Physiological Aspect of Tuberization in Potato Plant

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Potato is not only one of the major crops in the northern part of Japan but also an important winter crop after harvesting rice in southern Japan. The understanding of mechanism on tuberization of potato is a matter of scientific interest from a physiological point of view and also is practically important in the field of agriculture.

It has been generally accepted that potato tuber is morphologically one of the peculiar shapes of stem as a storage organ which is a rich accumulation in starch.

Furthermore the fact that the tuber formation of this plant is controlled with variations of environmental conditions as day-length and temperature, indicates that the tuber would be artificially formed at will on any part of the plant except on root, if the environmental condition is favorable for onset of tuberization.

This concept is supported with a number of evidences. As a typical instance of irregular tuberization, the so-called "sprout tuber" is readily formed on the top of sprout immediately emerged from the senile tubers.

Likewise evidence has been shown that the aerial tuber formation being found on the stem nodes of potato above the ground is a real common appearance, if plants are treated with girdling on the basal part of the stems to retard the downward transport of nutrient substances.

Accordingly, it seems safe to conclude that there are virtually numerous cases of tuberization in the potato plant. It would be, therefore, intriguing to know the fundamental principles of tuber formation of the potato plant from the physiological point of view.

I should like to take this opportunity to briefly review this problem and especially present a speculation to explain the specific effects of some growth substances on tuberization.

Relationship between tuberization and carbohydrates metabolism

In the normal growing phase of the potato plant, the stolon emerges from the node of stem under ground on the fifth day after sprouting, then concomitantly starts to grow linearly until onset of tuberization on the stolon tip. After an elongative growth of stolon for about two weeks or less, the stolon tips begin to swell afterwards to form tubers.

According to histological studies on the progressive development of the stolon and tuber, an accumulation of starch grains started to occur in the vicinity of the endodermis tissue of the stolon tips immediately after ceasing the stolon elongation, and subsequently starch grains spread out all over the tissues of the tuber including the cortex and the pith with an advance of tuber development.

Tagawa and Okazawa have advanced a view with respect to metabolism of carbohydrates in the tubers during their developmental

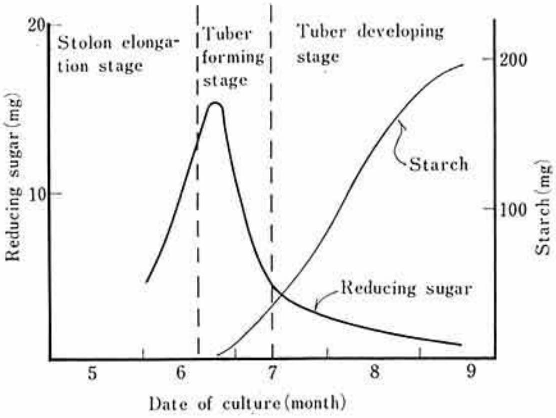

Fig. 1. Changes in reducing sugar and starch in stolon tip and tuber during the development stage

stage.

According to the summarized results of this investigation (Fig. 1), it was ascertained that a maximal amount of reducing sugar was accumulated in the stolon tips just before an initiation of their swelling accompanied with a high activity of their respiration, a gradual decrease of sugar content and an increasing accumulation of starch succeeded concomitant decline of respiratory activity, with a lapse of maturing process of the tuber.

Therefore, these must be the most important significance at the initial stage of tuberization as regards not only the metabolic pattern of carbohydrates but a morphogenesis of the stolon tip.

It also presented a similar evidence as to the initiation of sprout tuber formation, leading one to believe that a temporary accumulation of soluble sugar in the stolon tip may be a prerequisite for tuberization.

It may be concluded from these facts that this accumulated sugar evidently affords a raw material which is necessary for synthesis of the reserved starch in the tuber.

In addition, this tentative interpretation was thoroughly supported by the fact that a rapid decline of soluble sugar content in the stolon tips runs parallel to a gradual increase of starch accumulation immediately after the onset of tuberization (Fig. 1).

Effect of gibberellin on initiation of tuberization

Initiation of tuberization of this plant wholly depends on some environmental conditions such as short daylength, low temperature and so on. These facts are inconsistent with the nutritional theory on tuberization described above because of the unfavorable conditions for photosynthesis of carbohydrate in the potato leaves.

With reference to the evidence reported by Chapman, unfolding leaves of potato plants in the vicinity of the shoot apex have rather less photosynthetic activity than the old matured leaves but are apparently more sensitive to the short daylength responsible for tuberization than the matured ones.

Therefore, an accumulation of sugar in the stolon tips before starting tuberization is one of the analytical results as a consequence of the induction of tuberization.

In order to ascertain this problem, sterile cultures of potato stem segments were performed. The rate of tuber formation on the stem segments cultured on the medium apparently raised proportional to the increase of sucrose concentration in the medium.

However, no tuber formation occurred irrespective of the increase in the sugar content in the medium, if the apical tips obtained just after sprouting were used as cultural materials (Table 1).

Table 1. Effect of gibberellin on tuberization of cultured stem pieces

Materials		Sucrose concentration in the medium (%)			
		2	4	8	12
Stem segment (tuber induced)	−GA	−	±	+	+
	+GA	−	−	−	−
Apical piece of sprout (non-tuber induced)	−GA	−	−	−	−
	+GA	−	−	−	−

+ Means tuber formation and—no tuber formation GA = gibberellin

Accordingly, the tuber formation of potato *in vitro* could not be decided wholly by the excessive supply of carbohydrate from the nutrient medium, but it seems to be greatly depended on a physiological age of the stem tissue.

It failed to form any tuber on the medium being supplemented with gibberellin even when the tuber-induced stem segments were cultured regardless of supplying a suitable concentration of sucrose for tuberization (Table 1).

Therefore, gibberellin may play a more significant and principal role in controlling tuberization than nutrient factor as sugar.

On the other hand, there are accumulated several evidences on occurrence of natural gibberellin in the potato plant. Accordingly, it cannot exclude a possibility that an endogenous gibberellin in potato plants may regulate tuberization.

In fact, it was confirmed that the endogenous gibberellin shows certain variation in content in the leaf blades according to environmental conditions, e.g., a considerable decrease in the amount of gibberellin was recognized as resulting from subjection to short day (8-hr. daylength) and low temperature (13°C), both of which are the most favorable conditions for tuberization.

Similarly, a decline of gibberellin activity in the tuber also resulted, keeping pace with senility of tubers which are stored for a long duration of time over their dormant period.

When the senile tubers were exposed to diffused light in the green house for about a month, these tubers recovered their sprouting activity and also the rate of irregular tuber formation on the sprout declined sharply. The amounts of endogenous gibberellin contained in the treated tubers and sprouts were also found to have increased markedly (Fig. 2).

Furthermore, it was also clearly confirmed that there can be seen a retardation of irregular tuber formation on the senile tuber by soaking treatment with gibberellin solution.

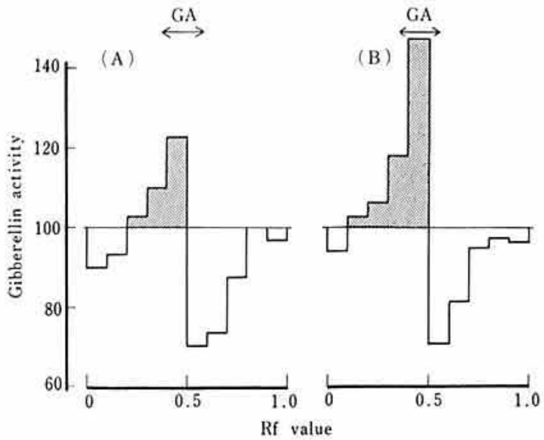

Fig. 2. Effect of light exposed treatment on gibberellin activity in the tuber
A=control, B=treatment

It would be consequently expected a possibility that the endogenous gibberellin may behave in a similar way as that of the exogenous gibberellin.

On the other hand, the tuberization of the non-induced potato plant was stimulated by the treatment with 2-chloroethyl trimethylammonium chloride (CCC), which acts as an inhibitor of gibberellin synthesis in the plant. These facts lead us to a conclusion that the necessity for lowering of gibberellin content to initiate the process of tuberization seems unmistakable.

Effect of cytokinin on initiation of tuberization

Palmer has demonstrated the fact that cytokinin is a stimulating factor of tuber formation of potato sprout cultured *in vitro*. The author has also confirmed the presence of endogenous cytokinin in the developing tuber, and there was a great tendency toward an accumulation of cytokinin in the young tubers (Fig. 3).

On the basis of another finding by means of the tissue culture, cytokinin is indispensable for inducing parenchymatous cells of potato tubers to divide. Accordingly, taking such a role of cytokinin into consideration,

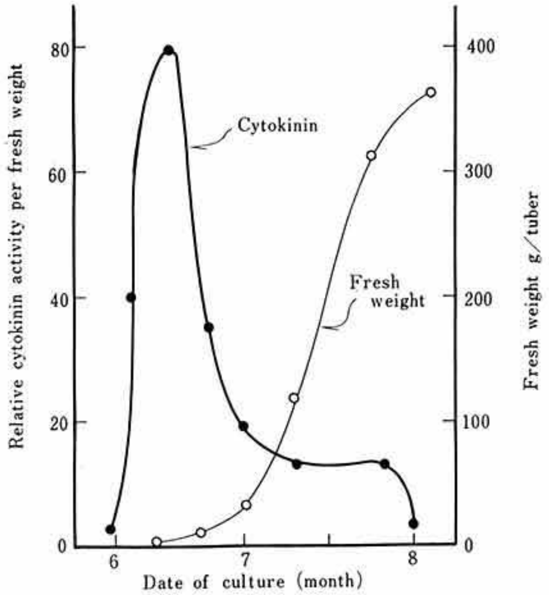

Fig. 3. Change in cytokinin activity and fresh weight of developing tubers

this accumulation of cytokinin seems to produce a beneficial effect on cell multiplication of newly formed tubers.

Several investigations have been reported that the cytokinin may be acting by creating a metabolic sink. This assumption is supported by the evidence pointed out in the earlier publication that the time of beginning of starch accumulation in the newly formed daughter tubers coincided practically with the period when a rapid decline of starch content in the mother tuber started.

The fact, considered with characteristic behavior of cytokinin as natural mobilizing agent of metabolites, supports the view that cytokinin in the tubers would stimulate to translocate the reserve starch from mother tubers to the daughter ones.

Conclusion

Although the mechanism of potato tuberization is not satisfactorily clarified, the several evidences at present are available to conclude that the initiation of tuberization is mainly due to the lowering of endogenous gibberellin activity in the stolon tips.

Increase in cytokinin may be a reflection of the initiation of tuberization, whereby a rapid cell proliferation in the formed tuber would be elicited and carbohydrates would also be mobilized to this locus for starch accumulation.

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