

APICAL DOMINANCE IN TUBERS OF POTATO
(*SOLANUM TUBEROSUM* L.)

N. LALLU and J.A. McWHA

Department of Botany, University of Canterbury,
Christchurch, New Zealand.

ABSTRACT

Apical dominance in the potato tuber shows many similarities with that exhibited in aerial shoot systems.

The apical bud of a tuber inhibits growth of the other buds. The degree of inhibition increases basipetally: buds immediately around the apex show only slight inhibition while those on the "heel" of the potato show only a small amount of growth. The buds can be released from the inhibition by isolation from the effects of buds nearer the apex. Isolated lateral buds commence growth with only a short delay while the basal buds show a significant delay, due possibly to their incomplete development.

The plant growth regulators indole-3-acetic acid and abscisic acid inhibit bud sprouting and growth while kinetin and gibberellic acid slightly promote it.

INTRODUCTION

The potato (*Solanum tuberosum* L.) tuber is a swelling at the apex of an underground stem. The tuber possesses an apical bud with leaf primordia and spirally arranged lateral buds ("eyes"), subtended by scale leaves.

The tubers are normally dormant at harvest and little or no bud growth occurs. When growth begins, it occurs more readily in the buds near the apex of the tuber (Appleman 1918). This phenomenon may be due to apical dominance, or it may indicate that the apical buds possess a less marked dormancy than do the laterals.

In the latter case, the longer rest period of the lateral buds could take the form of true dormancy of a morphologically fully developed bud, or it could be that the buds are morphologically immature and require a further period of development after harvest. Morphological studies by Goodwin (1967a, 1967b) indicate that the apical and lateral buds are morphologically indistinguishable, although the basal buds (those on the heel of the potato) are comparatively immature. It has been suggested (Appleman 1918, Michener 1942, Goodwin 1967a, 1967b, Goodwin and Cansfield 1967) that an apical dominance phenomenon exists in potatoes, and that the lateral buds are inhibited by the apical bud.

The object of the experiments reported here was to re-examine apical dominance in the potato tuber and to determine the possible role of some of the known groups of plant hormones.

MATERIALS AND METHODS

WHOLE TUBER EXPERIMENTS

Freshly harvested potatoes (var. Ilam Hardy) possessing a short rest period were used in this study. The potatoes were stored at 15-17°C in darkness for 16 days before the experiments were carried out.

Tubers of weight 15 to 18 g and with a uniform shape were selected; the apical bud was removed, and the tuber was cut transversely into two parts each with an equal number of "eyes". The tubers were then placed on moist sterilized sand or moist filter paper in a ventilated container at 16-18°C in darkness. Bud growth was examined under dim fluorescent light. Ten replicates were used for each treatment.

ISOLATED BUD EXPERIMENTS

Apical, lateral and basal buds were excised from the tubers as cylinders of tissue 14 mm in diameter and 8 mm in depth. The buds were placed in a 90 mm petri dish in an upright position on a disc of Whatman No. 1 filter paper moistened with 2 ml distilled water.

A representative of each of the major groups of plant growth regulators was applied to the buds. The treatments were indole-3-acetic acid (IAA) at a concentration of 2×10^{-5} M, and abscisic acid (ABA), gibberellic acid (GA₃) and kinetin at 4×10^{-5} M. All solutions were aqueous and while GA₃ was dissolved directly in distilled water, IAA and ABA, because of their low solubilities, were first dissolved in minimal amounts of methanol and then dispersed in water. The same procedure was adopted for kinetin, except that NN-dimethylformamide (DMF) replaced the methanol. In all cases, the appropriate solvent controls were included. Treatments consisted of the daily application of a 10 µl droplet of solution to the buds. Treatments were continued for 15 days and sprout length was measured every three days. Ten replicates were used for each treatment.

RESULTS

WHOLE TUBER EXPERIMENTS

The first visible indication of bud sprout was a swelling of the bud and, in all experiments, this swelling occurred at the same time in both apical and lateral buds. The swelling of the basal buds, however, occurred much later.

Immediately after sprouting, both the apical and lateral buds were of similar size, but the apical buds elongated more rapidly and after 13 days had achieved an average length of 4.0 mm compared with 2.1 mm for the laterals (Fig. 1a). In this experiment the buds immediately surrounding the apical bud were

also measured. These were termed the sub-apical buds, and were found to be intermediate in length between the apical and lateral buds (Fig. 1a). Growth of the basal buds was not apparent until day 17, and the subsequent rate of growth was very slow (Fig. 1a).

When the apical bud was removed, all other buds on the tuber showed an increased growth rate (Fig. 1b). This was particularly apparent in the case of the lateral and basal buds.

When tubers were cut in half transversely, a number of significant changes in bud growth occurred (Fig. 1c). The apical bud still grew significantly more than any other bud, but its growth was significantly greater than in the control tubers. The most interesting effect, however, was on those buds immediately adjacent to the cut surface. Those immediately above the cut were significantly inhibited compared with the lateral buds on the control tubers. The two buds below the cut showed significantly greater growth than the corresponding control buds and greater even than those on the tubers where the apical bud was removed. Their growth was comparable with that of the apical buds on the control tubers. Basal buds on the cut tubers showed only a slight promotion in growth.

EFFECT OF GROWTH REGULATORS ON ISOLATED POTATO BUDS

The time required for sprouting of isolated lateral buds was found to be only slightly greater than for apical buds (Table 1) although the subsequent rate of growth was markedly less for the lateral than for the apical buds (Table 2). Kinetin and GA_3 both promoted sprouting of apical and lateral buds. The basal buds exhibited a significant delay in sprouting which was overcome by kinetin but was apparently unaffected by GA_3 (Table 1). IAA and ABA delayed sprouting of all buds, although the effect of IAA was less marked on basal buds than on the other types of bud.

The rate of elongation of sprouted buds was increased by both GA_3 and kinetin, although GA_3 was the more effective promoter of elongation (Table 2). The apical buds showed the greatest response. ABA and IAA were both extremely effective inhibitors of bud elongation (Table 2).

TABLE 1. EFFECT OF PLANT GROWTH REGULATORS ON BUD SPROUTING. Values show percentage of excised buds sprouted 12 days after the commencement of daily applications of IAA, ABA, GA_3 , kinetin and solvent controls.

	Bud position		
	Apical	Lateral	Basal
Water	77	60	50
Methanol control	77	60	50
DMF control	77	56	40
ABA ($4 \times 10^{-5}M$)	50	44	0
IAA ($2 \times 10^{-5}M$)	60	43	38
GA_3 ($4 \times 10^{-5}M$)	100	89	40
Kinetin ($4 \times 10^{-5}M$)	100	80	75

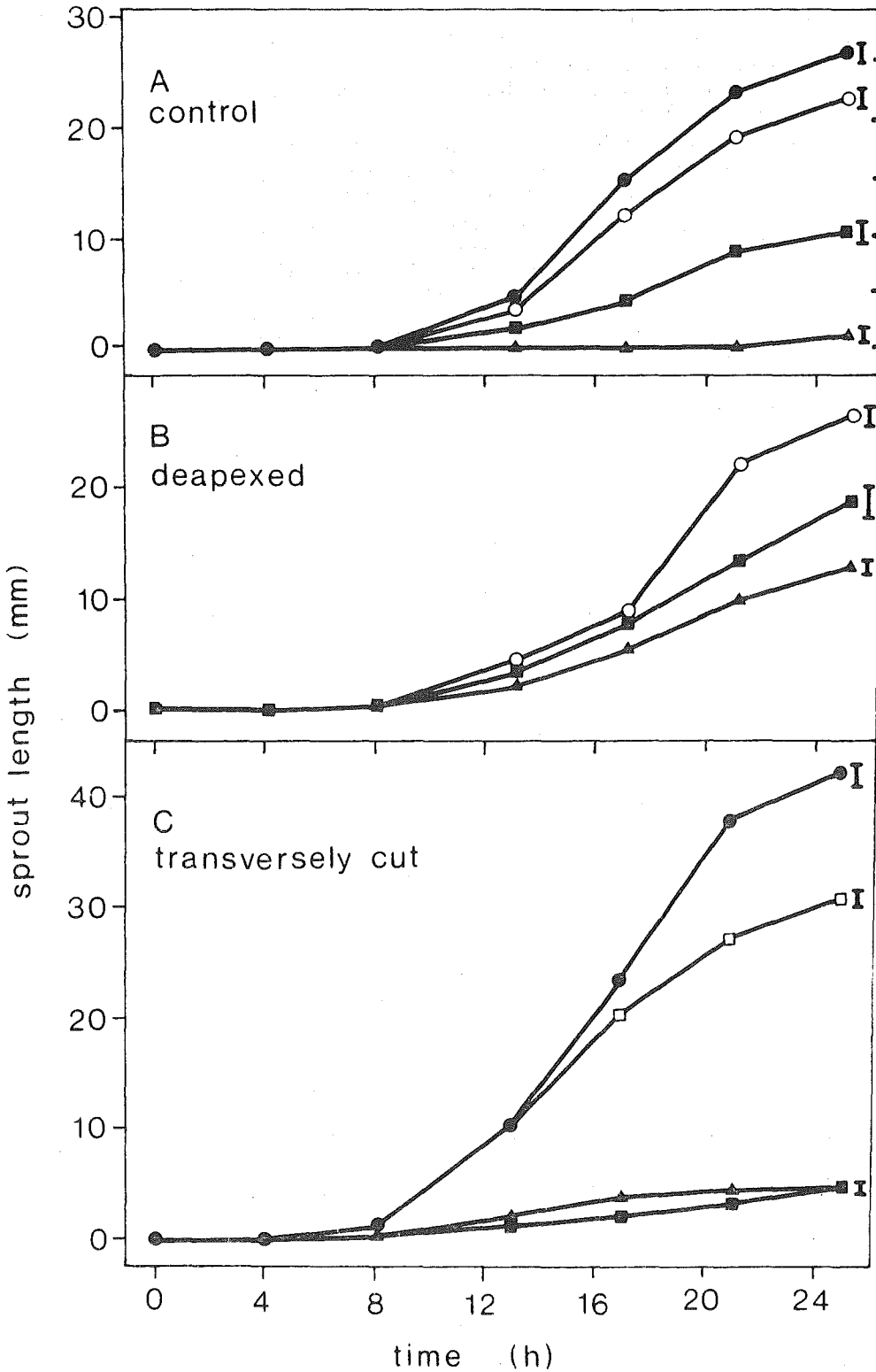


TABLE 2. EFFECT OF PLANT GROWTH REGULATORS ON SPROUT ELONGATION. Sprout length (mm) \pm standard error of excised potato buds 15 days after the start of daily treatments with IAA, GA₃, ABA, kinetin and solvent controls.

	Bud position		
	Apical	Lateral	Basal
Water	6.0 \pm 1.2	3.5 \pm 1.2	2.4 \pm 0.7
Methanol control	7.8 \pm 1.8	3.3 \pm 1.1	2.9 \pm 0.9
DMF control	5.2 \pm 1.2	2.5 \pm 0.8	1.2 \pm 0.3
ABA	2.6	1.1	0.0
GA ₃	32.9 \pm 1.4	16.0 \pm 2.9	4.5 \pm 2.3
K	10.2 \pm 1.1	8.3 \pm 0.3	5.0 \pm 1.2
IAA	1.94	1.4	1.2

DISCUSSION

The growth of both the lateral and basal buds on an intact potato tuber is less than that of the apical bud, and this appears to be the result of an inhibitory effect emanating from the apical bud. If the apical bud is removed, the other buds on the tuber show an increased growth, although those near the apex show more growth than the buds near the base or "heel" of the potato and frequently appear to exhibit dominance over them. These findings agree with the observations of Appleman (1918), Michener (1942) and Goodwin (1967a, 1967b), who reported that when dormancy has disappeared, bud growth commences in a basipetal sequence. Goodwin's initial observations, however, could infer either a basipetal sequence of dormancy disappearance or a lack of development at harvest in the more basal buds. He ruled out the latter possibility, as he could find no morphological difference between the apical and lateral buds, although the basal buds did appear less well-developed (Goodwin 1967a).

Fig. 1. Elongation of potato tuber buds in (a) whole tubers; (b) tubers with the apical bud removed and (c) tubers cut transversely in half; apical buds (solid circles); sub-apical buds (open circles), lateral buds (solid squares), basal bud (solid triangles). In Fig. 1c, lateral buds above the transverse cut are shown as solid squares whereas lateral buds below the cut are shown as open squares.

Vertical bars represent twice the standard error.

In this investigation we found that the lateral buds were capable of commencing growth as rapidly as the apical buds when isolated from the effects of apical buds by cutting the tuber transversely. This was confirmed using isolated buds. It was also noted in both whole tuber experiments and those using isolated buds that the subsequent rate of bud growth was consistently less for the lateral than for the apical buds. There is, nevertheless, clear evidence that the lateral buds are no more dormant than the buds near the apex, and are capable of commencing growth readily. The basal buds, however, require a longer period between their release from the effects of inhibition and the commencement of growth. This may be due to a lack of development at harvest as suggested by Goodwin (1967a), or to a more marked dormancy of these buds.

Michener (1942) also noted that apical and lateral buds were capable of commencing growth at the same time, and ascribed the apical dominance phenomenon to the production by and subsequent polar translocation of IAA from the apical bud to the more basipetal buds. Goodwin and Cansfield (1967), however, concluded that the inhibition was not brought about as a direct result of IAA inhibition, nor that it was a feature of the nutrient status of the bud. They supposed that there was an inhibitor produced under the influence of auxin and that the inhibitor was the active agent.

In our experiments, it was observed that both IAA and ABA were inhibitors of bud sprouting and of subsequent elongation, while kinetin and GA₃ exhibited promotory effects. El-Antably *et al.* (1967), who used a technique similar to ours, found no significant inhibition of sprouting in isolated buds by ABA. They ascribed this to difficulties with the technique, as the buds of intact tubers, when treated with ABA, showed no sprouting even after incubation for 14 days. Vanes and Hartmens (1969) used only apical buds, and found no effect on sprouting of either ABA or GA₃, although the effects on the subsequent elongation of sprouts were comparable with those reported here. However, their technique was different, and it is likely that there was a significant delay between application of the substances to the lower surface of the 8 mm deep cylinder of tuber and their arrival in physiological concentrations at the bud. This delay may have been sufficient to permit initial sprouting.

Rappaport *et al.* (1965) used a technique similar to ours, and found that GA₃ promoted sprouting while IAA at a similar concentration was inhibitory. They also bioassayed some supposed constituents of the inhibitor β complex (cinnamic, chlorogenic and caffeic acids and coumarin), but found that they did not inhibit sprouting. However, Blumenthal-Goldschmidt and Rappaport (1965) showed that inhibitor $-\beta$ when extracted from potato peel and reapplied to excised buds, inhibited sprouting. ABA is now believed to be a major constituent of inhibitor $-\beta$ (Milborrow 1968).

Goodwin and Cansfield (1967), on the other hand, believe that the component of the β -inhibitor fraction which is active in inhibiting sprout growth is an unstable "neutral" compound as opposed to an acid compound such as ABA.

Our work does not rule out this possibility, but it does demonstrate the remarkable similarities between apical dominance in the potato tuber and that which exists in the aerial shoot system of higher plants. It also demonstrates the ability of both IAA and ABA to function as inhibitors and indeed as the correlative inhibitor in this system.

LITERATURE CITED

- APPLEMAN, C.O. 1918. Physiological basis for the preparation of potatoes for seed. *Maryland Agricultural Experimental Station Bulletin* 212.
- BLUMENTHAL-GOLDSCHMIDT, S. and RAPPAPORT, L. 1965. Regulation of bud rest in tubers of potato *Solanum tuberosum* L. II. Inhibition of sprouting by inhibitor β complex and reversal of gibberellin A_3 . *Plant and Cell Physiology* 6: 601-608.
- EL-ANTABLY, H.M.M., WAREING, P.F. and HILLMAN, J. 1967. Some physiological responses to d, l abscisin (dormin). *Planta* 73: 74-90.
- GOODWIN, P.B. 1967a. The control of branch growth on potato tubers. I Anatomy of buds in relation to dormancy and correlative inhibition. *Journal of Experimental Botany* 18: 78-86.
- GOODWIN, P.B. 1967b. The control of branch growth on potato tubers. II The pattern of sprout growth. *Journal of Experimental Botany* 18: 297-307.
- MICHENER, H.D. 1942. Dormancy and apical dominance in potato tubers. *American Journal of Botany* 29: 558-568.
- MILBORROW, B.V. 1967. The identification of (+)-abscisin II (+)-dormin in plants and measurement of its concentrations. *Planta* 76: 93-113.
- RAPPAPORT, L., BLUMENTHAL-GOLDSCHMIDT, S., GLEGG, M.D. and SMITH, O.E. 1965. Regulation of bud rest in tubers of potato *Solanum tuberosum* L. I. Effect of growth substances on excised potato buds. *Plant and Cell Physiology* 6: 587-599.
- VANES, A. and HARTMANS, K.J. 1969. The influence of abscisin II and gibberellic acid on the sprouting of excised potato buds. *European Potato Journal* 12: 59-63.