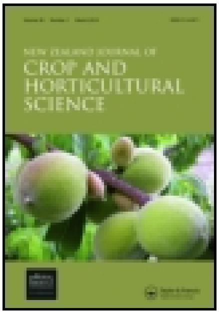

New Zealand Journal of Crop and Horticultural Science
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnzc20

Growth responses of potato (Solanum tuberosum) grown in a hot tropical lowland to applied paclobutrazol: 2. Tuber attributes

T. Tekalign [a] & P. S. Hammes [b]

[a] Department of Plant Production and Soil Science, University of Pretoria, Pretoria, 0002, South Africa E-mail:

[b] Department of Plant Production and Soil Science, University of Pretoria, Pretoria, 0002, South Africa

Published online: 22 Mar 2010.

New Zealand Journal of Crop and Horticultural Science, 2005, Vol. 33: 43–51
0014–0671/05/3301–0043

Growth responses of potato (*Solanum tuberosum*) grown in a hot tropical lowland to applied paclobutrazol: 2. Tuber attributes

T. TEKALIGN
P. S. HAMMES
Department of Plant Production and Soil Science
University of Pretoria
Pretoria 0002, South Africa
email: tekaligntsegaw@yahoo.com

Abstract The growth responses of potato (*Solanum tuberosum*) to leaf and soil applied paclobutrazol (PBZ) under the hot tropical climate of eastern Ethiopia was investigated in two field experiments. A month after planting, PBZ was applied as a foliar spray or soil drench at rates of 0, 2, 3, and 4 kg active ingredient (a.i.) PBZ/ha. A randomised complete block design with three replications was used. Averaged over the methods of application, PBZ increased tuber fresh mass, dry matter content, and specific gravity while promoting earlier tuber initiation and reduced tuber number. Root application of PBZ significantly increased crude protein content whereas both foliar and root PBZ applications extended the dormancy period. PBZ reduced the potassium and magnesium contents of the tubers. Tuber sulfur and copper contents were unaffected by either of the treatments. Foliar-applied PBZ increased the calcium content of tubers. Applying PBZ as a soil drench increased total tuber nitrogen. Both foliar and root applications increased tuber iron content while reducing phosphorus levels. PBZ increased tuber yield, improved quality attributes such as dry matter content, crude protein, and calcium (Ca) content and extended the dormancy period of potato tubers grown in the hot tropical lowlands of eastern Ethiopia.

Keywords dormancy; dry matter; nutrient composition; paclobutrazol; tuber quality; tuber yield

H04042; Online publication date 8 March 2005
Received 29 April 2004; accepted 30 October 2004

INTRODUCTION

Potato (*Solanum tuberosum* L.) tuberisation is a complex developmental process that requires the interaction of environmental, biochemical, and genetic factors (Kolomiets et al. 2001). Low mean temperatures (15–19°C) under a short photoperiod (12 h) are optimal for tuber initiation and early tuber growth (Vandam et al. 1996). High temperatures delay the onset of tuber initiation and bulking, decrease absolute tuber growth rate, and favour assimilates partitioning to the above-ground parts (Nagarajan & Bansal 1990; Gawronska et al. 1992; Vandam et al. 1996; Jackson 1999).

Under cool temperatures and short photoperiods, a transmissible signal is activated that triggers cell division and elongation in the sub-apical region of the stolon to produce tuber initials (Xu et al. 1998; Amador et al. 2001). In this signal transduction pathway, perception of appropriate environmental cues occurs in the leaves and is mediated by phytochrome and gibberellins (Van den Berg et al. 1995; Jackson & Prat 1996).

Potatoes grown under high temperatures are characterised by high levels of endogenous gibberellin (GA) (Vreugdenhil & Sergeeva 1999) that have a delaying or inhibitory effect on tuberisation (Abdella et al. 1995; Vandam et al. 1996). In addition, GA accumulation in tuber tissue can specifically impede starch accumulation (Booth & Lovell 1972; Paiva et al. 1983; Vreugdenhil & Sergeeva 1999), inhibit the accumulation of patatin and other tuber specific proteins (Hannapel et al. 1985; Vreugdenhil & Sergeeva 1999) and, in combination with other inhibitors, regulate potato tuber dormancy (Hemberg 1970).

In addition to the involvement of several endogenous growth substances, Koda et al. (1988) reported the existence of a specific tuberisation factor that is produced or activated in the leaves and translocated to the stolon where it exerts its effect. Hammes & Nel (1975) proposed that a balance between endogenous GA and tuber forming stimuli controls tuber formation; for tuberisation to occur the GA must be below a threshold level. This balance can be altered by the application of GA biosynthesis inhibitors such as 2-chloroethyl trimethyl ammonium chloride (CCC) (Menzel 1980) and B-995 (Bodlaender & Algra 1966). Recently, the *in vivo* and *in vitro* responses of potato to paclobutrazol (PBZ) have been reported (Balamani & Poovaiah 1985; Langille & Helper 1992; Simko 1994; Bandara & Tanino 1995).

Paclobutrazol ((2R, 3R+2S, 3S)-1-(4-chlorophenyl) 4,4-dimethyl-2-(1,2,4-triazol-1-yl)-pentan-3-ol) is a potent triazole plant growth regulator known to interfere with *ent*-kaurene oxidase activity in the *ent*-kaurene oxidation path to block GA synthesis (Rademacher 1997). It is hypothesised that PBZ blocks biosynthesis of GA in potatoes grown under elevate temperatures and increases productivity. This paper reports the effects of PBZ application methods and rates on tuber yield, quality, nutrient composition, and dormancy of potato grown in the hot tropical lowlands of eastern Ethiopia.

MATERIALS AND METHODS

Site description

Two similar field experiments were conducted under irrigation from January to July 2003 at Tony Farm, the research farm of Alemaya University, Ethiopia. The site is located at 41°50.4′E longitude, 09°36′N latitude, at an altitude of 1176 m. a.s.l. in the semi-arid tropical belt of eastern Ethiopia. During the growing period, the total precipitation was 230 mm and the mean monthly minimum and maximum temperatures were 18°C (ranging from 15.4°C to 21.3°C) and 31°C (ranging from 28.0°C to 34.4°C), respectively. The mean relative humidity was 50%, varying from 20% to 81%. The soil was a well-drained deep clay loam with 2.36% organic matter, 1.36% organic carbon (C), 0.12% total nitrogen (N), 14.15 ppm phosphorus (P), 1.08 meq 100 gm^{-1} exchangeable potassium (K), 0.533 mm hos cm^{-1} electric conductivity, and a pH of 8.6.

Plant culture

Treatments were laid down as two-factor (rate and method application) factorial experiments arranged in randomised complete block designs with three replications. In each plot (5.25 m × 2.1 m), 49 medium sized, well-sprouted tubers of 'Zemen' were planted at a spacing of 75 × 30 cm. Phosphorus was applied as diammonium phosphate at planting time at a rate of 150 kg ha^{-1} and N was side dressed after full plant emergence at a rate of 100 kg ha^{-1} in the form of urea. The plots were furrow irrigated regularly to maintain adequate moisture in the soil. Standard cultural practices for regional potato production were applied and no pests or diseases of significant importance were observed (Teriessa 1997).

Treatments

Thirty days after planting (early stolon initiation) the plants were treated with PBZ at rates of 0, 2, 3, and 4 kg active ingredient (a.i.) PBZ ha^{-1} as a foliar application or soil drench using the Cultar formulation (250 g a.i. PBZ per litre, Zeneca Agrochemicals SA (Pty Ltd, South Africa)). To prepare aqueous solutions, a given PBZ concentration was diluted in distilled water (250 ml $plot^{-1}$). For the foliar treatment, the solution was applied to each plant as fine foliar spray using an atomiser until run-off was reached. While applying the foliar treatment, the soil was covered with a plastic sheet to avoid PBZ seepage to the ground. The drench solution was applied to the soil in a ring around the base of each plant. The control plants were treated with distilled water at equivalent volumes.

Tuber parameters

Tuber initiation was recorded as occurring when the swollen portion of stolon tip attained a size of at least twice the diameter of the stolon (Ewing & Struik 1992). Potatoes were dug by hand. Tuber fresh mass and tuber numbers represent the average of 15 plants per plot.

Quality assessments

At harvest, samples of c. 5 kg tubers of all sizes from each plot were washed and dried. Tuber specific gravity was determined using the weight-in-air/weight-in-water method (Murphy & Goven 1959). For dry matter (DM) content determination the c. 3 kg tubers were chopped, pre-dried at a temperature of 60°C for 15 h and further dried for 3 h at 105°C in a drying oven. Tuber DM content is the ratio between dry and fresh mass expressed as a percentage. Separate samples (1 kg) were dried at 60°C to constant mass, ground and analysed for macro- and micronutrient contents. Total N was determined using the Macro-Kjeldahl method (AOAC 1984) and multiplied by a conversion of 6.25 to estimate tuber crude protein content (Van Gelder 1981). Following wet-ash digestion, P was determined by colorimetry, K by flame photometery, sulfur (S) by turbidimetry, and Ca, Mg, Fe, Cu, Mn, and Zn by atomic absorption.

Dormancy study

For dormancy evaluation, 10 uniform (70–105 g) and healthy tubers were selected from each plot and labelled. The samples were stored in a naturally ventilated diffused light store in a randomised complete block design with three replications. The average daily minimum and maximum temperatures during the storage period were 13.6°C and 22.8°C, respectively and relative humidity ranged from 34% to 70%. Tuber samples were monitored every 2 days to determine the dormancy period. The dormancy of a particular tuber was deemed to have ended when at least one 2-mm long sprout was present (Bandara & Tanino 1995). The average dormancy period of the 10 tubers is used to determine the dormancy period of a sample. The experiment was repeated once and all the procedures, techniques, and treatments used in experiment 1 were applied to experiment 2.

Statistical analysis

Analyses of variance were carried out using MSTAT-C statistical software (MSTAT-C 1991) and the means were compared according to the least significant differences (LSD) test at 1% probability level. Correlations between parameters were computed when applicable.

RESULTS

Combined analysis of variance of the two experiments revealed that there was no significant treatment by experiment interactions. Hence, pooled data are presented for discussion.

Regardless of the method of application, PBZ treatment significantly increased tuber fresh mass, DM content, specific gravity, and promoted early tuber initiation and reduced tuber number (Table 1). Irrespective of the concentration, PBZ-treated plants developed tuber initials c. 17 days earlier than the control (Fig. 1). Fresh tuber yield per hill was increased from 195 g for untreated plants to 314 g by applying 3 kg a.i. PBZ. PBZ treatment reduced tuber number by c. 21% compared with the control. Average tuber fresh mass significantly correlated with tuber number ($r = -0.98$, $P < 0.05$). Tuber DM content varied from 16.6% (control) to 18.0% (3 kg a.i. PBZ), and specific gravity from 1.061 (control) to 1.068 (3 kg a.i. PBZ). The means of PBZ concentration pooled over application method showed that application of 3 or 4 kg a.i PBZ increased DM content by c. 7.2% and specific gravity was increased from 1.061 to mean value of 1.067 by PBZ treatment.

Application method and PBZ concentration interacted significantly for tuber crude protein content and dormancy period (Table 2). Foliar spray of PBZ did not significantly affect crude protein content, whereas applying 4 kg a.i. PBZ as a soil drench increased content by c. 12% compared with the control. Regardless of the concentration, foliar PBZ extended the tuber dormancy period by 17 days, whereas applying 3 or 4 kg a.i. PBZ as a soil drench prolonged dormancy by c. 20 days.

The tuber mineral composition was significantly affected by both method of application and rate of PBZ (Table 3). Irrespective of the concentration, PBZ treatment reduced K and Mg contents of the tubers whereas Ca, S, Cu, and Zn concentrations were unaffected by either of the treatments. Compared to soil drench, foliar spray reduced K content but increased Ca content of the tubers.

A significant interaction between application method and concentration of PBZ was observed with N, P, Fe, and Mn content of the tubers (Table 4).

Table 1 Days to tuber initiation, fresh mass, number, dry matter (DM), and specific gravity of potato (*Solanum tuberosum*) tubers grown in a hot tropical climate as affected by concentration of applied paclobutrazol (PBZ). (a.i., active ingredient; SEM, standard error of the mean). Means within columns and rows sharing the same letters are not significantly different ($P < 0.01$).

Rate (kg a.i. PBZ ha^{-1})	Days to tuber initiation	Tuber fresh mass (g $hill^{-1}$)	Tuber no. (count $hill^{-1}$)	DM content (%)	Specific gravity (g cm^{-3})
0 (control)	54.0a	195c	7.6a	16.6c	1.061b
2	37.7b	300b	6.0b	17.5b	1.065a
3	37.3b	314a	6.1b	18.0a	1.068a
4	36.6b	305ab	6.0b	17.6ab	1.066a
SEM	0.48	3.26	0.09	0.09	0.0004

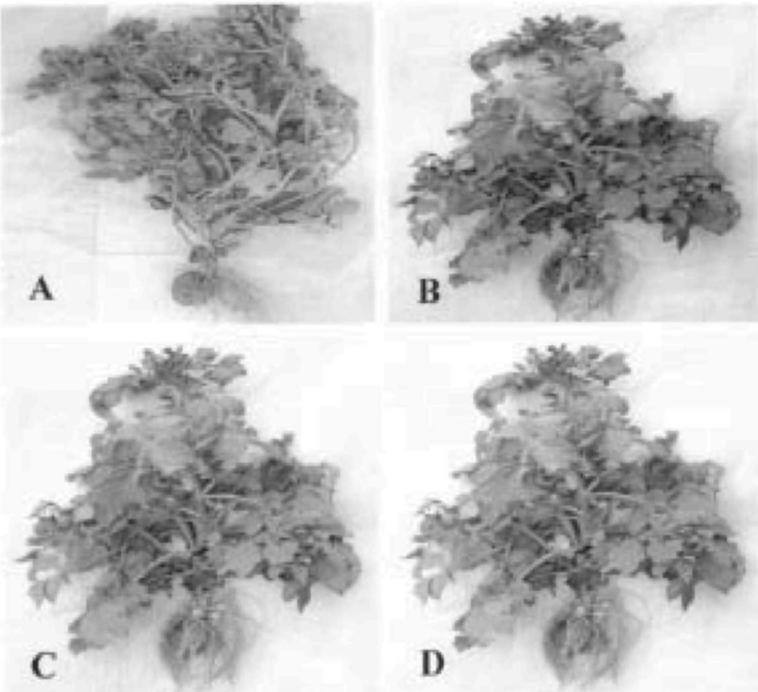

Fig. 1 Potato (*Solanum tuberosum*) plants 2 weeks after paclobutrazol treatment at rates of **A**, 0; **B**, 2; **C**, 3; and **D**, 4 kg a.i. ha^{-1}. Control plants had excessive top growth and no tuber formation, whereas the treated plants are characterised by reduced top growth and early tuberisation. (a.i., active ingredient.)

Table 2 Effects of application method and concentration of paclobutrazol (PBZ) on the crude protein and dormancy period of potato (*Solanum tuberosum*) tubers grown in a hot tropical condition. (a.i., active ingredient; DM, dry matter; SEM, standard error of the mean.) Means within columns sharing the same letters are not significantly different ($P < 0.01$).

Application method	Rate (kg a.i. PBZ ha^{-1})	Crude protein (% DM)	Dormancy period (days)
Foliar spray	0 (control)	11.67b	45.64c
	2	11.46b	61.99b
	3	11.88b	62.63b
	4	11.67b	63.32b
Soil drench	0 (control)	11.88b	45.33c
	2	11.67b	63.27b
	3	11.88b	65.89a
	4	13.34a	65.08a
	SEM	0.08	0.39

Foliar spray of any PBZ concentration did not increase N content, whereas application of 4 kg a.i. PBZ as a soil drench increased N concentration by 12%. Irrespective of the rate, foliar and soil drenching of PBZ reduced P concentration by c. 11 and 6% respectively compared with the control. Foliar spray of 3 or 4 kg a.i. PBZ increased tuber Fe content by c. 64%, whereas drench applications of 2 or 4 kg a.i. increased Fe content by c. 54% over the control. Treating plants with 3 kg a.i. as a foliar spray increased Mn concentration by c. 52%, whereas soil drenching of 3 or 4 kg a.i. PBZ increased the Mn content by c. 68% compared with the control.

DISCUSSION

For optimal yield and quality, potatoes prefer cool temperate climates with low mean temperatures (15–19°C) and a short photoperiod (12 h) (Vandam et al.

1996). Nevertheless, potato has been produced in many tropical climates under high temperature stress, resulting in significant yield reduction and quality deterioration. This is attributed to the synthesis of high amounts of endogenous GA, that in turn delay or inhibit tuber initiation, reduce partitioning of assimilates to the tubers, and impede the synthesis of starch and tuber specific proteins. This study investigated the effects of applied PBZ on the tuber yield and quality of potatoes grown in hot tropical lowlands of eastern Ethiopia.

Paclobutrazol treatments increased potato tuber yield and resulted in c. 57% yield advantage over the control which may be linked to early tuberisation, increased leaf chlorophyll content, enhanced rate of photosynthesis, and delaying the onset of senescence in response to PBZ treatment (Tekalign & Hammes 2004). The observed reduction in tuber number could be attributed to a decline in stolon number in response to a decrease in GA biosynthesis. The involvement of gibberellins in regulating stolon number through stolon initiation was reported by Kumar & Wareing (1972). Frommer & Sonnewald (1995) reported that the competition among tuber initials reduces the final tuber number. This interpretation is based on the observation that upon induction to tuberisation, multiple tuber primordials are initiated and during the early growth stage some tubers get a competitive advantage and thus outcompete other primordials and stop their further development. The strong association between tuber fresh mass and number signify that PBZ increased tuber yield by increasing individual tuber size at the expense of tuber count. In agreement with this finding, Balamani & Poovaiah (1985) and Simko (1994) reported an increased tuber dry weight per plant in response to PBZ treatment, although it was not clear if the increase was a consequence of

Table 3 Potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), copper (Cu), and zinc (Zn) concentrations (dry matter basis) within potato (*Solanum tuberosum*) tubers grown in a hot tropical climate as affected by application method and concentration of paclobutrazol (PBZ). (a.i., active ingredient; SEM, standard error of the mean.) Means within columns sharing the same letters are not significantly different ($P < 0.01$).

Main effects	Treatment	K (%)	Ca (%)	Mg (%)	S (%)	Cu (ppm)	Zn (ppm)
Method	Foliar spray	3.05b	0.14a	0.16a	0.52a	17.33a	34.16a
	Soil drench	3.15a	0.13b	0.16a	0.53a	14.83a	34.75a
	SEM	0.02	0.004	0.002	0.02	1.42	2.74
Rate (kg a.i. PBZ ha^{-1})	0 (control)	3.44a	0.13a	0.18a	0.55a	17.50a	31.33a
	2	2.98b	0.13a	0.15b	0.58a	15.50a	34.50a
	3	2.99b	0.13a	0.15b	0.50a	14.50a	40.33a
	4	2.99b	0.14a	0.15b	0.48a	16.83a	31.67a
	SEM	0.03	0.005	0.004	0.03	2.01	3.88

Table 4 Effects of application method and concentration of paclobutrazol (PBZ) on total nitrogen (N), phosphorus (P), iron (Fe), and manganese (Mn) content of potato (*Solanum tuberosum*) tubers grown in a hot tropical climate. Values are calculated on dry matter basis. (a.i., active ingredient; SEM, standard error of the mean.) Means within columns sharing the same letters are not significantly different ($P < 0.01$).

Application method	Rate (kg a.i. PBZ ha^{-1})	N (%)	P (%)	Fe (ppm)	Mn (ppm)
Foliar spray	0 (control)	1.87b	0.47a	60.33c	7.00d
	2	1.83b	0.41d	57.33c	6.67d
	3	1.90b	0.43bcd	102.00a	10.67ab
	4	1.83b	0.42cd	95.67ab	8.67bcd
Soil drench	0 (control)	1.90b	0.47a	70.67bc	7.33cd
	2	1.87b	0.44bc	101.33a	10.33bc
	3	1.90b	0.43bcd	91.67ab	11.00ab
	4	2.13a	0.45ab	115.67a	13.67a
	SEM	0.03	0.004	6.62	0.73

individual tuber size or number. However, Bandara & Tanino (1995) reported that PBZ nearly doubled the number of tubers per plant without affecting the total fresh weight of the tubers. This discrepancy may be explained by the difference in concentration, method of application, timing of PBZ application, and growing conditions (temperature and day length) of the plants in the course of experimentation. High temperature increases GA biosynthesis that reduces tuber sink strength to attract photoassimilate and may cause yield reduction (Booth & Lovell 1972). Krauss (1978) reported that gibberellin:abscisic acid (ABA) ratio controls tuberisation and subsequent tuber growth; relatively higher GA levels reduce or stop tuber growth, whereas higher ABA levels promote tuber growth.

Paclobutrazol increased the DM content of the tubers as clearly depicted by the higher DM% and specific gravity of treated tubers. This may be attributed to reduced tuber GA levels with a subsequent increase in sink strength enhancing starch synthesis and deposition. Booth & Lovell (1972) reported reduced sink strength of tubers resulting from high GA_3 accumulation in tuber tissue. Under conditions favourable for tuberisation, the activity of enzymes involved in starch biosynthesis such as ADPG-pyrophosphorylase, starch phosphorylase, and starch synthase increase (Visser et al. 1994; Appeldoorn et al. 1997). Mares et al. (1981) observed that exogenous application of GA_3 to growing tubers substantially reduced the activity of ADPG-pyrophosphorylase, whereas the activity of starch phosphorylase remained more or less constant. Similarly, Booth & Lovell (1972) observed that application of GA_3 to potato shoots reduced the export of photosynthates to the tubers, decreased starch accumulation, increased sugar levels, and resulted in a cessation of tuber growth. In this study, it is proved that specific gravity is an excellent indicator of tuber DM content with a significant positive correlation ($r = 0.99$, $P < 0.01$) concurring with the report of Tsegaw & Zelleke (2002).

Paclobutrazol application increased tuber crude protein content, probably because of blocking GA biosynthesis that is known to inhibit tuber protein synthesis. The increased total N concentration in tubers from PBZ-treated plants may be because of an increased uptake of N from the soil and/or remobilisation of N from other plant parts to the tubers. The negative effects of GA_3 on the synthesis of the major tuber protein (patatin) and other tuber specific proteins were reported by Park (1990) and Verugdenhil & Sergeeva (1999). The involvement of GA in the regulation of potato tuber starch and protein synthesis, along with a strong association between starch and protein content is reported by Paiva et al. (1983). Albeit not statistically significant, in this study a positive correlation between tuber DM content and crude protein ($r = 0.30$) was observed, indicating that increases in DM content might have contributed to some protein gain.

Paclobutrazol treatment extended seed tuber dormancy, probably by blocking GA biosynthesis and reducing ABA catabolism (Rademacher 1997) which could resulted in a low GA:ABA ratio in developing tubers. Dogonadze et al. (2000) observed that exogenous GA_3 treatment promoted tuber sprouting by enhancing RNA and DNA synthesis and Hemberg (1970) reported an inhibitory effect of ABA to tuber sprouting through inhibited RNA and DNA synthesis. The regulatory effects of GA and ABA on RNA and DNA synthesis are probably the major contributors to delayed sprouting (Shik & Rappaport 1970). It is suggested that the ratio of GA and ABA in the tuber is the most probable control mechanism of potato dormancy. Similar investigations revealed that PBZ is effective in extending the tuber dormancy period (Harvey et al. 1991; Simko 1994; Bandara & Tanino 1995).

In the current study, it was observed that untreated plants had thinner and longer roots compared to the treated plants, and PBZ increased root diameter by increasing the number of vascular elements as well as cortical cell row. This anatomical modification potentially might have altered mineral uptake and hence, tuber nutrition. PBZ treatment increased the concentration of tuber N, Fe, and Mn, but reduced K, P, Mg, and Cu. A close inspection of the data showed that there is a tendency for a slight increase in Ca, S, and Zn content. The decrease in mineral contents of the tuber in response to PBZ treatment may be a result of the reduced transpiration rate lowering mineral absorption from the soil and subsequently transport within the plant (Salisbury & Ross 1992). They reported that growing plants in greenhouses where there is reduced transpiration (from high humidity) may cause Ca deficiency in some tissues, whereas rapid transpiration may lead to a toxic build-up of some elements. In this study, PBZ increased potato tuber yield through individual tuber size and the observed reduction in some nutrient concentrations may be a "dilution effect". Reports on the effects of PBZ on mineral element content are not consistent and mainly studied on fruit crops. For instance, Yelenosky et al. (1995) observed that leaves from PBZ-treated citrus seedlings had higher concentration of N, Ca, B, Fe, and Mn. Wang et al. (1985) reported that PBZ treatment increased apple leaf N, P, K, Ca, Mg, Mn, Ca, Zn, and Sr concentration whereas the contents of Fe, Si, and Pb were unaffected. In contrast, Wieland & Wample (1985) reported that PBZ did not influence foliar content of N, P, K, and Mg, in apple and mineral composition of an apple fruit was unaffected by PBZ treatment (Steffens et al. 1985). Very recently, Yeshitela et al. (2004) reported that PBZ increased leaves Mg, Cu, Zn, and Fe content of mango without affecting the concentration of N, P, K, and Ca.

In conclusion, the results indicate that PBZ is an effective plant growth regulator that can be used to increase tuber yield and improve the tuber quality attributes of potatoes grown in lowland tropics, where there are elevated temperatures. However, it is crucial to point out that a detailed investigation must be done to detect the residual effects of PBZ in the tubers before they are used for commercial potato production. Prolonging tuber dormancy period with PBZ may be useful for the potato seed industry, particularly to reduce unnecessary sprouting of potato cultivars having a short dormancy period. However, the effect of residual PBZ on the performance of the next generation must be investigated. For all the parameters considered, little significant difference was observed between foliar spray and soil drench applications. Hence, foliar spray is suggested as a method of application.

ACKNOWLEDGMENTS

The study was sponsored by Alemaya University, Ethiopia, through a fund procured from World Bank. The authors are grateful to B. Nigatu, W. Tadesse, H. Berhan, H. Abeba, and others who directly or indirectly helped in the execution of the field and laboratory work.

REFERENCES

Abdella, G.; Guinazu, M.; Tizio, R.; Pearce, D. W.; Pharis, R. P. 1995: Effect of 2-chloroethyl trimethyl ammonium chlorides on tuberisation and endogenous GA_3 in roots of potato cuttings. *Plant Growth Regulation 17*: 95–100.

Amador, V.; Bou, J.; Martinez-Garcia, J.; Monte, E.; Rodriguez-Falcon, M.; Russo, E.; Prat, S. 2001: Regulation of potato tuberisation by day length and gibberellins. *International Journal of Developmental Biology 45(S1)*: S37–S35.

Appeldoorn, N. J. G.; de Bruijn, S. M.; Koot-Gronsveld, E. A. M.; Visser, R. G. F.; Vreugdenhil, D.; Van der Plas, L. H. W. 1997: Developmental changes of enzymes involved in sucrose to hexose-phosphate conversion during early tuberisation of potato. *Planta 202*: 220–226.

Association of Official Analytical Chemistry (AOAC) 1984: Official methods of analysis of the Association of Official Analytical Chemists. 14th ed. Washington D. C. Pp. 1141.

Balamani, V.; Poovaiah, B. W. 1985: Retardation of shoot growth and promotion of tuber growth of potato plants by paclobutrazol. *American Potato Journal 62*: 363–369.

Bandara, P. M. S.; Tanino, K. K. 1995: Paclobutrazol enhances mini tuber production in Norland potatoes. *Journal of Plant Growth Regulation 14*: 151–155.

Bodlaender, K. B. A.; Algra, S. 1966: Influence of growth retardant B995 on growth and yield of potatoes. *European Potato Journal 9*: 242–258.

Booth, A.; Lovell, P. H. 1972: The effect of pre-treatment with gibberellic acid on the distribution of photosynthate in intact and disbudded plants of *Solanum tuberosum*. *New Phytologist 71*: 795–804.

Dogonadze, M. Z.; Korableva, N. P.; Platonova, T. A.; Shaposhnikov, G. L. 2000: Effects of gibberellin and auxin on the synthesis of abscisic acid and ethylene in buds of dormant and sprouting potato tuber. *Prikladnaia Biokhimiia i Mikrobiologiia 36(5)*: 588–591.

Ewing, E. E.; Struik, P. C. 1992: Tuber formation in potato: induction, initiation, and growth. *Horticultural Review 14*: 89–198.

Frommer, W. B.; Sonnewald, U. 1995: Molecular analysis of carbon partitioning in solanaceous species. *Journal of Experimental Botany* 46 (287): 587–607.

Gawronska, H.; Thornton, M. K.; Dwelle, R. B. 1992: Influence of heat stress on dry matter production and photoassimilate partitioning by four potato clones. *American Potato Journal 69*: 653–665.

Hammes, P. S.; Nel, P. C. 1975: Control mechanisms in the tuberisation process. *Potato Research 18*: 262–272.

Hannapel, D. J.; Miller, J. C.; Park, W. D. 1985: Regulation of potato tuber protein accumulation by gibberellic acid. *Plant Physiology 78*: 700–703.

Harvey, B. M. R.; Crothers, S. H.; Evans, N. E.; Selby, C. 1991: The use of growth retardants to improve micro tuber formation of potato (*Solanum tuberosum* L.). *Plant, Cell, Tissue and Organ Culture 27*: 59–64.

Hemberg, T. 1970: The action of some cytokinin on the rest period and control of acidic growth inhibiting substances in potato. *Physiologia Plantarum 23*: 850–858.

Jackson, S. D. 1999: Multiple signalling pathways control tuber induction in potato. *Plant Physiology 119*: 1–8.

Jackson, S. D.; Prat, S. 1996: Control of tuberisation in potato by gibberellins and phytochrome B. *Physiologia Plantarum 98*: 407–412.

Koda, Y.; Omer, E. A.; Yoshihara, T.; Shibata, H.; Sakamura, S.; Okazawa, Y. 1988: Isolation of a specific potato tuber-inducing substance from potato leaves. *Plant Cell Physiology 29*: 969–974.

Kolomiets, M. V.; Hannapel, D. J.; Chen, H.; Tymeson, M.; Gladon, R. J. 2001: Lipoxygenase is involved in the control of potato tuber development. *The Plant Cell 13*: 613–626.

Krauss, A. 1978: Tuberisation and abscisic acid content in *Solanum tuberosum* as affected by nitrogen nutrition. *Potato Research 21*: 183–193.

Kumar, D.; Wareing, P. F. 1972: Factor controlling stolon development in potato plant. *New Phytologist 71*: 639–648.

Langille, A. R.; Helper, P. R. 1992: Effects of three anti-gibberellin growth retardants on tuberisation of induced and non-induced Katahdint potato leaf bud cuttings. *American Potato Journal 60*: 131–141.

Mares, D. J.; Marschner, H.; Krauss, A. 1981: Effect of gibberellic acid on the growth and carbohydrate metabolism of developing tubers of potato (*Solanum tuberosum* L.). *Physiologia Plantarum 52*: 267–274.

Menzel, C. M. 1980: Tuberisation in potato (*Solanum tuberosum* cv. Sebago) at high temperature: responses to Gibberellins and growth inhibitors. *Annals of Botany 46*: 259–266.

MSTAT-C. 1991: A microcomputer program for design management and analysis of agronomic research experiments. Michigan State University, East Lansing, MI, United States.

Murphy, H. J.; Goven, M. J. 1959: Factors affecting the specific gravity of the white potato in Maine. *Maine Agricultural Experiment Station Bulletin 583*. Orono.

Nagarajan, S.; Bansal, K. C. 1990: Growth and distribution of dry matter in a heat tolerant and a susceptible potato cultivar under normal and high temperature. *Journal of Agronomy and Crop Science 165*: 306–311.

Paiva, E.; Lister, R. M.; Park, W. D. 1983: Induction and accumulation of major tuber proteins of potato in stems and petioles. *Plant Physiology 71*: 161–168.

Park, W. D. 1990: Molecular approaches to tuberisation in potato. *In*: Vayda, M. E.; Park, W. D. *ed*. The molecular and cellular biology of the potato. Malkashim, United Kingdom, Redwood Press Ltd. Pp. 261–278.

Rademacher, W. 1997: Bioregulation of crop plants with inhibitors of gibberellin biosynthesis. *Proceedings of the Plant Growth Regulation Society of America 24*: 27–31.

Salisbury, F. B.; Ross, C. W. 1992: Plant physiology. 4th ed. The photosynthesis-transpiration compromise. California, United States, Wadsworth Publishing Company. Pp. 66–92.

Shik, C. Y.; Rappaport, L. 1970: Regulation of bud rest in tubers of potato (*Solanum tuberosum* L.) VII. Effect of abscisic and gibberellic acid on nucleic acid synthesis in excised buds. *Plant Physiology 45*: 33–36.

Simko, I. 1994: Effects of paclobutrazol on *in vitro* formation of potato microtubers and their sprouting after storage. *Biologia Plantarum 36(1)*: 15–20.

Steffens, G. L.; Wang, S. Y.; Faust, M.; Byun, J. K. 1985: Growth, carbohydrate, and mineral element status of shoot and spur leaves and fruits of 'Spartan' apple trees treated with paclobutrazol. *Journal of American Society for Horticultural Science 110*: 4–8.

Tekalign, T.; Hammes, P. S. 2005: Growth responses of potato (*Solanum tuberosum*) grown in hot tropical lowland to applied paclobutrazol: 1. Shoot attributes, assimilate production and allocation. *New Zealand Journal of Crop and Horticultural Science 33*: 35–42.

Teriessa, J. 1997: A Simple guide for potato production in Eastern Ethiopia. Ethiopia, Alemaya University.

Tsegaw, T.; Zelleke, A. 2002: Removal of reproductive growth increased yield and quality of potato (*Solanum tuberosum* L.). *Tropical Agriculture 79(2)*: 125–128.

Vandam, J.; Kooman, P. L.; Struik, P. C. 1996: Effects of temperature and photoperiod on early growth and final number of tubers in potato (*Solanum tuberosum* L.). *Potato Research 39*: 51–62.

Van den Berg, J. H.; Simko, I.; Davies, P. J.; Ewing, E. E.; Halinska, A. 1995: Morphology and (^{14}C)gibberellin A_{12} metabolism in wild-type and dwarf *Solanum tuberosum* spp. andigena grown under long and short photoperiods. *Journal of Plant Physiology 146*: 467–473.

Van Gelder, W. M. J. 1981: Conversion factor from nitrogen to protein for potato tuber protein. *Potato Research 24*: 423–425.

Visser, R. G. F.; Vreugdenhil, D.; Hendrix, T.; Jacobsen, E. 1994: Gene expression and carbohydrate content during stolon to tuber transition in potatoes (*Solanum tuberosum* L.). *Physiologia Plantarum 90*: 285–292.

Vreugdenhil, D.; Sergeeva, L. I. 1999: Gibberellins and tuberisation in potato. *Potato Research 42*: 471–481.

Wang, S. Y.; Byun, J. K.; Steffens, G. L. 1985: Controlling plant growth via the gibberellin biosynthesis system. II. Biochemical and physiological alterations in apple seedlings. *Physiologia Plantarum 63*: 169–175.

Yeshitela, T.; Robbertse, P. J.; Stassen, P. J. C. 2004: Paclobutrazol suppressed vegetative growth and improved yield as well as fruit quality of 'Tommy Atkins' mango (*Mangifera indica*) in Ethiopia. *New Zealand Journal of Crop and Horticultural Science 32*: 281–293.

Wieland, W. F.; Wample, R. L. 1985: Root growth, water relation and mineral uptake of young 'Delicious' apple trees treated with soil and stem applied paclobutrazol. *Scientia Horticulturae 26*: 129–137.

Xu, X.; Vreugdenhil, D.; Van Lammeren, A. A. M. 1998: Cell division and cell enlargement during potato tuber formation. *Journal of Experimental Botany 49*: *573–582*.

Yelenosky, G.; Vu, J. C. V.; Wutscher, H. K. 1995: Influence of paclobutrazol in the soil on growth, nutrient elements in the leaves, and flood/freeze tolerance of citrus rootstock seedlings. *Journal of Plant Growth Regulation 14*: 129–134.