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THE PHYSIOLOGICAL FOUNDATION OF THE TUBER FORMATION OF POTATO

By

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Although very extensive studies of the potato plant have been made, the development of tubers and stolon growth have received very little attention. Studies of the physiological foundation of stolon growth and tuber development are of scientific interest and knowledge of causal factors is of practical value.

Tuber formation of the potato plant arises as the enlargement of the tip of the sprout either underground or above ground in darkness.

Tuberization involves the enlargement of the tip of the rhizome which arises from the underground portion of the sprout and the beginning of tuber growth. Tuberization begins at about the time of flower anthesis. Many factors, including temperature, moisture supply, length of light period and carbohydrate reserve affect the formation and number of tubers. Lateral buds on the rhizomes develop into small tubers giving the appearance of a large set of tubers per plant. A comparatively small number of these, however, continues to grow and develop into large tubers.

The bud of the seed potato occasionally form tuber directly in the dark place, without sprout emergence.

It has also been shown that the seed potato treated with high concentration solution of alpha-naphthaleneacetic acid is arrested to emerge and it sprouts later or forms tuber directly.

Alpha-naphthaleneacetic acid and similar substances, known as growth substance, are now widely used for sprout inhibition of the seed potato and, on the other hand, they are used for the rejuvenescence of the degenerated seed potato to invigorate sprouting.

It may be assumed that the sprout emergence, stolon growth and tuber formation are dependent upon the nutritional condition of the seed potato and the progress of the whole plant, and as the regulator of the condensation and the translocaticn of the nutrients serves auxin, auxin precursor and the synthetic grcwth substances. The experiments are conducted to account for these relationships.

Review of Literature

In 1921, Clark reported that the time of the beginning of tuber formation coincided closely with the period of flower bud development. Studies of tubers of the Rural New Yorker No. 2 at 1-week intervals showed that most tubers that grew to exceed one-half an inch in diameter were formed at the beginning of the period of tuber development.

Jensen and Morris reported in 1931 that the stolon of the Russet Burbank were well started before the sprouts appeared above ground. Tubers one-fourth an inch in diameter were formed before the plants were 4 inches high, although the tuber enlargement did not keep pace with the growth of the plants.

Yamamoto and Noda reported in 1949 that the stolon of the Irish Cobbler emerged as soon as it sprouted (about the second day after sprouting). At the time of emergence the plant height was about 6 cm, the number of leaves 6-9, and the top weight 0.3-1.0 gram. The time of stolon emergence corresponds to that of the differentiation of flower organ in the growing point of the plant top. The elongation of stolon stopped on the 10 th or 15 th day after sprouting and began to swell, namely, a stolon began to change into a tuber at this period.

Edmundson reported in 1938 that throughout the 7 years that his studies were conducted, the stolons on the Rural New Yorker No. 2 began to form about 36 days after planting, and produced a fully developed stolon system in 20 to 25 days after the stolon bagan to form. Some Triumph stolons, growing in dry soil, become elongated, reaching the surface and developing aerial stems. Elongated stolons that reached the surface and produced aerial stems did not produce large tubers, but usually produced buds or tubers weighing frcm 5 to 10 grams. The stolons of the Rural New Yorker No. 2 develop slowly, the rate being governed chiefly by the amount of moisture in the soil. Although the stolon growth of the plant in the early- and late-irrigated plots started at about the same time, the growth and development were retarded when the soil did not contain sufficient mositure to keep the plants growing vigorously.

Kawada reported that the emergence of the seed potato treated with 0.1 per cent solution of alpha-naphthaleneacetic acid was arrested, and frequently later sprouted to form tuber on the apex directly.

Tejima and Naka reported that with regard to the tuber formation of the seed potato bud, the restricted soil moisture supply is the causal factor, but it is noteworthy that their materials are both degenerated seed.

Kawada has shown that the treatment with alpha-naphthaleneacetic acid rejuvenated the degenerated seed potato, and that the degree of rejuvenescence depended upon the concentration of the growth substance and the stage of maturity or the age of the seed potato.

Guthrie succeeded to inhibit sprouting of tubers in storage by means of the growth substances and to hasten with ethylene chlorhydrin.

Rosa reported that the dormant period of potato tubers were not an essential part of the life cycle. Some varieties of potatoes, when grown under conditions of high temperature and abundant moisture formed vegetative sprouts from partly grown tubers. Kolterman reported a similar development in Germany, following an unusual drought.

Materials and Methods

Seed potatoes of the variety Irish Cobbler, weighing 40-50 grams, were chosen for the experimental materials. Dormant period ended about the last of February or the first of March, 1951.

Tuber formation tests were conducted in the dark room, and the temperature was maintained at 15-20°C and the humidity at 90 per cent.

Tuberization and the Location of the Lateral Sprouts

Stolon, the subterranean lateral, is sometimes concluded to be the specially differentiated sprout to form tuber. Hence, the apically elongating main stem, without laterals, sprouted from the seed potato and the main stem, pinched back and sprouted laterals, are compared concerning the ability of tuber formation in the dark. Also the shift of the time of beginning of the tuber formation between the laterals is tested.

The seed potato was planted on April 17.

On May 4 the sprout elongated about 10 centimeters long. Of the half of the seed potatoes, the sprouts were pinched off of their apical two nodes. On May 15, the laterals sprouted out. The length of the growth of laterals showed the apical dominancy as generally seen.

On May 24, the tubers were ascertained to be formed on the weak laterals and not or few on the vigorous laterals. The nontreated main stem showed no sign of tuber formation.

The vigor of the laterals differed with their location on the main stem. Generally, the lowest lateral, being weakest, formed tuber earlier. The upper lateral remained elongate and failed to form tuber. (Fig. 1, and 2)

Tuber Formation on the Main Stem

Seed potatoes weighing 40-50 grams, were planted on April 27.

It is ascertained that the later emerged weak sprouts formed tubers along the lateral portion together on the apex. It may be concluded that the weakening of growth enables the sprout to form tuber either on the apex or lateral sides. (Fig. 3, Fig. 4, a, and b)

The Flower Formation in the Darkness

The etiolated sprout emerged from the seed potato, planted on April 27, formed flowers on the apex of the sprout or even on the apical end of the newly formed tuber. It is ascertained that the flower is formed in the dark and flower formation occurs almost simultaneously with tuber formation. (Fig. 5)

Vigor of the Sprout Growth and Tuber Formation

As shown in the above related experiment, the vigor of the sprout is correlated with tuber formation. The length and tuber formation of the sprouts, different in vigor, are examined.

The sprouts from the seed potatoes planted on April 27 were selected. On May 28, parts of them were either lightly pinched, or severely pruned back, and trimmed off from the seed potato. On June 5, their behavior was examined and photographed. A part of them was examined on June 27 to test the result of prolonged progress of growth.

On the lightly pinched sprouts, short laterals emerged, and on the severely pruned sprouts long laterals emerged. (Fig. 6, A, B, and Fig. 7, A) On June 5, no tuber was found on them. But on the corresponding sprouts those trimmed off from the seed potatoes, many tubers were found. (Fig. 6, C, D, and Fig. 7, B)

It is shown that even on the laterals emerged from severely pruned sprouts, tubers were formed depending upon their vigor. The laterals which bore the tubers were weak in growth as shown in Figure 8.

On June 27, after the progress of further growth numerous tubers were found upon the laterals which had born no tuber before. (Fig. 9)

It may be concluded that the vigor of the laterals emerged from the pruned back sprouts may vary depending upon the supply of moisture and nutrients including the growth substance. The supply of nutrients from the seed potatoes, in turn, may vary as time elapses.

A Certain Substance Which Favors Tuber Formation

On May 28, half of the sprouts, trimmed off from the seed potato, planted on April 27, was set in the right position and the other half was set upside

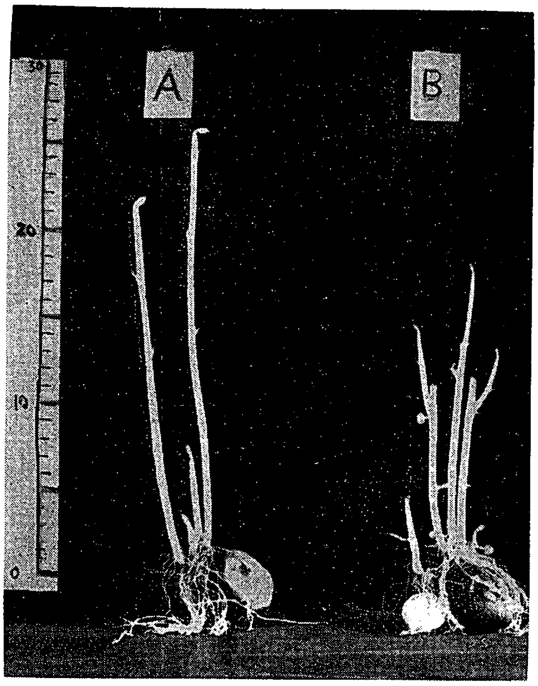


Fig. 1.

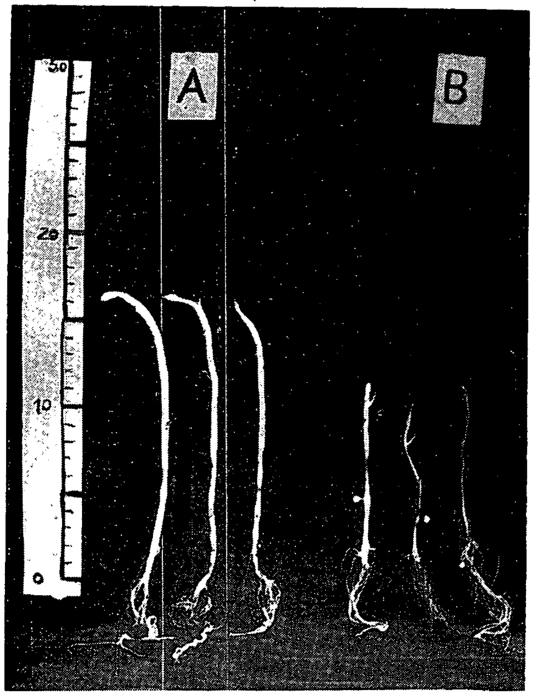


Fig. 2.

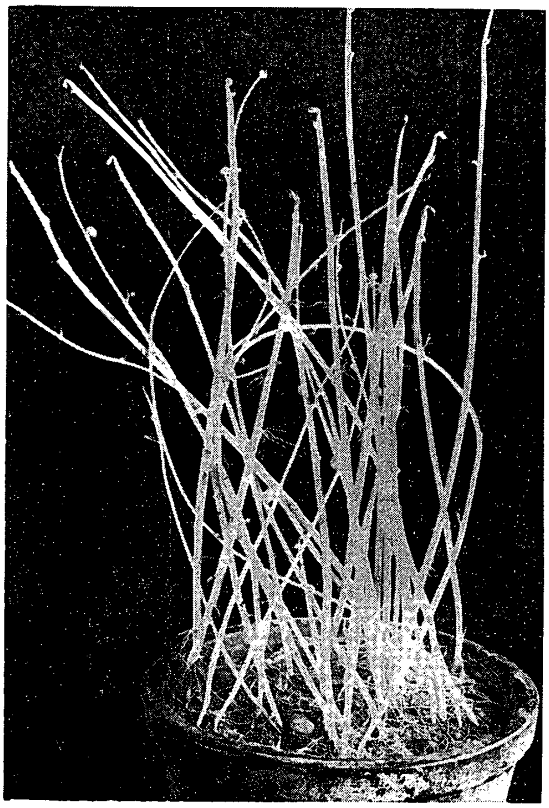
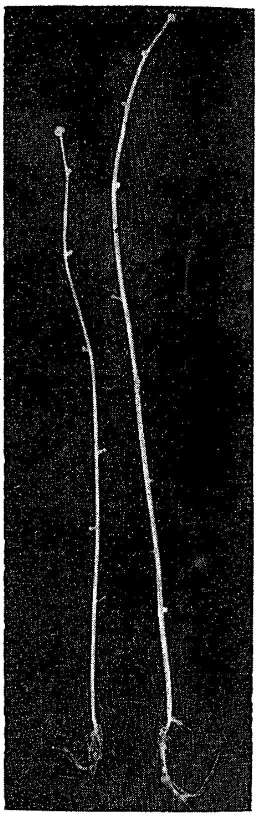


Fig. 3.

Fig. 1 Planted on April 17. Pinched on May 4. Photographed on May 24.
A Control.
B Pinched sprout.

Fig. 2 Sprouts trimmed off from the seed potato. Photographed on May 24.
A Control.
B Pinched sprout.

Fig. 3 Tuber formation on the apex. Planted on April 27. Photographed on June 5.



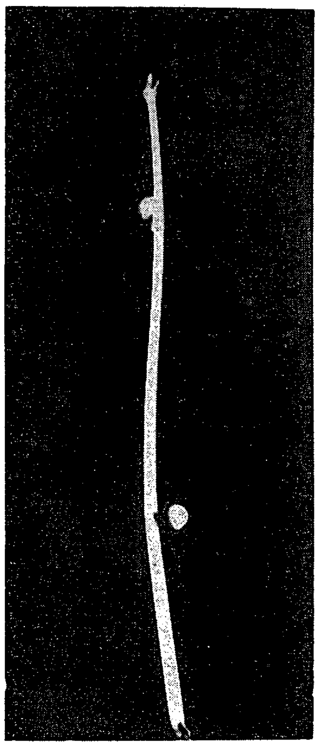


Fig. 4–a, Fig. 4–b

Tuber formation on the apex. The sprout is being trimmed off from the seed potato.

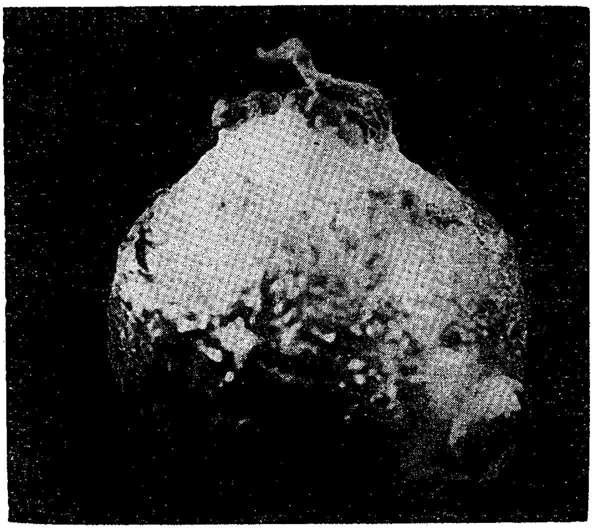


Fig. 5 The flower formation on the apical end of the newly formed tuber. Planted on April 27. Photographed on June 5. (×10)

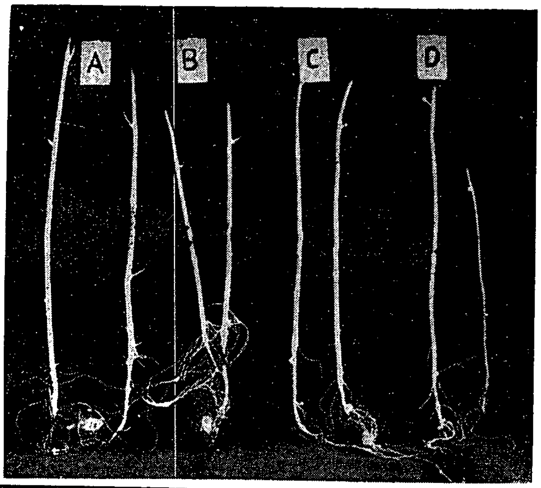


Fig. 6 Laterals and tubers on lightly pinched sprouts. Planted on April 27. Pinched on May 28 Photographed on June 5.
A, B Sprouts with the seed potato.
C, D Sprouts trimmed off from the seed potato.

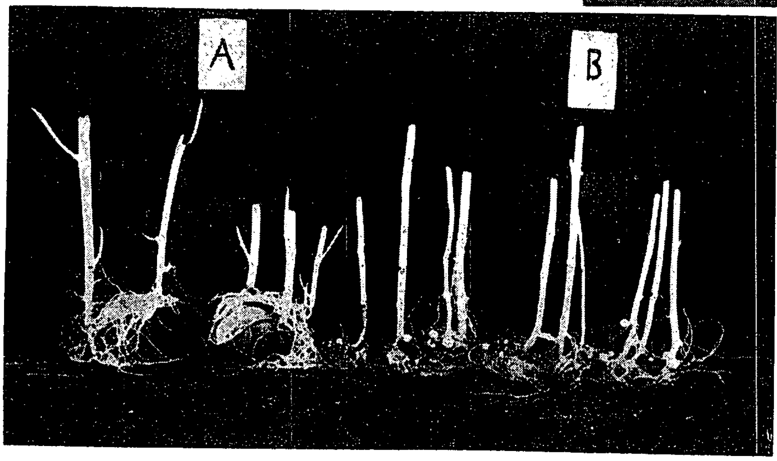


Fig. 7 Laterals and tubers on severely pruned sprouts.
Planted on April 27. Pinched on May 28. Photographed on June 5.
A Sprouts with the seed potato
B Sprouts trimmed off from the seed potato.

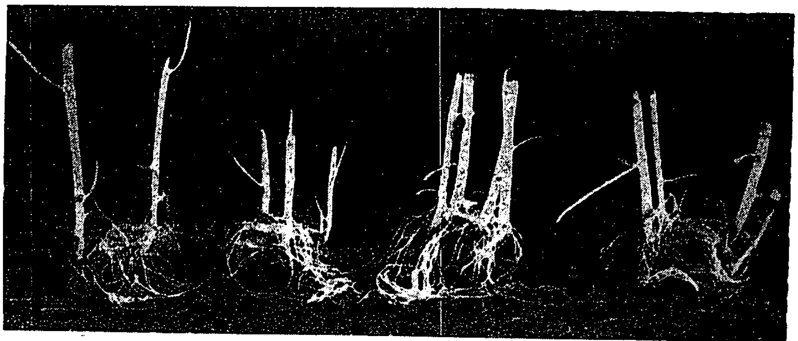


Fig. 8 Laterals different in vigor and tuber formation.
Photographed on June 5

Fig. 9 Tuber formation after the progress of further growth. Photographed on June 27.

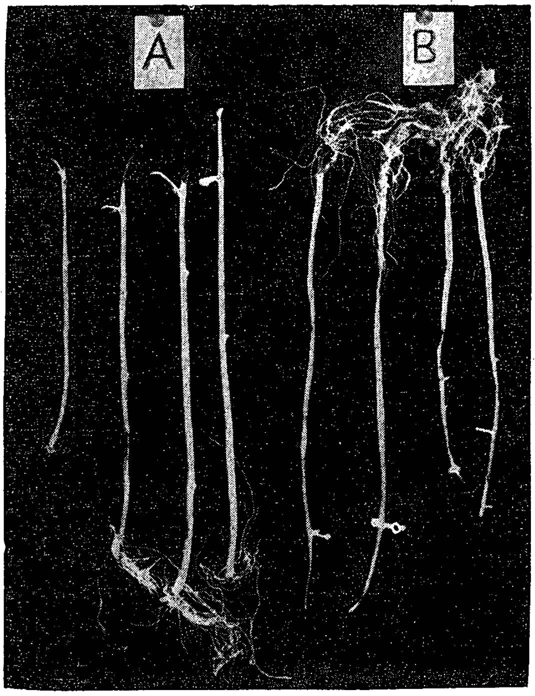


Fig 10 Tuber formation favored on the upside down position Set in the position on May 28. Photographed on June 11.
A Control
B Sprouts set in the upside down position.

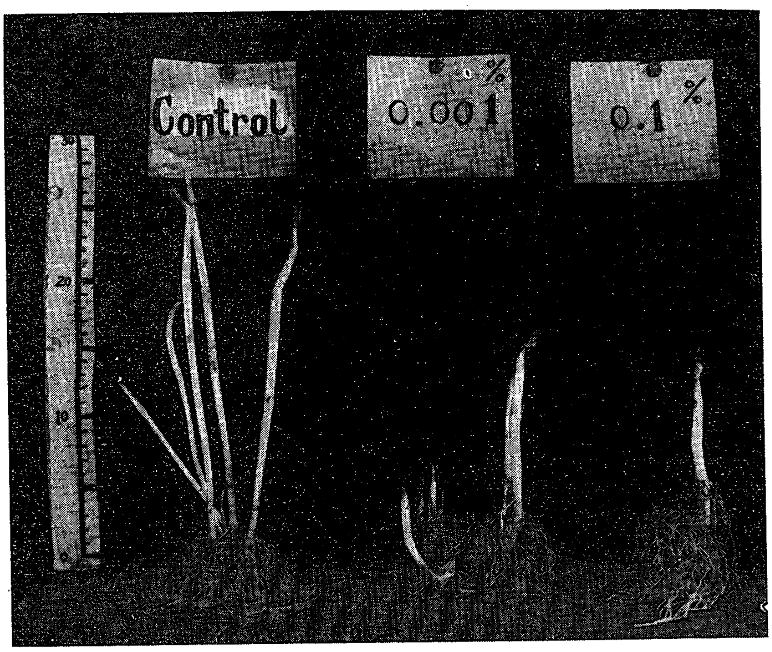


Fig. 11 Sprouting behavior induced by the different concentration solution of heteroauxin. Immersed 24 hours in the solution.
Planted on April 27.
Photographed on May 7.
Left Control: profuse sprouting; showing the breaking of apical dominancy
Centre Treated with 0.001 percent solution; showing a few sprouting
Right Treated with 0.1 percent solution; showing a single sprout, and completely restored apical dominancy

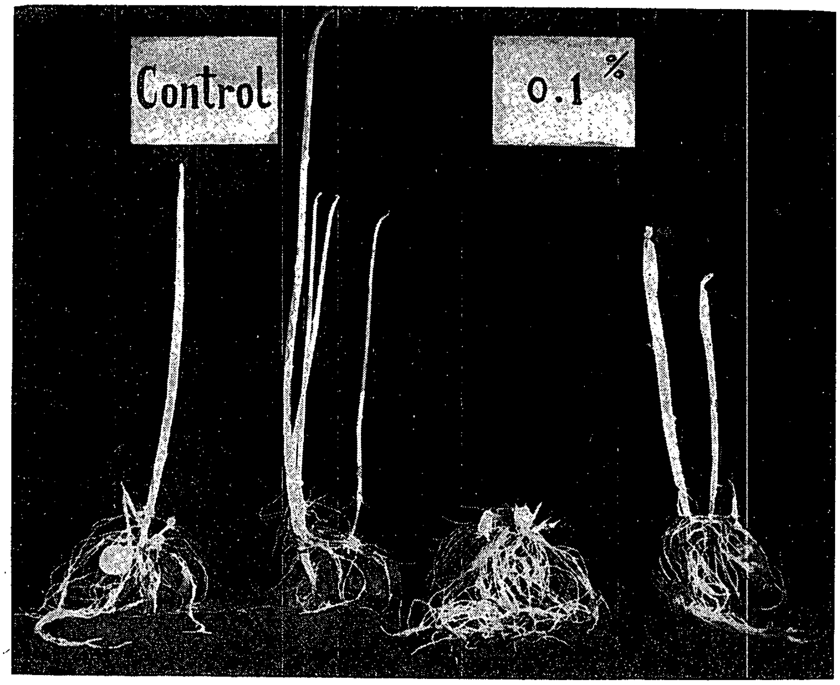


Fig. 12 Proliferous growth sprouted from heteroauxin treated seed potato (right) and normal growth from the control. Treated on April 27. Photographed on May 24.

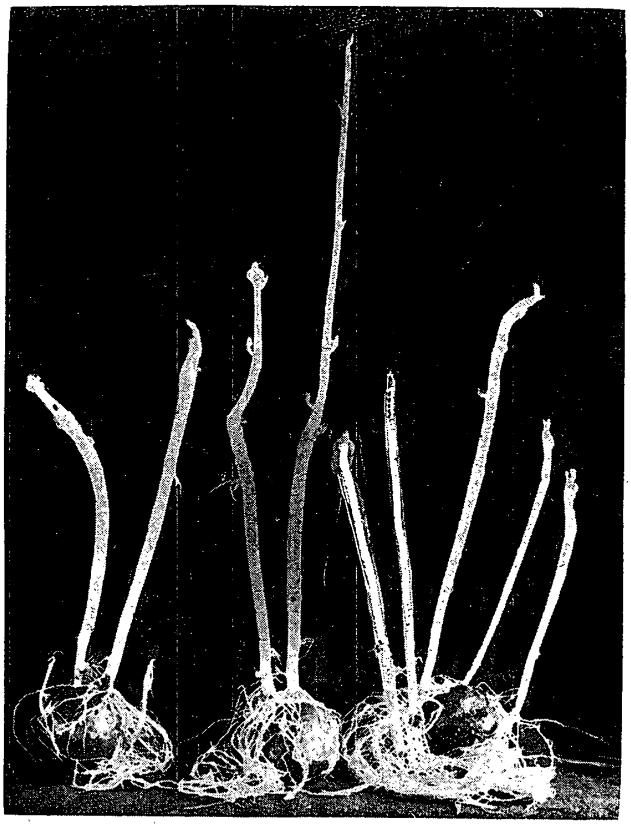


Fig. 13 Proliferous growth of the apex to which was added heteroauxin. Treated on May 5-7. Photographed on June 5.

A B

Fig. 14 Treated with TIBA on June 12.
Photographed on June 25.
A Control.
B Treated with TIBA.

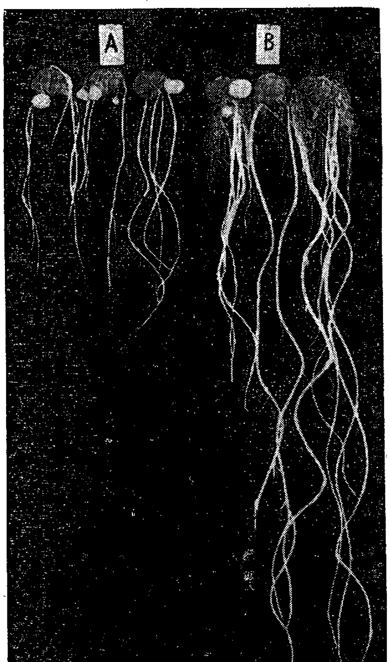


Fig. 15 The amount of soil moisture and tuber formation.
Planted on May 8. Photographed on June 27.
A. Restricted moisture supply plot
B. Abundant moisture supply plot

down. After 14 days of growth, the tubers were found on the upside down sprouts and not on the rightly set sprouts (Fig. 10)

Length growth of the laterals sprouted from the main stem showed apical dominancy even on the upside down position. Apical dominancy is thought to be due to the auxin distribution within the stem.

Tuber formation, favored on the upside down position, may be illustrated to be due to the downwards translocation of a certain substance which induces physiologically tuber formation.

Heteroauxin and Tuber Formation

The role of the growth substance as the sprout inhibitor of the tuber and for the rejuvenescence of the degenerated seed potatoes is already appreciated and is in practical use. (Fig. 11)

It is now assumed that there is a certain substance which favors tuber formation. For the purpose of identifying the property of the assumptive substance, action of heteroauxin on tuber formation is tested.

On April 27, the seed potatoes were immersed in 0.1 per cent solution of heteroauxin for 24 hours. 8 treated seed potatoes were planted in pots and placed in the dark room. Sprouts from 6 seed potatoes showed proliferous growth and 2 seed potatoes formed irregular tubers like shortened proliferous growth. On the other hand, from the control seed potatoes sprouted normal growth and only one seed potato formed tubers of the normal appearance. (Fig. 12)

To the sprouts emerged from the seed tubers, planted on April 27, 0.1 percent heteroauxin solution was added on the apical portion twice a day for three days (May 5-7) showed proliferous growth and on June 5 the tubers were found on half of them (Fig. 13). On June 11 the tubers were found on all of the seed potatoes.

0.1 percent solution of heteroauxin induces proliferous growth and tuber formation on the apex.

2-3-5 Triiodobenzoic acid and tuber Formation

Since tuber formation seems to occur highly correlated with the vigor of the sprout growth, the action of 2-3-5 triiodobenzoic acid that lowers the level of auxin action is tested as to whether it induces tuber formation.

On June 12, 100 p. p. m. solution of TIBA was added on the apical portion of the sprouts emerged from the seed potato planted on May 15.

The apical elongation of the treated sprouts being arrested, the apical portion enlarges and the laterals sprout out, showing the breaking of the apical dominancy evidently, but tuber is not yet formed on the apex. It seems that lateral growth proceeds more easily utilizing the nutrients from the seed potato rather than the progress of apical enlargement. (Fig. 14)

External Factors and Tuber Formation

It is suspected that external factors might be capable of inducing tuber formation as a causal factor.

Low temperature is thought to favor tuber formation. During the experiments the range in minimum temperature was above 15 degrees Centigrade and it seems that the temperature need not be below 15 degrees Centigrade for tuber formation. Low temperature is not the causal factor for tuber formation.

Higher concentration of carbon dioxide gas is thought frequently to favor tuber formation. Some seed potatoes were set in the desiccator for the purpose of raising carbon dioxide concentration.

The amount of moisture in the soil is known to govern the growth. It is assumed that dry soil induces tuber formation of the bud of seed potato directly. So, half of the seed potatoes were planted with abundant moisture supply and the other half with restricted moisture supply.

Restricted moisture supply favors tuber formation. (Fig. 15) Restriction of moisture supply arrests sprout growth, and it may be probably due to the low auxin production.

Edmundson reported that low moisture content of soil, retarding top growth, made the stolon elongate to reach the soil surface and to fail to form tuber. In this case, the retarded growth of the aerial portion may be probably resulted from low auxin production that may be due in turn to the water deficiency. The long length growth of subterranean laterals results from the retardation of the apical dominancy of the terrestrial portion, and vigorously elongating subterranean sprouts fail to form tuber.

It may be concluded that moisture supply, affecting auxin production, may either favor length growth or tuber formation. Moisture supply can not react in itself as the causal factor for tuber formation.

The atmospheric concentration of carbon dioxide gas also fail to prove to be the causal factor for tuber formation.

Discussion and Conclusion

Rosa investigated the condition of the bud primordia in tubers at different stages of maturity and at different times in the dormant period. The bud primordia develop considerably during the late stages of tuber growth and some development of the sprout proceeds even during the so-called dormant period, if the tubers are stored at temperatures favorable for growth. Some varieties of potatoes, when grown under conditions of high temperature and abundant moisture form vegetative sprouts from partly grown tubers. It is also reported that an unusual drought has caused a similar development. The dormant period of potato tubers probably is not an essential part of the life cycle. Dormancy must depend upon physical and chemical conditions within the tuber.

The inhibition of sprouting and the rejuvenescence of the degenerated seed potatoes by the external supply of the growth substances suggest that the shift of the physiological condition of the tuber may be dependent upon auxin.

It has been shown above that the treatment with the concentrated growth substances induces tuber formation and also, contrariwise, the buds of the degenerated seed potatoes form tubers directly instead of sprouting. It has been also shown that the cease in the length growth of the sprout induces the tuber formation.

Reduced growth of stems and decreased apical dominancy are symptoms which may be associated with decreased auxin supply.

We have found that a certain substance that migrates downwards within the sprout favors tuber formation, and that in the case of the decreased auxin supply the action of such a substance may be assumed.

The vegetative apical meristems are the dominating growth region of plants. Under conditions of a limited supply of cell building materials we recognize this dominance in polarity and inhibition. Length growth of the apical meristem is inversely correlated with cambial growth and the initiation of cambial growth may be expected whenever the length growth has been checked.

Flower formation is similarly correlated with the auxin action inversely, and may be brought about by the external supply of anti-auxin.

It may be concluded that when the level of auxin action or the dominating power of the apice is lowered, the length growth ceases and tuber and flower formation take place and lateral buds sprout, and, on the other hand, external supplies of the growth substances restore the length growth.

External supplies of the growth substances, however, when used at higher concentrations, inhibit the sprouting and induce tuber formation.

The assumptive substance, already referred to, may be assumed to be intimately related with auxin and is probably a sort of auxin-precursor.

It may be also assumed that the assumptive substance and auxin are changeable to each other as a reversible reaction.

In the case of the concentrated growth substance supply, from the outside, the assumptive substance within the sprout increases so much as to exceed the auxin action. In the case of the kohl-rabi, Deusse reports that auxin is not involved in tuberization which requires, according to Posesva's theory, a specific tuberization hormone.

According to Loomis, the growth substances increase the condensing power of meristems rather than serving directly as condensing agents, and inhibition of sprouting, induced by the action of the growth substance, may be regarded to be due to the excessive condensation conditions that accompany the prevention of the normal hydration or other difficulties. Dormancy may be assumed to be brought about by the similar physiological conditions.

In the case of tuber formation, the existence of a specific substance that is intimately related to the growh substances might be reasonably assumed as can be inferred from the foregoing description.

Stolons, being subterranean laterals, are under the influence of apical dominancy of the terrestrial, apical meristems, and arrested length growth respectively. As above stated, ceasing of the length growth induces tuber formation. Ceasing of the length growth of the subterranean laterals corresponds to the growth ceasing of the terrestrial portion, and remarkbly to the time of the flower bud formation. The flower bud formation, in turn, is induced by the ceasing of the length growth.

Stolon emergence and the beginning of the swelling start during 10-20 days after the sprouting of the seed potato. Hence, early vigor of growth is of significant importance, and early vigor is dependent on the vigor of the seed potato.

From the present experiments it can be summarizea that the sprouting and length growth is dependent upon auxin supply and flower and tuber formation occur under decreased auxin supply. The specific substance, that is intimately related to the growth substances and is changeable as a reversible reaction as already mentioned is assumed to react in the tuber formation.

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