem	Above-ground main stem	Sympo- dial branch	Mono- podial branch	Total**
D-1	5—6	13—14	—	—	19
D-2	7—8	(15—18)	10—12	16—17	34
N-1	5—6	15—17	5—7	11—12	37
N-2	6—9	(17—18)	7—8	14—16	36

D=Danshakuimo, N=Norin No. 1,

1=optimum planting (March 25),

2=late planting (June 30).

Figures in parenthesis were obtained from few cases.

*Arose out of lower portion on the main stem.

**Number of phytomers on the main stem in appearance.

branches arose chiefly at the portion below 10th node, and the maximum one reached about 80% in length for the main stem in appearance. This fact showed that these monopodial branches developed together with the main stem favorably in early stages of growth. On the contrary, in late planting, though the main stem in appearance was accelerated in length, the longest monopodial branch reached only about 60% to it.

If the main stem in appearance was measured with every ten node intervals, the height of 10th node in optimum planting was superior to that in late planting. But stem length of 10–20th or 20–30th node interval was respectively longer in late planting than in optimum planting. Besides, node positions at flower stalks or sympodial branches and relative relations in node position between two organs fell into disorder for both varieties in late planting.

Patterns of primary stolons were shown in Table 2 and Fig. 3. In optimum planting, they arose out of each node of the underground main stem without failing tuber formation corresponded with favorable monopodial branching at lower portion on the main stem. In late planting, there were sometimes found stolons which failed tuber formation corresponded with no branching at a few node on the base of the main stem. As a results, it may be concluded that leaves derived from lower phytomers either on the

Fig. 3. Tuber bearing patterns with special reference to phytomer unit at the stage of maximum vegetative growth in Danshakuimo.

Primary stolons arise at six phytomers on the underground main stem. Primary stolon (tuber); 1, 2, 3, 4. Secondary tubers; 5, 6, 7. Each stolon consists of several phytomers.

main stem or on the monopodial branches seemed to have a close relation with the development of stolon or tuberization. Final tuber yields were shown in Table 3.

These results justified a possibility to express plant types with 1) patterns of leaf length at each node on the main stem and 2) the growth patterns of sympodial branches on the main stem in appearance. Plant types thus obtained were: D-1; the main stem type having large and long leaves, D-2; the sympodial branching type having small and short leaves on the main stem, N-1; the sympodial branching type having large and long leaves on the main stem, N-2; the sympodial branching type having small and short leaves on the main stem.

Large and long leaves on the main stem might result from a normal growth in early stages. Generally, number of leaflets in a pinnate compound leaf increased with the node position upwards and the complete compound leaf appeared at 7–8th node for the first time. Vigorous monopodial branches usually initiated from the nodes having such a incomplete compound leaf at the lower portion of the main stem, and seems to have an important role for expanding leaf area in early stages of growth. When

Fig. 4. Changes of leaf length and stem thickness at each node on the main stem in appearance as affected by varieties and planting dates.

See legend of Table 1 for further explanation.

the growth in early stages is normal, subsequent growth tends to become favorable. Remarkable decline of leaf length at upper portion of the main stem suggests an effective translocation of photosynthate from the shoots to stem tubers.

On the contrary, small and short leaves on the main stem resulted from an abnormal growth in early stages and the later growth tended to become unfavorable. The growth of sympodial branches on the main stem in appearance was seriously influenced with the environmental conditions even though varietal differences were recognized.

Discussion

Establishment of tuber yields in potato plant starts with an initiation of stolons and follows their tuberization caused by the translocation of photosynthate from the leaves. Since stolons as well as leaves are component organs of a phytomer, the growing behavior can be considered as the accumulation of phytomers with changes of time. That is to say, tuber yields must be established with the connection of leaves (top) and tubers (underground portion).

Constancy in number of phytomers at the portion of underground main stem was supported by KURIHARA *et al.*⁸⁾ who

Fig. 5. Patterns of stem length, length of internode, branch length and flower stalks on the main stem in appearance as affected by varieties and planting dates.

Figures show node position on the main stem in appearance at which each branch arisen. *node position at which flower stalk born. ▶ Position of every tenth node.

observed primary stolons did not affected in number with different planting dates. The main stem was constant in number of phytomers maintained by TAGUCHI¹⁶⁾ who found no varietal differences on the date of the first flowering stage.

Number of phytomers in various parts of the shoot seems to be three as a greatest common measure. ARTSCHWAGER¹⁾ showed schematic traces of vascular bundles in potato plant and asserted that these traces could not exceed more than three internodes because of its phylotaxis. It is a matter of question to make clear the relation between morphological regularity and anatomical structures in near future.

Concerning translocation of photosynthates, sink and source concept has become a matter of discussion recently. MOORBY¹¹⁾ found daughter tubers quickly became as dominant "sink" for mineral nutrients soon after they appeared. HOPKINSON⁴⁾ outlined the changes of physiological function of each leaf in *Cucumis sativus* over the course of its life as a sink or a source of carbohydrate and nutrients. HOSHINO *et al.*⁵⁾ reported that the translocation of assimilated carbon from leaves was most rapid in a period of their rapid expansion with ladino clover (*Trifolium repense*). The same trend

was demonstrated by HOPKINSON⁴⁾ in his paper above mentioned.

Many works on patterns of translocation suggest that leaves near by the storage organ (sink) should contribute much more as a source than those far away (TANAKA,¹⁷⁾ PALMER¹³⁾ *et al.*, YOSHIDA *et al.*¹⁸⁾).

From these informations, leaves on the main stem or monopodial branches especially grew in earlier stages may much more contribute for the establishment of tuber yields. This is actually the case. High yield of tubers was obtained in such a plant type as having large and long leaves on the main stem. In addition, maximum monopodial branch reached about 80% in length as compared with the main stem in appearance.

Summary

1. A phytomer of potato plant consisted of, from top to bottom, leaf, upper root, internode, lower root, axillary bud and node in principle, and these organs were arranged with regular patterns (Fig. 1).

2. Constant relations in node position were found between flower stalks and branches. Flower stalk always appeared on a shoot apex whether on the main stem or any branches. As a results, the shoot so far known as a main stem was found to

Table 2. Some characters in primary stolons at each node on the underground main stem at the stage of maximum vegetative growth.

Node* position	Stolon length	No. of phytomers in stolon	Weight of tubers	Stolon length	No. of phytomers in stolon	Weight of tubers
	D-1			N-1		
1	34 cm	4	117 g	38 cm	5	238 g
2	17	4	113	70	4	197
3	42	5	117	40	3	216
4	61	5	120	42	3	30
5	40	4	85	—	—	—
	D-2			N-2		
1	—	—	—	—	—	—
2	—	—	—	—	—	—
3	7	6	14	30	8	—
4	10	5	—	65	8	—
5	8	3	—	3	3	66
6	16	10	17	2	3	9
7	10	5	—	31	5	—

*Number was arranged with node position upwards.

See legend of Table 1 for further explanation.

Table 3. Yield component derived from primary and secondary stolons.

	Number of tubers			Weight of tubers		
	Primary	Secondary	Total	Primary	Secondary	Total
D-1	4.9	1.1	6.0	708 g	38 g	746 g
D-2	4.0	2.0	6.0	284	58	342
N-1	5.8	1.8	7.6	984	20	1,001
N-2	3.3	0.3	3.6	242	31	273

See legend of Table 1 for further explanation.

consist of the main stem and sympodial branches grown subsequently. Moreover, monopodial branches arose from the node immediately below the sympodial branches and both ones grew together as if dichotomous branching. Monopodial branches also grew at the nodes which had incomplete pinnate compound leaf on the base of the main stem (Fig. 2).

3. Regular patterns were also found in number of phytomers in each portion of the shoots as following; the underground main stem, the main stem, sympodial branches either on the main stem in appearance or sympodial branches, and monopodial branches (Table 1, Table 2, Fig. 3).

4. Patterns of morphological regularity as stated above frequently fell into disorder under unfavorable conditions, *i.e.* late planting and some varietal differences were recognized.

5. It seemed reasonable to estimate the growth of potato plant with 1) patterns of leaf length at each node on the main stem, and 2) the growth of sympodial branches on the main stem in appearance. Vigorous growth in early stages could be known with large and long leaves on the main stem and was an essential factor to reach higher yield of tubers for any varieties (Fig. 4, Fig. 5, Table 3).

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〔和 文 摘 要〕

Phytomer (植物単位) よりみたジャガイモの形態的規則性と塊茎収量

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ジャガイモ個体を phytomer (植物単位) の集積と考え、個体における形態的規則性と塊茎収量との関係を明らかにしようとした。

1. ジャガイモの植物単位は、原則的に葉、上位根、節間、下位根、腋芽および節よりなり、これら諸器官の配列は規則的である。
2. 花梗は主茎、分枝を問わず茎端に着生する。しかしそれより 1～2 節下位から仮軸分枝が、またその 1 節下に単軸分枝が発生し、両者が並行的に伸長する。単軸分枝は主茎基部数節からも発生伸長する。
3. 地下主茎、地上主茎、仮軸分枝、単軸分枝の植物単位構成数は、生育が正常の場合それぞれほぼ一定であるが、正常でなくなる場合不規則となる。
4. 地上部の草姿は、1) 主茎 (第 1 花梗まで) 各節の葉の長さ及び、2) 見かけの主茎における仮軸分枝の生長程度であらわすことができ、主茎の葉が長大であることが多収の基本的条件であり、仮軸分枝の適度の伸長は、さらに収量を高める附加的条件である。