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Acid & Neutral Gibberellin-Like Substances in Potato Tubers [1, 2]

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Gibberellin-like substances occur in many higher plants (11). At least four gibberellins (A_1, A_5, A_6, & A_8) have been isolated from Scarlet Runner bean (*Phaseolus coccineus* L. [*P. multiflorus* Lam.]) and identified (6). Characteristically, separation of gibberellin-like substances is performed at low pH, below the pKa value of gibberellins A_1 and A_3. This is an heritage of the procedures used to extract gibberellins from cultures of *Gibberella fujikuroi* (Saw.) which are most productive of gibberellins at pH 2.5. Heretofore, no gibberellins have been found in plant extracts prepared at neutral or higher pH. However, Wierzchowski and Wierzchowska (18) recently found two gibberellin-like substances in the neutral fraction of an extract of the broth of *Gibberella fujikuroi* (Saw.) Wr. The greater gibberellic acid activity in extracts allowed to stand at low pH for 24 hours, as compared to 8 hours, led Lazer, Baumgartner, and Dahlstrom (4) to believe that gibberellic acid occurred in a bound or derivative form. They suggested that this increase may be the result of hydrolysis of a precursor. Murakami (9) reported the formation of a GA_3 glucoside that is hydrolyzed by acid or emulsin.

Naturally occurring gibberellins may be intimately involved in controlling rest period in potato (*Solanum tuberosum* L.) tubers (1, 14, 15, 16). However, the research reported heretofore was based entirely on the activity of gibberellin-like substances extracted at low pH. The fact that the pH of extracted potato tuber sap is about 6.5 spurred an investigation of the possible occurrence of gibberellins at higher pH.

Previous research in this laboratory on gibberellin-like substances utilized orthodox methods of extraction, essentially those of West and Phinney (17). However, the present study shows that peelings of potato tubers contain several gibberellin-like sub-

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stances that are extractable at low and neutral pH. Perhaps most significant is the activity shown in the neutral fraction (2).

Materials & Methods

► Extraction: The method of extraction and separation of gibberellin-like substances from potato tubers is shown in a flow diagram (fig 1). Potato peelings and buds were reported by Okazawa (10) and Smith (16) to contain the bulk of gibberellin activity in the potato tuber. Therefore, buds and peelings from well-sprouted tubers were used in this study.

Peelings (1,000 g fr wt) were homogenized in a Waring blendor and extracted in 3,000 ml of methanol for 48 hours at 0 C (fig 1). The methanol was changed once after 24 hours. The combined methanol extract (final concentration: about 75 % methanol) was filtered through a Büchner funnel, evaporated to the water phase, and the pH adjusted to 7.5 with $NaHCO_3$. The residue was discarded. The water phase was extracted several times with alcohol-free ethyl acetate which was then separated from the water phase.

The ethyl acetate fraction was washed with 1 % H_2SO_4 and dehydrated with anhydrous sodium sulfate. The ethyl acetate fraction contained neutral

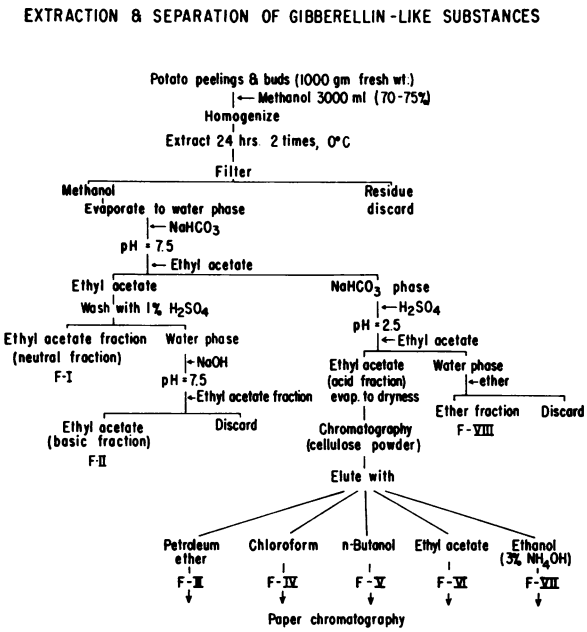


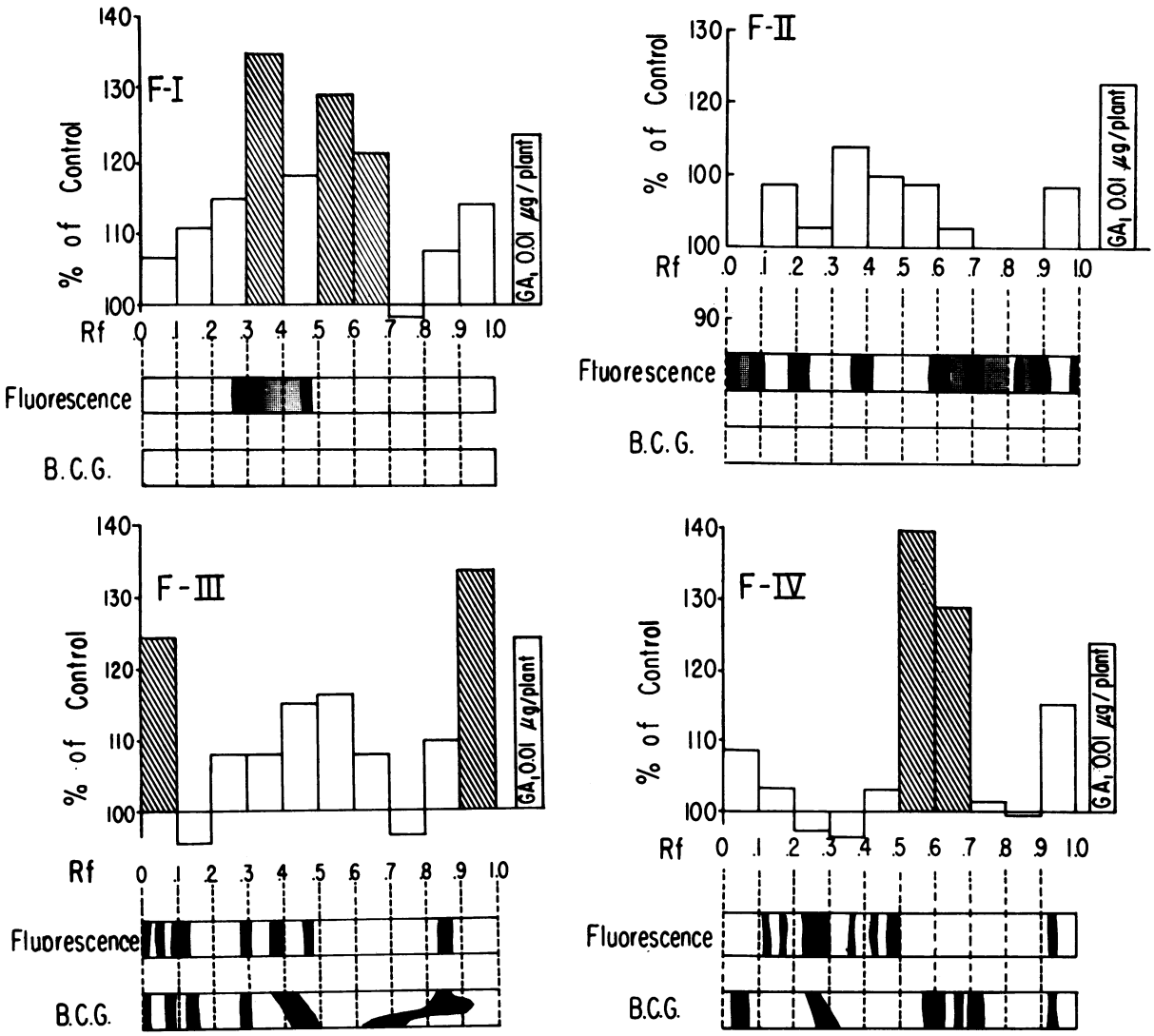
Fig. 1. Flow diagram showing procedure for extraction and separation of gibberellin-like substances from potato peelings and buds. Isopropyl alcohol, ammonium hydroxide, and water 10 : 1 : 1 v/v was used as developing solvent.

substances (F-I). The water phase was adjusted to pH 7.5 with NaOH and extracted with ethyl acetate, yielding the basic fraction (F-II). The water phase was discarded.

Fractions F-III to F-VIII came from the water phase which had been adjusted to pH 7.5 with $NaHCO_3$. This phase was adjusted to pH 2.5 with H_2SO_4 and extracted three times with ethyl acetate. The ethyl acetate fraction was mixed with 2 g cellulose powder, and evaporated to dryness. The dried fraction was placed on a cellulose powder column (3.3 × 25 cm) which had first been purified with 1 N HCl, distilled water, and methanol. The column was developed with 400 ml aliquots of petroleum ether (F-III), chloroform (F-IV), *n*-butyl alcohol (F-V), ethyl acetate (F-VI), and 3 % ammonium hydroxide in ethyl alcohol (F-VII). Fraction (F-VIII) was prepared by partitioning the water phase with ether after separation of the ethyl acetate fraction.

All fractions were concentrated to a volume of about 2 ml and streaked on Whatman No. 3 mm paper (46 × 57 cm). They were then developed at 22 C in a chromatographic cabinet by a descending solvent system containing isopropyl alcohol, ammonium hydroxide (specific gravity 0.90), and water (10 : 1 : 1 v/v). The chromatograms were removed when the solvent reached about 45 cm from the origin. A strip 2 cm wide was cut from one edge and checked for fluorescence with a 275 mμ ultra violet light, and for color development with bromcresol green (B.C.G.). Only GA_3 is known to fluoresce, but only in the presence of H_2SO_4. However, fluorescence was checked in order to detect other substances, such as fluorescent inhibiting compounds, that migrate to the same Rf's as gibberellin-like substances. Zones exhibiting different colors of fluorescence are so indicated by different shadings on the figures. Bromcresol green, an indicator in the pH range of 4.0 to 5.6, was used in order to detect acid substances including possible gibberellins. The remainder of the chromatogram was cut into 10 sections according to Rf and eluted by shaking 5 hours with 150 ml of methanol. The eluates were filtered and evaporated to dryness. These fractions were then dissolved in 0.05 % Tween-20 (polyoxyethylene sorbitan monolaurate) in 50 % aqueous ethanol solutions for bioassay.

► Bioassay: The primary bioassay used in this test was the dwarf pea grown under red light. It was developed by Reinhard, Kato, and Lang (13), based on the observation of Lockhart (5) that gibberellins reverse the red light inhibition of elongation of dwarf peas. The test is sensitive to all gibberellins (fig 3) but not to coumarin, trans-cinnamic, 3-indoleacetic (10^{-5} M), or myristic acids (Rappaport, unpublished data). Peas (cv. Morse's Progress No. 9) are soaked for 6 to 8 hours in running water and then planted in the dark at 27 C. After 4 days, seedlings 2.75 to 3.5 cm long (measured from the cotyledonary node to the highest visible node) are transferred to water culture under red light. The radiation source,



Figs. 2 through 9. Response of dwarf peas (cv. Morse's Progress No. 9) to gibberellin-like substances extracted from potato peelings and buds with different solvents (refer to flow diagram, fig 1).

Fig. 2 (*upper left*). Neutral fraction—F-I.

Fig. 3 (*upper right*). Basic fraction—F-II.

Fig. 4 (*lower left*). Acid petroleum ether fraction—F-III.

Fig. 5 (*lower right*). Acid chloroform fraction—F-IV.

45 cm above the plants, consisted of two 48-inch pink fluorescent tubes above three sheets of red cellophane on a frosted-glass plate. The plants are treated 24 hours later with a measured droplet (usually 5, 10, or 20 µl) of extract or known gibberellin. After 5 days the distance between the cotyledonary node and the highest visible node is measured. Ten single plant replications are used per fraction. Activity greater than 120 % of the Tween-20 control is significant.

Dwarf maize d-1, d-3, and d-5 (hereafter referred to as d-1, d-3, or d-5) in ten single plant replications were also used for bioassay of gibberellin-like substances (12). A measured droplet (usually 0.05 ml) containing extract or known gibberellin is delivered into the cup formed by the elongating leaf sheaths.

The distances between the prop root and the ligules of the first and second leaf sheaths are measured to determine gibberellin-like activity.

Results

Figures 2 through 9 show the activity on dwarf peas of gibberellin-like substances in extracts of potato peelings and buds.

► Neutral Fraction F-I: Surprisingly, fraction F-I contained at least two zones showing gibberellin activity on dwarf peas, at Rf 0.3 to 0.4 and Rf 0.5 to 0.7 (fig 2). These zones will be provisionally termed potato factors I and II. These fractions, however, were not active on d-1 or d-5 (table I). The Rf 0.3 to 0.4 fraction showed fluorescence but no color development. It is not clear at present whether this fluorescence is from potato factor I or from another substance at the same Rf. This extraction was repeated five times, with activity of the neutral substances ranging from 20 to 50 % over the control.

Table I

Effect of Neutral Fractions (Rf 0.3–0.6) on Elongation of Dwarf Maize d-1 & d-5, & Dwarf Pea*

Rf	% Elongation		
	Dwarf maize		Dwarf pea
	d-1	d-5	
0.3–0.4	100.2	110.6	122.1
0.4–0.5	84.9	103.8	112.7
0.5–0.6	82.9	103.4	115.6

* Average of ten single plant replications.

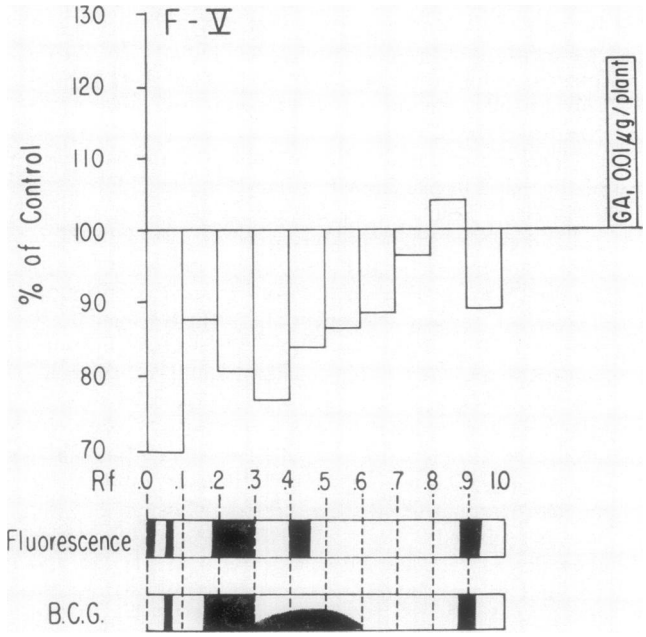
► Basic Ethyl Acetate Fraction F-II: Fraction F-II (fig 3) contains several severely toxic zones and no significantly active zones. Perhaps inhibitors overcame stimulating effects of gibberellin-like substances. Several fluorescent zones were seen, but no color development was found with bromcresol green.

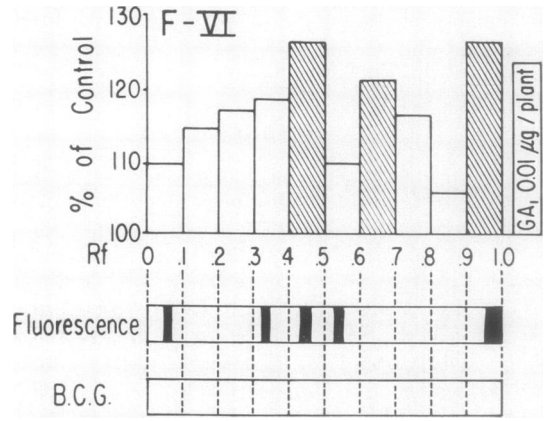
► Petroleum Ether Fraction F-III: The column was first developed with petroleum ether to remove substances that might be inhibitory or toxic to peas. Experience has shown that potato tubers contain many toxic substances. The gibberellins are not known to be soluble in petroleum ether, yet this fraction contains at least two active zones, at Rf 0.1 to 0.2 and 0.9 to 1.0 (fig 4). Activity at Rf 0.1 to 0.2 was reported previously by Murakami (8) who used the same solvent system. Certainly, more information on the solubility properties of the gibberellins is needed, especially of A_5 to A_9. Fluorescence and color development were seen at Rf 0.9 to 1.0, but the low activity on the plants discounts the likelihood that the color was due to the active compound.

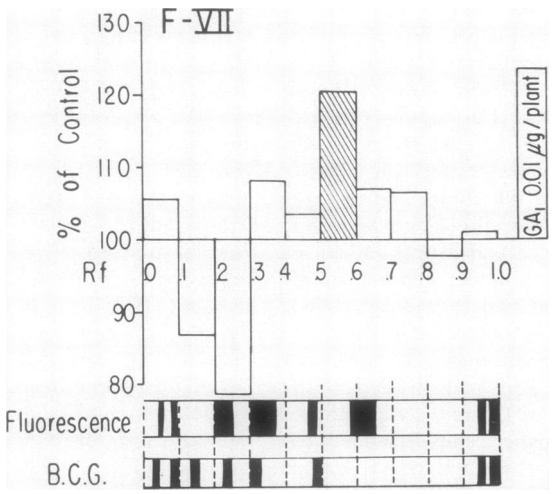
► Chloroform Fraction F-IV: Strong gibberellin-like activity was seen in the chloroform fraction at Rf 0.5 to 0.7 (fig 5). This was entirely unexpected in view of the generalization that gibberellins are not soluble in nonpolar solvents, including chloroform. Indeed, chloroform has been used as a background solvent for column chromatography of gibberellin-like substances.

This surprising activity prompted an investigation of the solubility of known gibberellins in chloroform (fig 10). Solutions of known gibberellins, except A_2, which was not available, were dissolved in 0.1 M phosphate buffer at pH 8.0, shaken three times for 3 minutes with distilled chloroform, and partitioned. The water phase was sequentially adjusted to pH 6.0, 5.0, and 2.5 and the same extraction procedure repeated at each pH. The combined chloroform fractions from each pH extract were evaporated to dryness and the residue dissolved in 0.05 % Tween-20. Measured droplets were applied to dwarf peas and the comparative activity (solubility) of gibberellins in chloroform after partitioning from phosphate buffer was determined. Both gibberellins A_5 and A_7 were partially extractable with chloroform at pH 2.5 and 5.0, and A_7 was partially extractable at pH 6.0. Gibberellins A_1, A_3, and A_5 migrate to Rf 0.5 to 0.7 in the standard solvent system. The comparative activity of the chloroform fraction on dwarf peas and d-1, d-3, and d-5 was studied in the following experiment.

► Comparative Activity of Acid Chloroform Fraction F-IV on Dwarf Peas & Dwarf Maize d-1, d-3, & d-5: The data of figure 10 are from a chloroform fraction prepared in a separate experiment. The aim was to study the comparative effect of Rf 0.5 to 0.7 of the chloroform fraction on bioassays sensitive to gibberellin-like substances. Dwarf maize d-1, d-3, and d-5 and Morse's Progress No. 9 dwarf pea were used to detect activity of gibberellin-like substances. The chromatographic method was different from that already described in that isopropyl alcohol, ammonium hydroxide, and water were used in the ratio of 8:1:1 instead of 10:1:1 v/v. In addition, one-half (A) of the extract was streaked on Whatman No. 3 mm paper, eluted immediately, and the eluates tested for activity on dwarf peas and d-1 (fig 11A). The other half (B) was stored at −10 C for about one month, chromatographed, and the eluates tested on dwarf peas and d-3 and d-5 (fig 11B). Thus direct comparisons are difficult to make except as they may be related to the activity on dwarf peas in the data of figure 11A. As seen in figure 11A, the chloroform fraction contained a zone between Rf 0.5 and 0.7 that was active on dwarf peas, but not on d-1. The complete lack of activity on d-1 is surprising in view of the relatively high activity on the peas. However, the fraction was not diluted and inhibitors may have obscured activity on d-1, although no symptoms of toxicity were seen on the maize. The chloroform fraction (B) contained activity at Rf 0.45 to 0.55 on dwarf peas, and d-3 and d-5 (fig 11B). The activity was noticeably different from that of (A) after 1-month's storage at −10 C. The Rf of the active fraction in (B) was slightly lower than in (A), and a portion of the active zone disappeared.







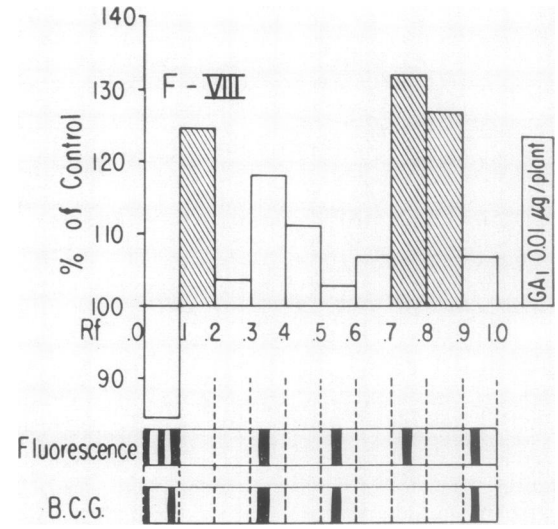


Fig. 6 (*upper left*). Acid *n*-butyl alcohol fraction—F-V.
Fig. 7 (*upper right*). Acid ethyl acetate fraction—F-VI.
Fig. 8 (*lower left*). Acid ethanol, 3 % ammonium hydroxide fraction—F-VII.
Fig. 9 (*lower right*). Acid ether fraction—F-VIII.
Chromatograms developed with isopropyl alcohol, ammonium hydroxide, and water (10:1:1 v/v). Data are average of ten single plant replications. Differences in colors of fluorescence and color detection were shown by differences in shading.

► *n*-Butyl Alcohol Fraction F-V: The *n*-butyl alcohol fraction (fig 6) contained many substances that inhibited elongation of peas. Therefore, the presence of gibberellin-like substances was not ascertained. Both fluorescence and color development were seen in this fraction at several Rfs.

► Ethyl Acetate Fraction F-VI: That ethyl acetate is an excellent solvent for gibberellins is confirmed by the amount of activity seen in different zones in the F-VI fraction (fig 7). Activity is seen at Rf 0.4 to 0.5, 0.6 to 0.7, and 0.9 to 1.0 In addition, other fractions (0.2–0.4 & 0.7–0.8) approached significant activity. Whereas the gibberellin-like substances found at Rf 0.3 to 0.5 and 0.6 to 0.7 are reminiscent of Rf's of known gibberellins, the activity at 0.9 to 1.0 cannot be attributed to that of any known gibberellin. None are known to migrate with the solvent front. The fluorescence at Rf 0.35 and 0.45 is likely not due to the gibberellin-like substance because of the relatively low activity on the bioassay.

► Ethyl Alcohol—3 % NH_4OH Fraction F-VII: One peak of activity, at Rf 0.5 to 0.6, was detectable in this fraction. It corresponds to gibberellins A_3 and A_1 (fig 8).

► Ether Fraction F-VIII: After ethyl acetate extraction at pH 2.5, the water phase was reextracted with ether (F-VIII) as a check on the completeness of extraction of gibberellin-like substances by ethyl acetate. Obviously, the initial ethyl acetate extraction only partially dissolved the gibberellin-like substances, since the ether fraction contained activity at Rf 0.1 to 0.2 and 0.7 to 0.9 (fig 9).

Discussion

Numerous papers describe gibberellin-like substances in many higher plants. Okazawa (10) reported an active substance from potato tubers at the same Rf as gibberellin A_1 or A_3, and Smith and Rappaport (14, 15) and Smith (16), using Mitchell's solvent (7), detected activity in potato peelings of acid gibberellin-like substances at Rf's comparable to those of gibberellins A_1 or A_3, and A_5. Activity was also seen at Rf 0.1 to 0.2 and 0.9 to 1.0.

However, the array of gibberellin-like substances described in this paper has not been detected from potato tuber extracts before. Most significant is the discovery of gibberellin-like substances extracted from potato peelings at neutral pH (fig 2). However, the failure of potato factors I and II to stimulate elongation of dwarf maize requires explanation. This failure may simply be due to low concentration, although the partially purified extract from as much as 50 g of peelings was applied per plant, enough for marked stimulation of pea plants by acid gibberellins from the same amount of tissue. Hayashi and Rappaport (3) have shown the chemical conversion of potato factor I to an acid gibberellin-like substance. This prompts the speculation that dwarf peas may possess an efficient mechanism for converting this neutral substance to an acid substance, whereas d-1 and d-5 may not. However, differences in absorption of the compound by the two plants cannot be overlooked.

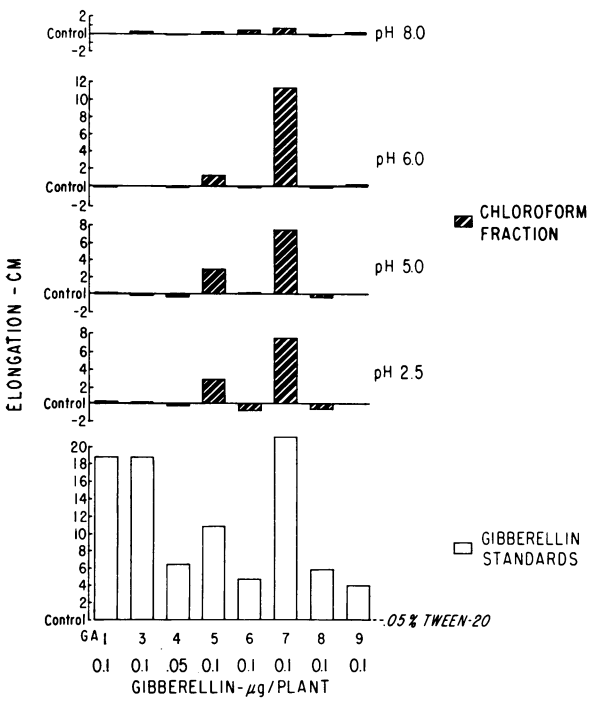


Fig. 10. Solubility of gibberellins A_1 and A_3 to A_9 in chloroform after separation from water at pH 8.0, 6.0, 5.0, and 2.5. The bottom histogram shows the effect of the different gibberellins on elongation of Morse's Progress No. 9 dwarf pea. Average of ten single plant replications.

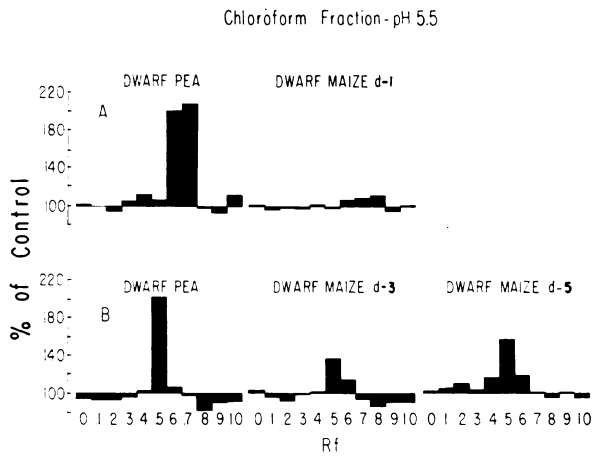


Fig. 11A. The response of dwarf pea and dwarf maize d-1 to gibberellin-like substances extracted at pH 5.5 with choloroform. Extracts applied immediately after preparation to ten single plant replications.

Fig. 11B. The response of dwarf pea and dwarf maize d-3 and d-5 to the same extract applied one month after storage at —10 C. Average of ten single plant replications.

The nature of the neutral substances is unknown at present; however, their possible significance cannot be overlooked. It is unlikely that gibberellins occur as free acids in plants because of their low pKa values, and it is not original to speculate that they occur in a bound or precursor form. In fact Lazer, Baumgartner, and Dahlstrom (4) have suggested this possibility, and it does not come as a complete surprise that Murakami (9) showed the in vitro formation of a complex between glucose and GA_3. The glucoside moiety was hydrolyzable with dilute HCl or emulsin (β glucosidase). The neutral substance at Rf 0.3 to 0.4 is at the same Rf as Murakami's GA_3 glucoside. Partial identification of two neutral gibberellin-like substances was presented in a note by Wierzchowski and Wierzchowska (18). However, judging from their technique, it seems possible that their compounds are basic, rather than neutral. The chemical nature of neutral substances in potato tubers is under investigation, and reports of their chemical and physiological properties will follow.

The gibberellin-like activity of the chloroform

fractions in the data of figures 11A and 11B was unexpected, since heretofore gibberellins had not been shown to be soluble in chloroform. Both gibberellins A_5 and A_7 are soluble in chloroform (fig 10). Fraction (A) contained substances that stimulated dwarf peas but not d-1, and fraction (B) contained substances active on dwarf peas, and d-3 and d-5. Smith and Rappaport (14) and Smith (16) showed that some acid extracts of potato peelings were more active on d-5 than d-1, while Smith and Rappaport (15) found others that were equally active on d-1, d-3, and d-5. West and Phinney (17) showed that bean factor II (GA_5) was more active on d-5 than d-1. MacMillan, Seaton, and Suter (6) found gibberellin A_5 but not A_7 in runner beans. Based on Rf, greater activity on d-5 than d-1 and solubility of gibberellins A_5 and A_7 in chloroform, the gibberellin found in the chloroform fraction may be A_5 or A_7, most likely A_5. The possibility of using chloroform to separate certain gibberellins should not be overlooked (see fig 10).

Two differences were seen in chloroform fractions (A) and (B) after storage for one month at −10 C: the Rf of the active zone was lower in (B), and part of the activity was lost. Since the chromatograms were prepared a month apart, environmental differences during chromatography may account for the differences in Rf. However, the loss of activity is surprising, since in our experience gibberellins A_3 and A_1 are stable for long periods when stored at −10 C. The nature of this change is worthy of further investigation.

The other active substances found in potato peelings are also under investigation, with the special aim of determining their identity and, hopefully, physiological action.

Summary

Gibberellin-like substances were found in extracts of potato peelings and buds made with various organic solvents at low (2.5) and neutral (7.3) pH. A solution of isopropyl alcohol, ammonium hydroxide, and water (10:1:1 v/v) was used as developing solvent. Dwarf peas grown under red light and dwarf maize d-1, d-3, and d-5 were used for bioassay. A neutral fraction contained a zone at Rf 0.3 to 0.4 that was active on peas but not on d-1 or d-5. Gibberellin-like substances at Rf 0.5 to 0.7 in a chloroform extract were active on dwarf pea, and d-3 and d-5 but not on d-1. Gibberellins A_5 and A_7 were soluble in chloroform at pH 2.5 and 5.0, and A_7 was soluble at pH 6.0. The possible significance of neutral gibberellin-like substances is discussed.

Acknowledgments

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