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Control mechanisms in the tuberization process

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Summary

Experiments were conducted with the cultivar Up-to-date to study the relationship between gibberellin level and tuber initiation. Tuberization resulted in case of all treatments which led to a decrease in the endogenous gibberellin level. This observation is also applicable to most of the results published by other research workers. It is postulated that a balance between gibberellins and other endogenous growth substances (especially inhibitors) controls the tuberization process, and that tuber initiation results as soon as the gibberellin content decreases beneath a threshold level.

Introduction

The process of tuberization has interested scientists for decades, and numerous hypotheses have been advanced to explain the control mechanism.

One of the earliest research workers considered tuberization the result of a symbiotic reaction between the potato plant and a fungus (Bernard, 1902). Inevitably it was also linked directly with the C:N-ratio (Wellensiek, 1929; Werner, 1935). The work of Gregory (1956), emphasizing the probable existence of a specific hormone-like tuber-forming substance, led to a renewed and redirected interest in the subject. As early as 1962 Okazawa & Chapman suggested that a balance between an inductive stimulus and natural gibberellins controls tuberization. The probable role of endogenous gibberellins in the control mechanism is emphasized in various recent publications (Racca & Tizio, 1969; Smith & Rappaport, 1969; Pont Lezica, 1970; Tizio, 1971).

Indications were found that other growth substances such as abscisic acid (El-Antably et al., 1967), cytokinins (Palmer & Smith, 1969, a, b) and ethylene (Garcia-Torres & Gomez-Campo, 1973; Palmer & Barker, 1973) may also be involved.

A generally accepted theory regarding the mechanism of tuber initiation still does not exist, though an increasing number of research workers are slowly reaching concensus on a number of important aspects. Significantly, many present workers are thinking in terms of a balance between two or more growth substances, gibberellin being one of them. This approach is in line with the contemporary school of thought that many growth and developmental processes in plants are controlled by a balance

of growth substances, generally phytohormones and inhibitors, rather than by specific hormones (Kefeli & Kadyrov, 1971).

Experiments conducted at the University of Pretoria have shown that the tuberization process of many of the South African potato cultivars is very sensitive to photoperiod. Up-to-date plants grown under long-day conditions could be induced to tuberize by only one inductive short-day cycle, while eight inductive cycles led to very good tuberization (Hammes, 1972). Plants grown from isolated tuber buds responded to inductive photoperiods at a very early stage of development, and tubers of 1 cm diameter were present 30 days after emergence of plants. When grown under 15-hour photoperiods the first tubers of Up-to-date plants developed approximately 60 to 70 days after emergence (Hammes et al., 1974). Inductive short days, even after this stage, led to improved tuberization. It is, thus obvious that any hypothesis regarding the mechanism of tuber initiation must explain the role of environmental factors such as photoperiod and temperature.

In an experiment to localize the site of perception of the photoperiodic stimulus in potatoes (Hammes & Beyers, 1973), tubers were produced in non-inductive photoperiods when the young leaves and meristematic stem apices were removed. Tuberization in these plants could be inhibited by application of gibberellic acid. It was concluded that the leaves seem to produce a substance, probably gibberellin, which delays tuberization under long-day conditions.

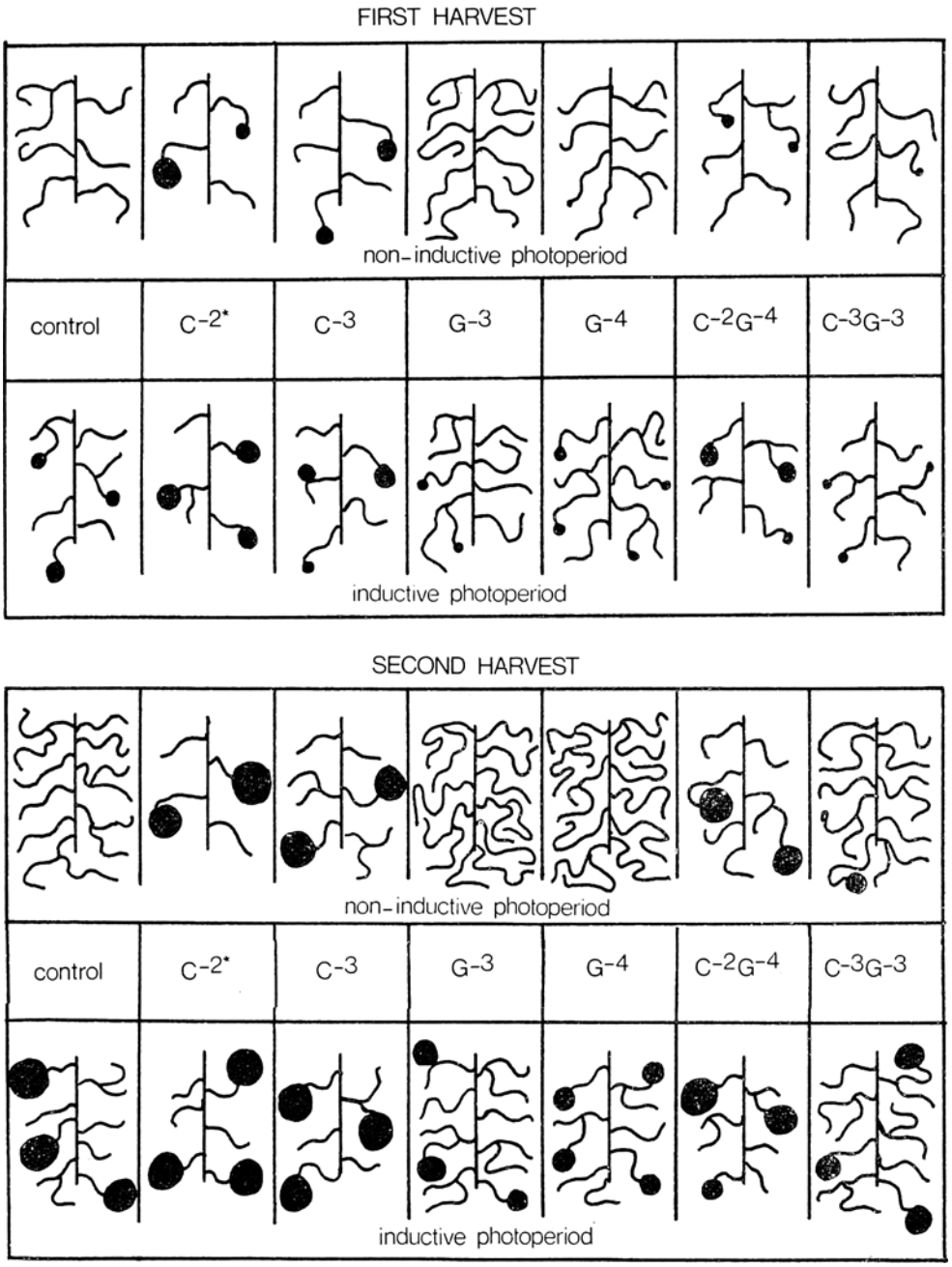
With a view of obtaining more information on the relationship between gibberellin level and tuber initiation, both under long and short days, a further experiment was conducted. The present paper is a report on the results of this latter experiment. A probable control mechanism is also postulated.

Procedure

The experiments were conducted in PGW-36 plant growth chambers, on the experimental farm of the University of Pretoria. Uniform potato plants, cv. Up-to-date, grown from tuber buds, were planted in pots containing washed sand and watered weekly with a nutrient solution. The plants were kept under non-inductive long-day conditions for 50 days before the treatment period of 9 days, and afterwards for 6 and 26 days, respectively, until the time of the two harvests.

Day and night temperatures of 20 and 15°C in a 12-hour cycle were maintained continuously. The non-inductive photoperiod consisted of 12 hours of high light intensity (180 W/m^2), followed directly by 6 hours of low light intensity (6W/m^2) and a dark period of 6 hours.

The treatments which were applied are shown in Fig. 1. In the case of the inductive short days the photoperiod was 12 hours. Differences in total radiation between long-day and short-day treatments were small. Growth substances were applied once, namely when the short-day treatments started. Gibberellic acid (GA_3) was applied to the young leaves at rates of 0.1 ml 10^{-3} *M* or 0.1 ml 10^{-4} *M* per plant (codes G^{-3} and G^{-4}). CCC (2-chloroethyltrimethylammonium chloride), at rates of 100 ml 10^{-2} or 10^{-3} *M* (Codes C^{-2} and C^{-3}), was applied to the root medium.


FIRST HARVEST
non-inductive photoperiod
control
C-2*
C-3
G-3
G-4
C-2G-4
C-3G-3
inductive photoperiod
SECOND HARVEST
non-inductive photoperiod
control
C-2*
C-3
G-3
G-4
C-2G-4
C-3G-3
inductive photoperiod

Results

The reaction of the plants on the various treatments were similar for the two harvest periods, as can be seen in Table 1 and Fig. 1.

In the case of plants induced to tuberize by 9 short-day cycles, treatment with CCC tended to improve tuberization, while application of gibberellic acid significantly decreased the dry mass of tubers.

Where plants were continuously kept in non-inductive photoperiods, application of CCC consistently led to good tuber formation, whereas controls and plants treated with gibberellic acid produced no tubers. Practically the same degree of tuberization was achieved by means of CCC application as when tuberization was induced by short photoperiods. When gibberellic acid and CCC were applied simultaneously the reaction depended on the relative concentrations of the applied growth substances. A relatively high CCC concentration led to good tuberization, while on the other hand tuber formation was poor when the GA level was high.

Comparing the results of the two harvests, it is clear that inductive photoperiods as well as treatment with CCC advanced tuber initiation by more than 20 days. The applied substances also had an effect on the rate of tuber development. The dry mass of individual tubers of CCC-treated plants increased on the average by more than 2 g from the first to the second harvest (non-inductive photoperiod). Where the lower level of CCC was combined with the higher level of GA (treatment 10^{-3} *M* CCC + 10^{-3} *M* GA) the increase in tuber mass was only 0,2 g. The gibberellic acid seemed to have retarded the growth of tubers appreciably. Application of gibberellic acid had a deleterious effect on the time of tuber initiation, on the number of tubers initiated, and on tuber development. It is important to note that long days magnified the effect of gibberellin, while short days magnified the effect of CCC and reduced the effect of gibberellin.

Plants that did not produce tubers had very long stolons of up to 268 cm per plant after gibberellic acid treatment. As soon as tuber initiation occurred the growth of stolons summarily ceased. The result was that treatments which improved tuberization led to less stolon development. As can be deduced from Table 1 the stolons of

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Fig. 1. Diagrammatic representation of the effect of gibberellic acid and CCC on stolon and tuber formation (to scale).
*C^{-2} = 100 ml 10^{-2} M CCC per plant/*pro Pflanze/par plante;* C^{-3} = 100 ml 10^{-3} M CCC per plant; G^{-3} = 0.1 ml 10^{-3} M GA per plant; G^{-4} = 0.1 ml 10^{-4} M GA per plant.

First harvest – *Erste Ernte – Première récolte*
Non-inductive photoperiod – *Nicht induktive Photoperiode – Photopériode non-inductive*
Control – *Kontrolle – Témoin*
Second harvest – *Zweite Ernte – Seconde récolte*
Inductive photoperiod – *Induktive Photoperiode – Photopériode inductive*

Abb. 1. Diagram über den Einfluss von Gibberellinsäure und CCC auf die Stolonen- und Knollenbildung (massstabgerecht).
Fig. 1. Effet de l'acide gibberellique et du CCC sur la formation de stolons et de tubercules.

Table 1. Effect of photoperiod and treatment with growth substances on tuberization and other plant characteristics.

Code	Number of tubers[1]	Dry mass of tubers[2]		Average tuber mass[3] (g)	Tubers as % of total mass[4]	Stolon length[5] (cm)	Dry mass of stolons[6] (g)	Plant height[7] (cm)	Number of internodes[8]	Dry mass[9] (g)		tal
		g	SD ±							haulms[10]	roots[11]	
First harvest[12]												
Inductive photoperiod[13]												
C^{-2}	2.7	1.70	0.22	0.66	37.5	27.9	0.35	22.7	14.7	1.69	0.52	4.26
C^{-3}	2.3	1.66	0.34	0.76	37.4	38.7	0.36	20.3	16.7	1.88	0.51	4.41
G^{-3}	2.3	0.38	0.12	0.17	10.7	77.9	0.46	38.0	19.0	2.08	0.60	3.52
G^{-4}	4.3	0.98	0.16	0.23	22.4	77.8	0.63	26.7	18.0	2.25	0.53	4.36
$C^{-2}G^{-4}$	2.3	1.25	0.17	0.65	30.0	36.3	0.45	26.3	16.3	2.07	0.44	4.21
$C^{-3}G^{-3}$	2.7	0.52	0.12	0.20	15.6	55.0	0.44	30.3	18.7	1.81	0.59	3.34
Control[14]	3.3	1.03	0.22	0.31	23.8	73.3	0.61	25.0	15.0	1.82	0.72	4.31
Average[15]	2.9	1.07	–	0.44	25.4	55.2	0.47	27.0	16.9	1.94	0.56	4.06
Non-inductive photoperiod[16]												
C^{-2}	1.7	1.00	0.22	0.69	26.8	30.3	0.55	22.3	17.3	1.69	0.52	3.77
C^{-3}	2.0	0.70	0.54	0.35	16.8	45.7	0.57	27.3	15.3	1.80	0.87	3.95
G^{-3}	–	–	–	–	–	119.9	0.75	40.7	14.3	2.39	0.78	3.92
G^{-4}	0.3	0.12	–	0.12	3.7	82.8	0.76	34.7	16.3	1.93	0.66	3.49
$C^{-2}G^{-4}$	1.7	0.53	0.10	0.35	16.1	53.1	0.62	28.3	16.7	1.74	0.43	3.33
$C^{-3}G^{-3}$	0.3	0.04	–	0.04	1.1	72.1	0.60	37.3	18.0	1.95	0.83	3.42
Control	–	–	–	–	–	62.0	0.58	23.0	16.3	2.16	0.81	3.55
Average	0.9	0.34	–	0.51	12.9	66.6	0.63	30.5	16.8	1.95	0.70	3.65
LSD_T**(5%)	–*	0.64***	–	0.49***	–*	33.9	NS	9.1	–*	0.69	0.37	NS
Second harvest[17]												
Inductive photoperiod												
C^{-2}	3.3	6.28	1.64	1.95	63.7	32.1	0.24	27.3	22.3	2.25	1.00	3.76
C^{-3}	3.3	6.10	1.04	1.86	58.2	34.7	0.30	28.3	21.7	3.08	0.96	3.43
G^{-3}	3.0	3.26	0.96	1.24	42.0	144.4	0.89	37.3	25.0	2.84	0.89	3.89
G^{-4}	4.0	4.98	0.74	1.33	51.3	65.9	0.73	36.0	21.7	2.91	1.07	3.69
$C^{-2}G^{-4}$	2.3	5.21	0.75	2.02	55.1	38.9	0.40	25.7	21.3	2.79	1.04	3.43
$C^{-3}G^{-3}$	2.7	4.03	1.34	1.79	41.7	123.5	1.13	38.0	27.0	3.27	1.14	3.57
Control	2.7	5.96	1.16	2.35	59.7	64.9	0.44	30.3	23.0	2.52	1.03	3.94
Average	3.1	5.12	–	1.90	53.1	72.1	0.59	31.9	23.1	2.81	1.02	3.53
Non-inductive photoperiod												
C^{-2}	1.7	4.36	0.37	2.84	50.4	34.4	0.52	27.7	23.7	2.55	1.23	4.66
C^{-3}	2.0	4.64	1.07	2.32	49.4	57.3	0.69	27.0	22.0	2.94	1.11	4.35
G^{-3}	–	–	–	–	–	268.7	2.18	43.0	25.3	2.69	1.57	4.44
G^{-4}	–	–	–	–	–	215.4	1.87	31.0	24.0	2.86	1.77	4.50
$C^{-2}G^{-4}$	2.0	3.05	0.43	1.78	40.2	55.5	0.91	29.3	23.7	2.79	0.84	4.59
$C^{-3}G^{-3}$	1.3	0.49	0.47	0.24	7.1	137.2	1.17	46.3	26.3	3.32	1.73	4.70
Control	–	–	–	–	–	184.1	1.72	30.7	22.0	2.64	1.31	4.66
Average	1.0	3.13	–	1.79	36.8	136.1	1.29	33.6	23.9	2.83	1.36	4.70
LSD_T**(5%)	–*	1.81***	–	NS***	–*	69.2	0.79	10.5	–*	NS	0.64	2.64

* Data not analysed statistically – *Angaben nicht statistisch analysiert – Données non analysées statistiquement.*

** LSD values valid for comparison between growth substance treatments within photoperiod treatments – *Grenzdiffe werte gültig für Vergleich zwischen Wachstumssubstanzverfahren innerhalb der Tageslänge-Verfahren – Valeurs LSD petite différence significative) utiles pour la comparison entre les traitments aux substances de croissance dans les traite de photopériode.*

***LSD values only valid for inductive photoperiod data – *Grenzdifferenzwerte nur gültig für Daten der induktiven T länge – Valeurs LSD seules utiles pour les données de photopériode inductive.*

[1] *Anzahl Knollen – Nombre de tubercules;* [2] *Trockensubstanz der Knollen – Masse sèche des tubercules;* [3] *Durchschnitt Knollenmasse – Masse de tubercules moyen;* [4] *Knollen in Prozent der Gesamtmenge – Tubercules en % de la masse t* [5] *Stolonenlänge – Longuer des stolons;* [6] *Trockensubstanz der Stolonen – Masse sèche des stolons;* [7] *Pflanzenhöhe – Ha des plantes;* [8] *Anzahl Internodien – Nombre d'internoeuds;* [9] *Trockensubstanz – Masse sèche;* [10] *Stengel – Tiges;* [11] *Wurz Racines;* [12] *Erste Ernte – Première récolte;* [13] *Induktive Tageslänge – Photopériode inductive;* [14] *Kontrolle – Témoin;* [15] *A – Moyenne;* [16] *Nicht induktive Tageslänge – Photopériode non inductive;* [17] *Zweite Ernte – Seconde récolte*

Tabelle 1. Einfluss von Tageslänge und Behandlung mit Wuchsstoffen auf die Knollenbildung und andere Pflanzene schaften.

Tableau 1. Effet de la photopériode et du traitement avec des substances de croissance sur la tubérisation et d'a caractéristiques des plantes.

CCC-treated plants were appreciably thicker than those of GA-treated plants.

The total dry mass of all plants with good tuber development was much higher than that of plants without tubers. The short-day control plants had twice the mass of the long-day control plants, in spite of the fact that there were no detectable differences in the size of stems and leaves. The same observation was made in a number of other experiments – the presence of tubers (metabolic sinks) caused an increase in the net rate of photosynthesis.

Discussion

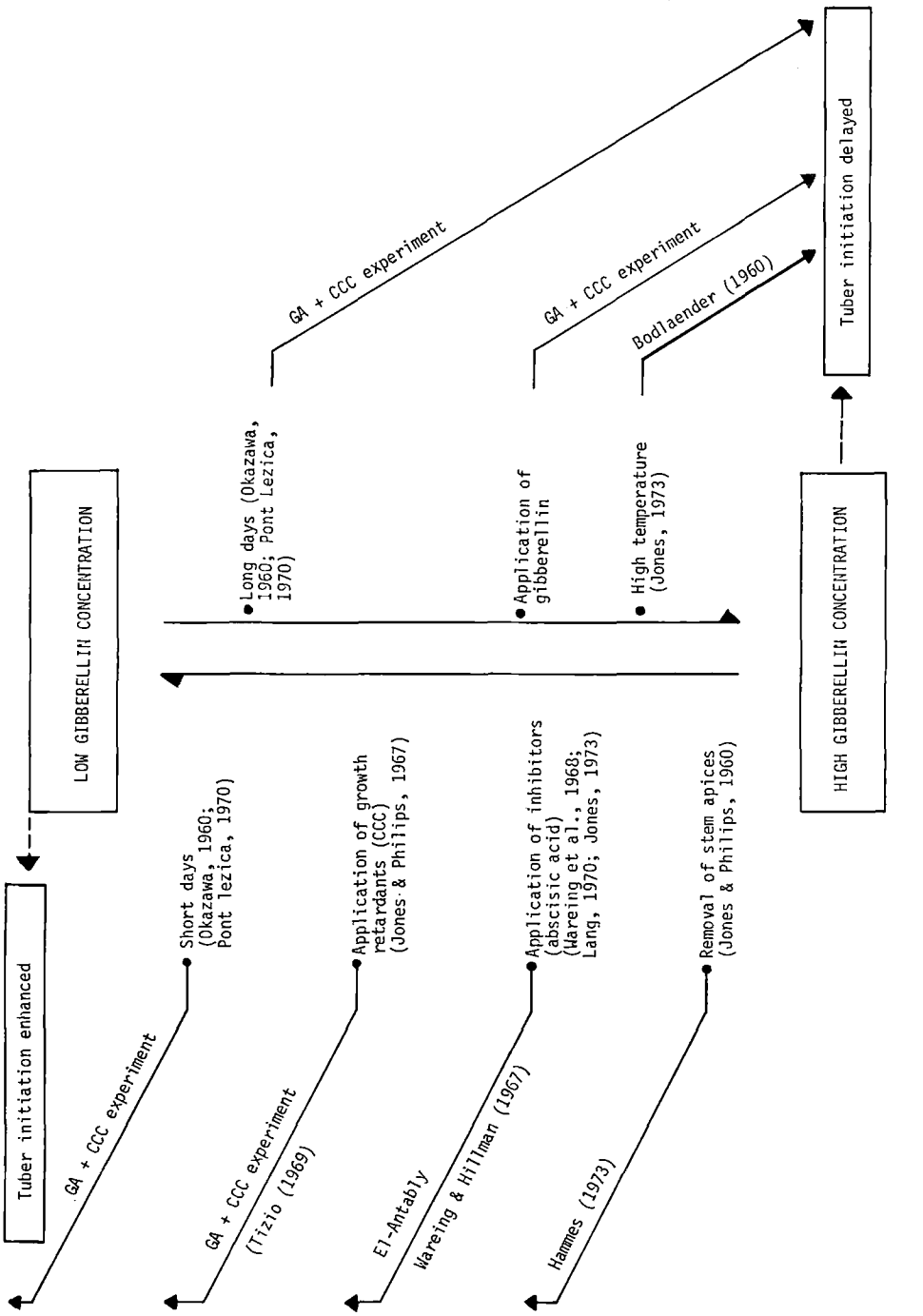
In these and other experiments it was noted that tuber initiation was always accompanied by an increase in total dry mass, although the growth of haulms, stolons and roots were reduced compared with plants without tubers. These correlated growth reactions seem to indicate that the induced condition exists in all the organs of the plant and that interdependent control mechanisms stop the growth of stolons, induce tuber initiation, limit the activity of the apical meristem of the haulms and increase the rate of photosynthesis, possibly by mobilizing carbohydrates from the leaves to the tubers. These observations indicate that a balance between various growth substances is involved in the control mechanism, rather than a single tuberization hormone. It is in agreement with the conclusion of Palmer & Barker (1973) that a 'hormonal complex' controls stolon growth and tuber initiation.

The apparently divergent results of growth substance treatments reported by a number of research workers can be ascribed to such an intricate endogenous growth substance interaction in the plant. It can be expected that application of a number of growth substances may influence this balance and thus have a direct or indirect influence on tuberization. The same holds true for environmental conditions, variations in nutritional levels, etc.

In accordance with the results of a number of scientists the foregoing experiment suggest that gibberellin or gibberellin-like substances are a dominant factor in tuber initiation. Apparently the ability of CCC to stimulate tuber formation is due to its anti-gibberellin action. The results obtained in this study with natural growing plants compare very well with those obtained by Tizio (1969) with tuber sprouts grown in vitro.

It is postulated that tuberization is normally prohibited by high effective gibberellin levels, and that the tuberization process commences as soon as the gibberellin level is lowered. Improved tuberization can probably directly be associated with a low level of active gibberellin in the plant. Supporting evidence for this hypothesis is schematically summarized in Fig. 2. Drastic fluctuations occur in the endogenous gibberellin level of plants, and various growth and developmental responses can without doubt be associated with the level of active gibberellins. In a review of the physiological role of gibberellins Jones (1973) refers to the possible importance of conjugated GAs (GA-glucosides) as regulators of the level of free GA. Low temperature as well as abscisic acid increase the level of conjugated gibberellins.

Exactly how the low level of gibberellin is associated with tuber initiation is at pres-


Tuber initiation enhanced
LOW GIBBERELLIN CONCENTRATION
HIGH GIBBERELLIN CONCENTRATION
Tuber initiation delayed
GA + CCC experiment
Short days (Okazawa, 1960; Pont Lezica, 1970)
GA + CCC experiment
(Tizio (1969)
Application of growth retardants (CCC) (Jones & Philips, 1967)
El-Antably
Application of inhibitors (abscisic acid) (Wareing et al., 1968; Lang, 1970; Jones, 1973)
Wareing & Hillman (1967)
Removal of stem apices (Jones & Philips, 1960)
Hammes (1973)
Long days (Okazawa, 1960; Pont Lezica, 1970)
GA + CCC experiment
Application of gibberellin
Bodlaender (1960)
High temperature (Jones, 1973)

ent unclear. A tempting explanation is that a direct balance between endogenous gibberellins and inhibitors (abscisic acid (El-Antably et al., 1967); inhibitor-β (Holst, 1971); the 'root factor' (Racca & Tizio, 1969)) determines the active gibberellin level in the plant. As soon as the gibberellin concentration is lowered beneath a critical value tuberization results, due to the release (synthesis, activation?) of a substance(s) such as cytokinins (Palmer & Smith, 1969a, b; Stallknecht, 1972) or ethylene (Garcia-Torres & Gomez-Campo, 1973) or even a specific unknown tuberization hormone. It is clear, however, that if a specific tuber forming substance is involved it is normally present in potato plants. (Tuberization can be achieved in plants grown in non-inductive environmental conditions by application of growth retardants such as CCC, or by removal of stem apices and young leaves.) Although the existence of a specific tuberization hormone seems unlikely, it can not be ruled out at present. The fact that the tuberization stimulus can be transmitted by grafting small pieces of stem from induced onto non-induced shoots (Kumar & Wareing, 1972) still argues in favour of such a specific substance.

The proposed mechanism of control over the process of tuber initiation is reconcilable with the results of the foregoing experiments, but it is not the only possible interpretation of the available data. The inhibition of gibberellin biosynthesis or some other anti-gibberellin action can not be assumed to be the only or even the most important effect of CCC. Teltscherova (1968, 1969, 1970) found that application of CCC to *Chenopodium* plants led to an increase in the extractable amounts of cytokinins and auxin, as well as a decrease in the gibberellin content. Application of gibberellin resulted in a decrease in the cytokinin level. The complex effect of applied growth substances on the concentration and activity of endogenous growth substances com-

Fig. 2. Schematic representation of the probable role of gibberellin in the tuberization process.

Tuber initiation enhanced – *Gesteigerte Knollenbildungsbereitschaft – Initiation accrue de la tubérisation*
Low gibberellin concentration – *Niedrige Gibberellin-Konzentration – Basse concentration en gibberelline*
GA + CCC experiment – *GA + CCC-Versuch – Essai GA + CCC*
Short days – *Kurze Tage – Jours courts*
Application of growth retardants (CCC) – *Anwendung von Wachstumshemmern – Application de retardeurs de croissance*
Application of inhibitors (abscisic acid) – *Anwendung von wachstumsverhindernden Stoffen (Abscisinsäure) – Application d'inhibiteurs (acide abscissique)*
Removal of stem apices – *Entfernung der Stengelspitzen – Enlèvement des sommets de tiges*
Long days – *Lange Tage – Jours longs*
Application of gibberellin – *Anwendung von Gibberellin – Application de gibberelline*
High temperature – *Hohe Temperatur – Haute température*
High gibberellin concentration – *Hohe Gibberellin-Konzentration – Haute concentration en gibberelline*
Tuber initiation delayed – *Verzögerte Auslösung der Knollenbildung – Initiation de la tubérisation retardée*

Abb. 2. Schematische Darstellung der wahrscheinlichen Rolle von Gibberellin im Knollenbildungsprozess.
Fig. 2. Représentation schématique du rôle probable de la gibberelline dans le processus du tubérisation.

plicates the interpretation of such treatment effects. It will be difficult to prove whether particular growth substances are directly or indirectly involved in the tuberization process.

Zusammenfassung

Kontrollmechanismen im Knollenbildungsprozess

An der Universität von Pretoria wurden mit der Kartoffelsorte Up-to-Date Versuche durchgeführt, um den Zusammenhang zwischen dem Gibberellinniveau und der Auslösung der Knollenbildung zu untersuchen. In nicht induktiven Photoperioden erfolgte eine Knollenbildung, wenn die junge Blätter und die meristematischen Spitzen entfernt wurden. In diesen Pflanzen konnte die Knollenbildung durch Anwendung von Gibberellinsäure gehemmt werden. Die sich entwickelnden Blätter schienen unter Langtagbedingungen eine Substanz, wahrscheinlich Gibberellin, zu entwickeln, welche die Knollenbildung verzögerte.

Beigabe von CCC zum Wurzelnährboden führte zum fast gleichen Grad der Knollenbildung, wie wenn die Pflanzen durch kurze Tageslängen zur Knollenbildung angeregt wurden. Diese Wirkung des CCC wurde durch Anwendung von Gibberellinsäure zu den jungen Blättern nahezu ganz aufgehoben. Verwendung von Gibberellinsäure zu Pflanzen, die unter Kurztagbedingungen zur Knollenbildung angeregt wurden, hatte auch eine nachteilige Wirkung auf die Knollenbildung. Wenn GA und CCC gleichzeitig angewendet wurden, hing die Reaktion von den jeweiligen Konzentrationen der angewendeten Mittel ab (siehe Tabelle 1 und Abb. 1).

Es wird vorausgesetzt, dass Knollenbildung normalerweise durch hoch wirksame Gibberellin niveaux verhindert wird und dass eine Knollenbildung erfolgt, sobald das Gibberellinniveau auf ein kritisches Mass herabgesetzt wird. Wenn eine spezifisch knollenbildende Substanz mit im Spiele ist, dann ist sie auch in nicht induzierten Kartoffelpflanzen vorhanden. Umweltbedingungen können das Gleichgewicht zwischen den Gibberellinen und den endogenen Hemmern (und wahrscheinlich andern Wachstumssubstanzen) beeinflussen, indem sie ihr Niveau oder ihre Aktivität beeinträchtigen. Ein deutlicher Beweis für die wahrscheinliche Rolle des Gibberellins im Knollenbildungsprozess wird in Abb. 2 dargestellt.

Résumé

Contrôle des mécanismes des processus de tubérisation

Des espériences ont été exécutées à l'Université de Pretoria, sur le cultivar Up-to-Date, dans le but d'étudier la relation entre le niveau de gibberelline et l'initiation des tubercules. La tubérisation était réalisée en photopériodes non-inductives alors que les jeunes feuilles et les sommets méristématiques de tiges sont enlevés. On pouvait inhiber la tubérisation dans ces plantes par application d'acide giberrellique. Les feuilles en développement semblaient produire une substance dans des conditions de jours longs, probablement la gibberelline, qui retardait la tubérisation.

L'application de CCC au système radiculaire provoquait un degré presque identique de tubérisation que lorsque l'induction était provoquée par de courtes photopériodes. Cet effet du CCC est presque complètement annihilé par l'application d'acide gibberellique aux jeunes feuilles. L'application d'acide gibberellique aux plantes à tubérisation induite par de courtes photopériodes a également un effet opposé à la tubérisation. Lorsqu'on applique simultanément GA et CCC, la réaction dépend des con- (voir tableau 1 et fig. 1).

Il est admis que la tubérisation est normalement inhibée par de hauts niveaux de gibberelline active et que la tubérisation se déclenche

aussitôt que le niveau gibberellique est abaissé en-dessous d'un seuil critique. Si une substance spécifique formatrice de tubercules est impliquée, elle est également présente dans les plantes de pomme de terre non induites. Les conditions de milieu peuvent influencer l'équilibre entre les gibberellines et les inhibiteurs endogènes (et probablement d'autres substances de croissance) en agissant sur le niveau ou l'activité de quelques-uns d'entr'eux. La fig. 2 apporte quelque preuve du rôle probable de la gibberelline dans le processus de tubérisation.

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