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Review Classics

Studies on plant growth substances in Japan before 1945

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Abstract The idea that a specific chemical stimulus is involved in some processes of plant development was introduced by European plant scientists in the early 20th century. After the discovery of auxin by Went in 1926, this hormone became a subject of intensive studies in the physiology of plant growth and development. In Japan, studies on auxin started in the middle of the 1930s. At that time, gibberellin was discovered in Japan. Unfortunately, gibberellin was regarded as a fungal toxin and no special attention was paid to its physiological significance. The first paper on auxin in Japan was published by Masayuki Nagao in 1936, dealing with its transport in the root, which was then a subject of dispute. Before World War II (~1940) there were only about ten auxin researchers, excluding those in applied areas. In this article I will introduce their studies and some of the applied studies. I will also pay special attention to a series of work by Sadao Yasuda who was a pioneer researcher of plant reproductive physiology in Japan. He studied self-incompatibility (1927–1932) and parthenocarpy (1930–1940) which are related to plant growth substances. He demonstrated that a special substance (inhibitor) was involved in self-incompatibility. This is probably the first case in Japan for demonstrating the involvement of a regulatory inhibitor in plant development. In his study on parthenocarpy he concluded that "pollen hormone" and auxin are identical in their physiological nature.

Key words: Early auxin studies, inhibitor of self-incompatibility, plant hormone studies in Japan, pollen hormone

Studies on plant hormones in Japan, mostly on auxins, started around the middle of the 1930s. Gibberellin was discovered in Japan in 1933. Although it was shown to exhibit various interesting physiological effects on plant growth, it was treated as a fungal toxin and no special attention was paid to its physiological significance before World War II (~1940). In the book, "Shokubutsu Horumon (Plant Hormones)" written by Sumiki (1943), the author called gibberellin "Shokubutsu tocho horumon (Plant hyper-elongation hormone)" because a very small amount of gibberellin induces abnormal hyper-elongation in plants and is quite different from the effects of the growth hormone, auxin. At that time this prominent effect alone attracted much attention by researchers.

By 1950 several Japanese books on plant hormones had been published (Kinoshita 1938; Sumiki 1943; Koshimizu 1944; Sugiyama 1947). Essays and review articles in Japanese dealing with plant hormones, including those for applied studies, were also written in various journals (Koketsu 1926, 1934; Shibata 1934; Yamaguchi 1937; Yasuda 1935, 1940a,b, 1941; Shibuya 1939; Kawada 1942a, b, c; and others). The earliest detailed review in Japanese on the idea of plant hormones was written by Koketsu (1926). He actually wrote the article in 1925 based on his lecture at a meeting when the discovery of "Wuchsstoff (growth substance/auxin)" had not yet been reported by Went in 1926. In this article he introduced hypotheses of hormones involved in growth correlation, cell division/tissue formation, and tropism, which were controversial subjects among plant physiologists in Europe.

The history of early auxin studies in Japan was introduced by Nagao (1975). According to him there were less than ten auxin researchers (excluding those in applied areas) before World War II. As to studies on gibberellin, the book by Sumiki (1943) and its revised edition (1951) covered a wide range of early studies, including applied areas.

In this article I will introduce mainly auxin studies including applied studies. Special attention is also paid to a series of Yasuda's work on self-incompatibility and parthenocarpy which are related to plant growth regulators.

Early auixn studies

The idea that a specific chemical stimulus is involved in some developmental processes of plants had been presented before the discovery of "Wuchsstoff" by Went. In 1909, Fitting found that an exudate from the pollen mass of orchids smeared on orchid stigmas induced the same post-floral phenomena as observed at the time of pollination; he assumed the presence of some chemical

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stimulant in the pollen and named it "pollen hormone". When a plant is injured, cell proliferation occurs at the site of the injury and wound tissue is formed. Harberlandt assumed that some hormone-like substance is produced in the wound tissue, and named it "wound hormone" (1921a, 1922). He also proposed the presence of "necro hormone" which he thought was produced at the time of the death of plant tissue (1921b). In 1931, Kögle and Haagen Smit gave the name of "auxin" to the Wuchsstoff, and isolated IAA (then termed "heteroauxin") from human urine as a substance which has the same effect as Wuchsstoff. As IAA had already been synthesized, it soon became popular among researchers and was intensively used in experiments for various aspects of plant growth regulation. Although IAA had been suggested to be the auxin obtained from higher plants, it was years before IAA was actually isolated from immature corn kernels in crystals and identified (Haagen Smit et al.1946). In 1925, Majima and Hoshino of Tohoku University synthesized IAA starting from indolyl-magnesium iodide via indolyl-acetamide as a novel synthetic method. Later it was synthesized from indole by way of the Grinyard reaction by Tanaka of Takeda Nutrition Chemistry, Co. Ltd. (1940), from cyanopropionaldehyde by Takei and Takano of Kyoto Imperial University (1941) and from ethylformate and succinic acid ester by Tamari of Tokyo Imperial University (1941).

Masayuki Nagao (1908–1999), who was professor of Tohoku University, took advantage of utilizing a specimen of IAA (then called hetero-auxin) obtained from Prof. S. Fujise which had been synthesized by Majima and Hoshino and kept in the laboratory, and started studies on auxin transport in the root. He published a series of papers under the title of "Studies on plant growth hormones of plants I∼VI" (Nagao 1936, 1937a,b, 1938, 1942b, 1943). At that time auxin transport in the root was a subject of dispute. The most conflicting results were about whether the root tip could produce a growth substance. Thimann (1934) and others had denied its production in root tips, and concluded that growth substance was acropetally transported to the root tip. On the other hand, Cholodny (1934) had concluded that growth substance produced in the root tip is transported basipetally. Nagao's paper in 1936 is probably the first research paper on IAA published in Japan. Nagao demonstrated using various seedlings that their root apices have the ability to produce auxin or activate it, and suggested that auxin moves basipetally through the growth zone of the root (1936, 1937b, 1938, 1939). By observing root growth inhibition of decotyledonized sunflower seedlings with auxin applied to their cut surfaces, he also concluded that auxin produced in the aerial part of the plant is transported acropetally in the root (Nagao 1937a). Later he obtained the same conclusion using pea seedlings with their epicotyls excised (Nagao 1942a). This conclusion is our present understanding about the flow of auxin transport in the plant axis.

Perhaps reflecting the then trend of auxin studies in America and Europe, several experiments on auxin transport and distribution in the tissue were also reported by other researchers around the same period. Yamane conducted a series of experiments to analyze the relationship between the phototropic movement of *Fatsia* (Yatsude) leaf blades and auxin (Yamane 1938, 1939, 1940, 1941, 1944). He demonstrated that leaf blade movement observed when the leaf surface receives unequal radiation is the result of the curvature of the petiole due to unequal distribution of auxin in the petiole. In positive phototropic movement, auxin content was higher on the dark side, and in negative phototropic movement higher on the light side. He suggested that the main path of auxin transport is the vascular bundle. Onaka (1942) assayed auxin content by the *Avena* test in the branch of pine (*Pinus thunbergii* Parl.) seedlings. He reported the following results. The distribution of auxin was restricted to near the cambium, more auxin was detected in the upper side of inclined stems accompanied with thickening growth, and in the main stem and root rather than their lateral axes. Leaf removal decreased auxin content. Acropetal transport was observed in summer, and basipetal transport in autumn–winter with a reduced content in the latter seasons.

An experiment on the relationship between electric potential and auxin transport using sunflower hypocotyls and pea epicotyls was reported by Kinoshita (1939a). Electric potential was higher in the tissue where storage substances were found and in the high growth region, where the center of auxin synthesis is assumed to be. By observing that a higher gravitropic response of a horizontally placed hypocotyl was obtained after 20 h, when an electric current was applied from its base rather than applied from the tip, he concluded that auxin transport was affected by a change in electric potential distribution due to electric application. In parallel with this experiment, Kinoshita also studied the effect of IAA on the plasmodium of *Didymium nigripes* in a series of experiments (Kinoshita 1938, 1939b; Watanabe et al. 1939a, b). This plasmodium shows a marked positive chemotaxic response to IAA. The IAA given to the head of the plasmodium increased electric potential between the head and the tail and respiration of the cytoplasm, resulting in protoplasmic streaming toward the head. However, the specificity of this IAA effect was not examined. Referring to this IAA effect on the plasmodium, he hypothesized that auxin transport in the gravitropic response of the sunflower hypocotyl was due to polarized protoplasmic streaming caused by electric stimulus (Kinoshita 1939a). Yamaki (1941) took up as his study subject a well-known phenomenon about potato stems where invertedly placed stems develop adventitious buds at their bases which cannot be observed in those in the upright position. He reported that an active auxin and its presumable precursor which acted as an inhibitor existed in the diffusible auxin fraction obtained from the stem as assayed by the *Avena* curvature test, and that both substances existed more in the tip region of the stem. This was marked in inverted stems. When an electric current was applied to the cut surfaces of horizontally placed internode segments, the precursor moved to the positively charged end and accumulated. He also showed that purified IAA applied to the cut surface of an internode segment was transported basipetally. But the transport polarity disappeared with time. His finding is in accordance with the general idea that polarity in adventitious roots/buds formation is established with polar transport of auxin. Relationship between polarity in lateral root formation and auxin was also studied by Nagao (1942b). He demonstrated that in a sterile culture of decapitated root segments of pea seedlings, auxin stimulated lateral root formation especially near the tip.

Studies on the presence of growth inhibitors and their roles were also reported in the early 1940s. Okabe (1940a, b) reported that in diffusates from the stem and petiole of fig, ginkgo, mulberry, tea and willow, some substance(s) which caused positive curvature in the *Avena* curvature test was found, and more auxin existed in young tissues and more inhibitors in aged tissues. The idea that the balance of the amount of the growth promoting substance (auxin) and inhibitors plays an important role in morphogenesis was presented in Nakano and Kinoshita's study on the germination inhibitors of *Avena* seeds and aerial tubers of *Batatus* sp. The formation of aerial tubers is associated with a decrease in the growth rate of the shoot apex. When the ratio of the amount of auxin to that of inhibitors is kept at higher values, normal lateral buds are formed, while aerial tubers are formed when the ratio drops to an appropriate value. If the ratio becomes too large during tuber formation, they germinate on the plant, but if it becomes too small, they enter into complete dormancy (Nakano and Kinoshita 1942).

The growth stimulating effect of auxin was also studied in other plant materials. Nagao (1937a) reported that an IAA paste applied to the cut surface of cotyledons or decapitated hypocotyls of sunflower seedlings inhibited the elongation of the hypocotyl and caused a marked swelling of the hypocotyl several mm below the cotyledons while a slight stimulation of elongation was observed in the middle portion of the hypocotyls. He also tested IAA, indole-3-propionic acid, NAA and phenylacetic acid on the growth of rice coleoptiles in water (Nagao 1943). IAA and NAA were most effective, phenylacetic acid being much less active.

Kojima (1940) reported that in pea seedling roots kept in IAA solutions, elongation was inhibited and thickening was promoted, and lateral root formation seemed to be associated with the growth inhibition of the main root. IAA inhibited cell division and elongation. However, at IAA concentrations where growth was severely inhibited, cell division was stimulated near the elongation zone and lateral root formation was promoted. Stimulation of cell elongation was also reported by Yamaguchi (1937) and Yamada (1939).

Whether auxin can stimulate cell enlargement (elongation) or cell division or both was a topic of disputes. At that time auxin was thought not to stimulate cell division, but to stimulate cell wall extension (reviewed by Shibata 1934), and stimulation of cell wall extension was said to depend on the sensitivity of the cell wall (Kinoshita 1941).

The mechanism of auxin-induced cell elongation was a controversial subject in America and Europe. Changes in wall properties, acid-induced growth and involvement of the plasma membrane in relation to cell wall extensibility, which were the main topics in auxin physiology in the 1960s–70s had been discussed intensively (reviewed by Yamaguchi 1937,Yamada 1939).

Evidence for stimulation of cell division by auxin was accumulating in the studies of morphogenesis such as parthenocarpy, root formation, cambial activity, etc. Auxin-induced stimulation of cambium activity in sunflower stems was reported by Snow (1935a,b). Yasuda (1937a,b,1939) found that a *Petunia* pollen diffusate injected to the region near the cambium of the stem of *Kalanchoe pinnata* stimulated cell division. The diffusate was supposed to contain "pollen hormone" which was concluded later to be the same as growth hormone (auxin). Actually, Yasuda examined the effect of auxin on parthenocarpy in *Petunia*. He injected a solution of Belvitan which contains IAA (Bayer) to *Petunia* ovaries and found that IAA stimulated division of egg cells and expansion of nucellus cells (1940c). He thus confirmed that auxin can stimulate both cell expansion and cell division. Hirose (1939) also found that an IAA paste directly applied to tree cambium stimulated cell proliferation. He utilized this IAA effect to stimulate the formation of graft unions (1940, 1941). Kawada reported that by NAA treatment, cell division and cell enlargement were stimulated in mung bean and rape, while their growth was inhibited (1942d).

In the late 1930s various synthetic auxins were synthesized and studies on structure-activity relationship were conducted intensively in the U.S.A. In Japan, Prof. Takei's group of Kyoto Imperial University synthesized naphthoic acid and its hydroderivatives and tested their auxin activity in rooting of *Petunia*. They found 3,4-dihydronaphthoic acid was most active, and suggested that the presence of the double bond in the ring is important to the expression of auxin activity (Mitsui et al. 1944).

Studies on self-incompatibility and parthenocarpy by Yasuda

Sadao Yasuda (1895–1950), Professor of Taihoku Imperial University, started his physiological studies on fertilization using *Petunia violacea* in 1927 (Yasuda 1927a,b, Yasuda and Arai 1927) (Figure 1). In one line of experiments he pursued the presence of an inhibitory substance(s) of self-incompatibility. There had been many reports concerning the notion that a specific substance which exists in the pistil affects pollen germination and pollen tube growth. His study on this inhibitory substance is probably the first case in Japan for demonstrating the involvement of regulatory inhibitor(s) in plant development. He scrupulously and systematically designed a series of experiments on this subject. First, he questioned if such a specific substance exists. For this purpose he devised a method of employing droplet suspension of a liquid medium containing a test material and sugar for pollen germination and growth (Yasuda 1928a), and found that the secretion of the stigma of self-incompatible individual contained a special substance(s) which was inhibitory to the pollen germination of the self to some extent (Yasuda and Arai 1927; Yasuda 1928b). Later he confirmed the existence of such an inhibitory substance in the style (1931a, b) and also in the ovary (Yasuda 1932). He concluded that in the pistil of self-incompatible plants there undoubtedly exists a substance which inhibits self-fertilization. Then, he conducted experiments to see where the inhibitor is produced, employing a technique to graft the style to the ovary with gelatin (Figure 2, quoted from 1931a, b). Since pollen growth was affected by the nature of the ovary but not by that of the style, he concluded that the inhibitor is mainly secreted from the ovary (Yasuda 1931c). By examining juice from various parts of the ovary, the substance was found to be most abundant in the placenta. He thought that the distance that the ovary-produced inhibitor ascends in the style determines whether pollen growth inhibition occurs at the stigma, in the style or in the ovary (Figure 3, quoted from 1933a). He also examined the timing of the production of the inhibitor and its nature (Yasuda 1930a). The inhibitor was not detected in the pistil of young buds. It seemed to be produced after or immediately before flowering. The

Figure 1. Professor Sadao Yasuda (1895–1950). Photograph provided through the courtesy of Dr. Kenji Yasuda.

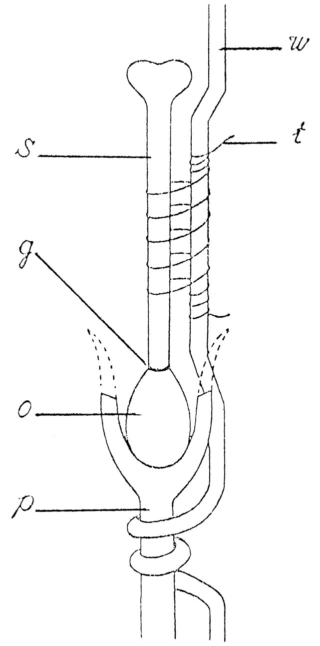

Figure 2. Grafting operation. *s*: style; *o*: ovary; *p*: peduncle; *g*: gelatine; *w*: iron wire; *t*: spider's thread (quoted from Yasuda, 1931a, b).

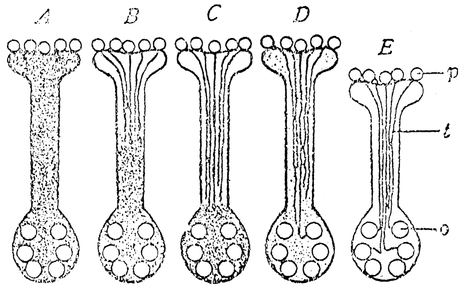

Figure 3. Diagram showing the relation between the special substances and pollen tube growth. *p*: pollen; *t*: pollen tube; *o*: ovule. (A) The special substances have reached the stigma, and inhibition of pollen germination takes place. (B) The special substances stay in the ovary, and inhibit pollen tube growth in the ovary. (C) Pseudoself-fertility is caused by the poor production of special substances. (D) The result of bud pollination: self-fertilization due to the lack of special substances. The special substances are distributed more in the darker regin. (quated from Yasuda. 1933a)

inhibitor was water soluble, because it could diffuse through a gelatin layer in the grafting experiments. It remained active in a dried residue of a water extract of the pistil and also in the dried powder of the pistil. In addition, although it inhibited the growth of the pollen of the self, it conversely stimulated the growth of other strains (Yasuda 1932b). The existence of such an inhibitor in cabbage was also suggested by Kakizaki (1930a,b). After more than half a century, gametophytic self-incompatibility is known to be controlled in the simplest cases by the highly polymorphic *S* locus, and arrest of pollen tube growth in the style occurs when one of the two *S* alleles of the pistil matches the *S* allele of the pollen. Putative *S* allele proteins which are RNases had been identified. In 1994, Lee et al. finally demonstrated that *S*-RNases control the self-incompatibility behavior of the pistil in *Petunia inflata* (Lee et al. 1994).

Yasuda later (from 1930–1940) conducted a series of experiments on a factor in pollen which can induce parthenocarpy, and came to the conclusion that "pollen hormone" is identical with auxin (1934c, 1939). Yasuda injected an exudate of *Petunia* pollen to the ovaries of egg plant and *Nicotiana*, and found that the ovaries became thickened and resulted in parthenocarpy (1933b, 1934a,b; Yasuda et al. 1930). He also demonstrated that a pollen exudate of cucumber injected into the ovary of cucumber easily induced seedless fruit (Yasuda et al. 1935). The result showed the presence of some substance in pollen which could stimulate the growth of the ovary. In further experiments he denied the possibility that the substance was a kind of "wound hormone" of Haberlandt (1934, 1935) or a kind of "necro hormone" produced with the death of pollen (1936). Yasuda demonstrated clearly that the growth of the ovary initiated by pollination is due to a stimulant, "pollen hormone" which is contained in live pollen.

Whether "pollen hormone" is identical with auxin or not was controversial. Laibach (1932) and Laibach and Maschmann (1933) concluded that the two were the same on the basis of the following two pieces of evidence. A pollen exudate of orchid applied to the cut surface of decapitated *Avena* coleoptiles stimulated their growth, and auxin applied to the stigma of orchid plants induced post-floral phenomena. At that time, as mentioned earlier, auxin was believed to induce expansion of the cell wall but not to induce cell division. Laibach also believed "pollen hormone" had no activity in stimulating cell division. However, Yasuda had noticed that cell division clearly occurred when the ovary started to grow after the stimulus of "pollen hormone" was given. He thought it could be possible that the "pollen hormone" he examined was a different substance which could stimulate cell division. However, he finally demonstrated that the "pollen hormone" could stimulate both cell expansion and cell division (Yasuda 1937, 1939, 1940) and concluded that auxin and the "pollen hormone" are identical to one another in their physiological nature. He explained that the dual activity of the same substance is due to the nature of the tissue which receives the stimulus of the substance. He assumed that in young cells with high mitotic potential, cell division is stimulated, while in aged cells with less mitotic activity, cell wall expansion is stimulated.

Applied studies

From the late 1930s to the early 1940s, rooting and induction of parthenocarpy were the most popular subjects examined as auxin actions especially in applied fields. Tamari synthesized more than 20 compounds and tested their rooting activity (Tamari 1941). Several compounds including IAA, IBA and NAA markedly stimulated rooting of *Cryptomeria japonica*, *Daphne* odora and *others*. Yasuda and Nagai of Horticultural School of Tokyo Prefecture (1939) examined the effect of IAA on the rooting of more than 10 kinds of ornamental garden plants and found only half of them such as Margaret, plum tree and *Piracanthus* were stimulated to root. Shibuya (1938c) reported on a detailed examination of the IAA effect to induce root formation in tea cuttings. Kinoshita and Kasahara (1939) reported that IAA in combination with Vitamin B1 markedly stimulated rooting of *Thea sinensis* (Japanese tea), *T. sinensis* var. *macrophylla* (Chinese tea) and *Ripa nustrutium aquaticum*, which are usually difficult to be induced. But, in chrysanthemum, which is easy to be induced, Vitamin B1 had no effect. They thought that those plants which are easy to have induced roots contain a large amount of "Rhizocaline", a hypothetical root-forming substance named by Went (1934), and that Vitamin B1 is "Rhizocaline".

Hirose (1939) conducted application experiments on wound tissue formation, graft union formation, artificial parthenocarpy, abnormal growth of fruit and flower, branch curvature and rooting of cuttings as affected by IAA using various plants. In further experiments on IAA-stimulated graft union formation he showed that IAA induced cell division in the pith and/or cambium of various woody plants (1940, 1941). The rooting activity of IAA in cuttings was examined and reported by a number of researchers engaged in application studies of various fruit-trees and ornamental trees. These reports are referred to the book of Sumiki (1951).

The activity of IAA in parthenocarpy induction and fruit growth was also examined and reported for various tree fruits such as persimmon, loquat, plum, pear, etc. and vegetables such as egg plant, and *Cucurbitaceae* plants including cucumber and pumpkin. IAA was applied either by spraying water solutions or smearing lanolin pastes to the stigma (refer to the book of Sumiki in1951 in which these reports are listed.).

In addition to the above-mentioned phenomena, feeding tests of IAA were conducted by a number of researchers in applied fields to see if there were any effects using various plant materials such as fruit, seed, tuber, flower, etc. One of the interesting reports is that IAA could induce germination of peanut which usually shows dormancy (Shibuya 1938a, b). Shibuya of Taihoku Imperial University supported the hypothesis that a hormone existing in the endosperm moves to the embryo to initiate germination. He also reported that IAA treatment of seeds could induce a vernalization-like effect. Another interesting effect is that IAA when applied as lanolin paste to the tips of the petal and/or calyx induced a large-sized corolla in *Solanum melongena*, *Zephyranthes candida*, *Farfugium japonicum*, *Zinnia elegans* and *Aster tataricus* (Hirose 1939).

The use of 2,4-D as a herbicide was initiated by the work of Hamner and Turkey in 1944 who reported on the effect of 2,4-D and 2,4,5-T to induce the death of the root apex in *Fallopia concoluvulus*. In Japan, the start of studies on herbicides had to wait until after World War II. In 1948, large-scale applied studies of 2,4-D in paddy and dry field farming were conducted as a Grant-in-Aid project from the Ministry of Education.

Studies on gibberellin

Physiological and application studies of gibberellin before World War II were few. This is partly due to a limited supply of gibberellin, which was produced at the laboratory of Yabuta and Sumiki of Tokyo University by a small-scale static culture of the fungus, *Gibberella fujikuroi*. As I mentioned in the beginning, researchers at that time did not foster the idea that gibberellin was a plant growth hormone. Yabuta's group conducted feeding experiments on various cultivated plants for possible utilization in agriculture. These early studies are listed in Sumiki's book (1943). One interesting effect of gibberellin was reported by Hayashi (1940). He showed that amylase activity in seeds of barley, wheat and rye increased by gibberellin treatment, and suggested the possibility of utilizing it in industrial malt production. Intensive studies on gibberellin both in basic and applied fields in Japan started only after the mass production of fungal gibberellin became possible in tank culture by Kyowa Hakko Co., Ltd. after World War II. Such a historical review is referred to the book, "A miracle plant hormone–gibberellin (Kiseki no shokubutsu horumon–gibberellin)" (1980). Early gibberellin studies were also collected as a book (Stodola 1958). When gibberellin was found, Japanese researchers who were interested in the physiology of plant growth phenomena might have adhered to a doctrine, "without auxin, no growth (Ohne Wuchsstoff, kein Wachstum)". It was unfortunate that no-one had the idea that at that time gibberellin might be a plant hormone. Nagao writes in his article (1975) that Japanese researchers at that time thought it a virtue (of scientists) not to have interests in the research fields of others. But they might have unconsciously had a disposition to admire Occidental trends even in science, as Nagao also guessed.

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