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Response of potato grown under non-inductive condition to paclobutrazol: shoot growth, chlorophyll content, net photosynthesis, assimilate partitioning, tuber yield, quality, and dormancy

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Abstract

The effect of foliar and soil applied paclobutrazol on potato were examined under non-inductive condition in a greenhouse. Single stemmed plants of the cultivar BP1 were grown at 35(±2)/20(±2) °C day/night temperatures, relative humidity of 58%, and a 16 h photoperiod. Twenty-eight days after transplanting paclobutrazol was applied as a foliar spray or soil drench at rates of 0, 45.0, 67.5, and 90.0 mg active ingredient paclobutrazol per plant. Regardless of the method of application paclobutrazol increased chlorophyll *a* and *b* contents of the leaf tissue, delayed physiological maturity, and increased tuber fresh mass, dry matter content, specific gravity, dormancy period of the tubers. Paclobutrazol reduced the number of tubers per plant. A significant interaction between rates and methods of paclobutrazol application were observed with respect to plant height and tuber crude protein content. Foliar application gave a higher rate of net photosynthesis than the soil drench. Paclobutrazol significantly reduced total leaf area and increased assimilate partitioning to the tubers. The study clearly showed that paclobutrazol is effective to suppress excessive vegetative growth, favor assimilation to the tubers, increase tuber yield, improve tuber quality and extend tuber dormancy of potato grown in high temperatures and long photoperiods.

Introduction

High temperature is an important factor limiting potato production in some areas of the world (Morpurgo and Ortiz 1988). The optimum temperatures for foliage growth and net photosynthesis are 20–25 °C and 16–25 °C, respectively. Low mean temperatures (15–19 °C) and short photoperiods (12 h) are favorable for tuberization and early tuber growth (Vandam et al. 1996). High temperatures inhibit tuberization in both short and long day conditions, especially under long photoperiods (Jackson 1999).

The carbon budget for potatoes developed by Leach et al. (1982) indicate that plant growth rate is strongly related to net photosynthesis and dark respiration. At elevated temperatures foliage growth is promoted, rate of photosynthesis declines rapidly, assimilate partitioning to the tubers is reduced and dark respiration increases (Thornton et al. 1996). Tuber growth is completely inhibited at 29 °C, above which point the carbohydrates consumed by respiration exceeds those produced by photosynthesis according to Levy (1992). Like high temperatures, long photoperiod also decreases partitioning of assimilates to the tubers and increases partitioning to other parts of the plant (Wolf et al. 1990).

The most noticeable morphological features of potato grown under high temperatures or long

photoperiods are taller plants with longer internodes, increased leaf and stem growth, the leaf: stem ratio decrease, leaves are shorter and narrow with smaller leaflets, and partitioning of assimilates to the tubers declines (Ben Khedher and Ewing 1985; Manrique 1989; Struik et al. 1989).

Induction to tuberization is promoted by short days, more specifically by long nights (Gregory 1965) and cool temperatures (Ewing 1981). Under such conditions 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, the perception of appropriate environmental cues occurs in the leaves and is mediated by phytochrome and gibberellins (Van den Berg et al. 1995; Jackson and Prat 1996).

Amador et al. (2001) reported that endogenous gibberellin is a component of the inhibitory signal in potato tuberization under long days. Previous studies on GA showed that the levels of GA-like activity decrease in leaves of potato upon transfer from long day to short day conditions (Railton and Wareing 1973). Under short day conditions gibberellin biosynthesis is reduced (Amador et al. 2001). Van den Berg et al. (1995) reported that a dwarf potato mutant tuberizes under long days due to the incorporation of gene that partially blocks the conversion of 13-hydroxylation of GA_{12}-aldahyde to GA_{53} and treatment with gibberellin biosynthesis inhibitors enhance tuberization in *andigena* spp. under long day conditions (Jackson and Prat 1996).

Potato plants grown under non-inductive conditions are characterized by high levels of endogenous gibberellins (Vreugdenhil and Sergeeva 1999) that promote shoot growth (Menzel 1980) and delay or inhibit tuberization (Abdella et al. 1995; Vandam et al. 1996). In addition, the accumulation of gibberellin in tuber tissue can specifically impede starch accumulation (Booth and Lovell 1972; Paiva et al. 1983; Vreugdenhil and Sergeeva 1999), inhibits the accumulation of patatin and other tuber specific proteins (Vreugdenhil and Sergeeva 1999), and in combination with other inhibitors it regulates potato tuber dormancy (Hemberg 1970).

Previous studies showed the hormonal balance controlling potato tuberization could be altered using gibberellin biosynthesis inhibitors such as 2-chloroethyl trimethyl ammonium chloride (CCC) (Menzel 1980), B 995 (Bodlaender and Algra 1966), and paclobutrazol (Simko 1994). Paclobutrazol (2RS, 3RS)-1-(4-chloro-phenyl)-4,4-dimethyl-2-(1H,2,4-triazol-1-yl)-pentan-3-ol (PBZ) is a triazole plant growth regulator known to interfere with *ent*-kaurene oxidase activity in the *ent*-kaurene oxidation pathway (Rademacher 1997). Interference with the different isoforms of this enzyme could lead to inhibition of GA biosynthesis and abscisic acid (ABA) catabolism. In addition, it induces shoot growth reduction (Terri and Millie 2000; Sebastian et al. 2002), enhance chlorophyll synthesis (Belakbir 1998; Sebastian et al. 2002), delay leaf senescence (Davis and Curry 1991) and increase assimilate partitioning to the underground parts (Balamani and Poovaiah 1985; Davis and Curry 1991; Bandara and Tanino 1995).

It is postulated that PBZ blocks gibberellin synthesis in potato plants grown under non-inductive growing conditions and modifies its growth to increase the productivity of the crop. Accordingly, in the present study we have investigated the effect of foliar and soil applied PBZ on shoot growth, leaf chlorophyll content, assimilate production and allocation, tuber yield, quality, and dormancy period of tubers of plants grown under conditions of high temperature and long photoperiod. Ultimately, to generate information to use it as a possible intervention to introduce potato culture to the marginal area where high temperatures and/or long photoperiods are limiting factors.

Materials and methods

Plant culture

Two similar experiments were conducted in 2002 on the experimental farm of the University of Pretoria, South Africa. Potato tubers of medium maturing commercially cultivated variety BP1 were allowed to sprout and seed cores of approximately 15 g containing the apical sprout were excised. Seed pieces were planted in crates with vermiculite and kept in a growth chamber at 35/20 °C day/night temperatures and 16 h photoperiod. After a week, uniform plants were trans-

planted to 5 l plastic pots filled with sand and coconut coir (50:50 by volume) and grown in a greenhouse at 35(±2)/20(±2) °C day/night temperatures, an average relative humidity of 58%, and a 16 h photoperiod. The photoperiod was extended using a combination of Sylvania fluorescent tubes and incandescent lamps (PAR: 10 μmol m^{-2} s^{-1}). In both experiments the pots were arranged in a randomized complete block design with three replications and each replicate contained seven pots per treatment. Plants were fertilized with standard Hoagland solution and watered regularly to avoid water stress.

Treatments

Twenty-eight days after planting (early stolon initiation) the plants were treated with PBZ at rates of 0, 45.0, 67.5 and 90.0 mg active ingredient (a.i.) per plant as a foliar spray or soil drench using Cultar (250 g a.i. paclobutrazol per liter, Zeneca Agrochemicals SA (PTY.) LTD., South Africa). For the foliar treatment the solution was applied as a fine spray using an atomizer. The drench solution was applied to the substrate around the base of the plants. The control plants were treated with distilled water.

Data recorded

Net photosynthesis and chlorophyll content
Two weeks after treatment application the rate of net photosynthesis was measured using portable photosynthesis system (CIRAS-1, 1998, UK) and leaf chlorophyll content was determined. From each treatment three plants were randomly selected and rate of net photosynthesis measured on the terminal leaflet of the three fully expanded younger leaves. The photon flux density incident at the level of the leaf in the cuvette was 1050–1220 μmol s^{-1} m^{-2} (PAR). Average saturated vapor pressure of water at cuvette temperature was 34.5 mbar and vapor pressure deficit of the air in the course of measurements was 6.05 mbar. To determine the concentrations of chlorophyll *a* and *b* spectrophotometer (Pharmacia LKB, Ultrospec III) readings of the density of 80% acetone chlorophyll extracts were taken at 663 and 645 nm and their respective values were assessed using the specific absorption coefficients given by MacKinney (1941).

Assimilate partitioning and total leaf area
Two, four, six, and eight weeks after treatment application one pot of each treatment combination was harvested and separated into leaves, stems, tubers, and roots and stolons. Leaf area was measured with a LI-3000 leaf area meter (LI-inc, Lincoln, Nebraska, USA) and the plant tissues oven dried at 72 °C to a constant mass. Dry matter partitioning was determined from the dry mass of individual plant parts as a percentage of total plant dry mass.

Plant height, senescence, tuber fresh mass and number
Plant height refers to the length from the base of the stem to shoot apex. Plants were regarded as physiologically mature when 50% of the leaves senescenced. Tuber fresh mass and number represent the average tuber mass and count of three plants per treatment, respectively.

Quality assessment
At harvest a representative tuber sample from each treatment group was taken and washed. Tuber specific gravity was determined by weighing in air and under water. For dry matter content determination the samples were chopped and dried at a temperature of 60 °C for 15 h and followed by 105 °C for 3 h. Dry matter content of the tubers is the ratio between dry and fresh mass expressed in percentage. Samples dried at 60 °C and analyzed for total nitrogen (Macro-Kjeldahl method, AOAC 1984) and tuber crude protein content assessed by multiplying total nitrogen by a conversion factor of 6.25 (Van Gelder 1981).

Dormancy study
For dormancy period study six healthy tubers per treatment were selected and labeled. Each treatment was replicated three times and samples were randomly distributed on shelves in a dark room. 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 and Tanino 1995). Procedures, techniques and treatments in experiment 2 were similar to experiment 1.

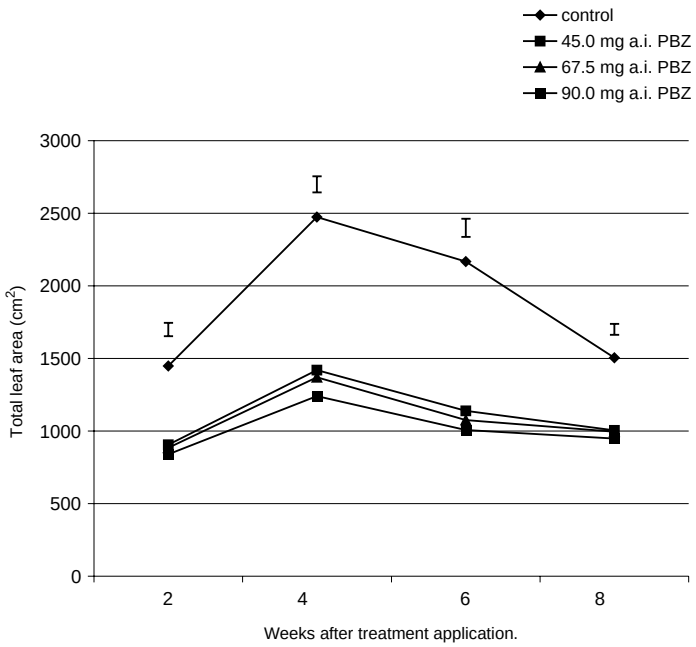

Figure 1. Potato total leaf area as influenced by different rates of paclobutrazol. The vertical bar represents least significant difference (LSD) at 1% probability level.

Data analysis

The analyses of variance were carried out using MSTAT-C statistical software (MSTAT-C 1991). Combined analysis of variance did not shown significant treatments by experiment interaction. Hence, for all of the parameters considered, the data of the two experiments were combined and presented for discussion. Means were compared using the least significant difference (LSD) test at 1% probability level. Correlations between parameters were computed when applicable.

Results

Shoot growth and senescence

PBZ treatment considerably reduced leaf area per plant. Irrespective of the rates of application 2, 4, 6 weeks after application the leaf area of PBZ treated plants were typically 50% smaller than the control (Figure 1). A significant interaction was observed between rates and methods of PBZ application with the soil drench resulted significantly shorter plants than the foliar spray (Table 1). Application of 67.5 or 90 mg a.i. PBZ per plant as a foliar spray and soil drench brought about 46 and 63% height reduction compared to the control, respectively.

Chlorophyll content

Regardless of the method of application PBZ significantly increased chlorophyll *a* and *b* contents of the leaf tissue (Table 2). The highest chlorophyll *a* (0.86 mg g^{-1} FW) and chlorophyll *b* (0.31 mg g^{-1} FW) values were obtained at the highest rate of PBZ application. An increase in chlorophyll *a* and chlorophyll *b* were observed with increasing rate of application. Irrespective of the methods of application PBZ significantly prolonged the time to physiological maturity (Table 2). The treated plants retained photosynthetically active leaves longer and delayed the date to 50% senescence by approximately 20 days compared to the control.

Net photosynthesis and assimilate partitioning

Leaf net photosynthesis was significantly affected by rate and method of PBZ application (Table 2). The highest net photosynthesis was observed in

Table 1. Potato plant height as affected by methods and rates of PBZ application.

Rate (mg a.i. PBZ plant^{-1})	Plant height (cm)	
	Foliar spray	Soil drench
0 (control)	58.16a	59.32a
45.0	37.96b	27.45de
67.5	33.35c	23.78ef
90.0	29.53cd	20.52f
SEM	1.15	

SEM, standard error of the mean.
Means within column and row sharing the same letters are not significantly different ($p < 0.01$).

plants treated with 67.5 mg a.i. PBZ per plant. Foliar treated plants showed higher net photosynthesis than soil drench treated plants. PBZ significantly affected total dry matter production and assimilate allocation to the different plant parts (Table 3). Compared to the control, at all harvesting stages PBZ treatment greatly reduced partitioning of assimilate to the leaves, stems, and roots and stolons, and increased partitioning to the tubers. Application of 67.5 or 90 mg a.i. of PBZ resulted in the highest tuber dry mass (%) at all harvesting dates. There was no consistency in the effects of methods of application on the pattern of assimilate production and allocation.

Regardless of the method of application PBZ treatment significantly increased tuber fresh mass, dry matter content, and specific gravity but reduced tuber numbers (Table 4). Tuber fresh mass per pot ranged from 71.9 (control) to 155.6 g (67.5 mg a.i. PBZ) showing that the treatment brought about 116% yield advantage over the control. Without considering the concentration PBZ treatment boosted dry matter content and specific gravity by an average value of 20 and 1.4%, respectively compared to the control. There was a tendency towards reduced tuber fresh mass, dry matter content and specific gravity at the higher rate of application. Increasing the rate of PBZ application resulted a concomitant reduction in tuber number. Average over the methods of application, treatment with 45.0, 67.5 and 90 mg a.i. PBZ decreased tuber number by 23, 33 and 43%, respectively, as compared to the control.

PBZ significantly extended tuber dormancy period regardless of the method of application (Table 4). As the mother plants were grown under constant high day and night temperatures the tubers had a relatively short dormancy period. Irrespective of the concentration PBZ treatment extended the dormancy period nearly by a month as compared to the control.

A significant interaction between rates and methods application was observed for tuber crude protein content (Table 5). Applying 45.0 or 67.5 mg a.i. PBZ as a foliar spray increased crude protein content by about 11% compared to the control. On the other hand, a dose of 67.5 or 90.0 mg a.i. PBZ applied as a soil drench resulted in an approximate increase of 22% over the control.

Discussion

Triazoles are potent plant growth regulators that inhibit shoot growth at low concentrations. PBZ

Table 2. Chlorophyll *a* and *b* contents of leaf tissue, leaf net photosynthesis and days to physiological maturity as influenced by methods and rates of PBZ application.

Main effects	Treatment	Chlorophyll *a* (mg g^{-1} FW)	Chlorophyll *b* (mg g^{-1} FW)	Leaf net photosynthesis (μmol m^{-2} s^{-1})	Days to physiological Maturity
Method	Foliar spray	0.69a	0.22a	10.50b	96.13a
	Soil drench	0.71a	0.20a	9.54a	96.00a
	SEM	0.02	0.02	0.29	0.41
Rate	0 (control)	0.50c	0.14b	6.79b	81.48c
	45.0 (mg)	0.67b	0.15b	10.74a	99.71b
	67.5 (mg)	0.78ab	0.23ab	11.65a	100.70ab
	90.0 (mg)	0.86a	0.31a	10.91a	102.39a
	SEM	0.03	0.03	0.41	0.58

SEM, standard error of the mean.
Means of the same main effect within the same column sharing the same letters are not significantly different ($p < 0.01$).

Table 3. Dry matter distributions (%) in different parts of potato as influenced by rate and method of PBZ application.

Main effect	Treatment	Leaf	Stem	Root & stolon	Tuber	Leaf	Stem	Root & stolon	Tuber
		Harvest I				Harvest II			
Method	Foliar spray	41.32a	23.59a	19.16a	15.93b	35.54a	23.93a	16.19b	24.34a
	Soil drench	41.83a	23.73a	18.06b	17.38a	36.00a	23.95a	17.48a	22.57b
	SEM	0.48	0.34	0.31	0.29	0.33	0.31	0.29	0.19
Rate	0 (control)	45.79a	33.18a	19.21a	1.82c	45.50a	27.53a	18.04a	8.93c
	45.0 (mg)	39.65b	21.15b	19.12a	20.08b	33.56b	23.14b	15.88b	27.42b
	67.5 (mg)	39.40b	20.08b	18.81ab	21.71a	32.02b	22.57b	16.54ab	28.86a
	90.0 (mg)	39.45b	20.22b	17.30b	23.02a	32.01b	22.52b	16.86ab	28.61a
	SEM	0.68	0.48	0.43	0.41	0.46	0.44	0.41	0.37
		Harvest III				Harvest IV			
Method	Foliar spray	35.52a	25.71b	14.71a	24.06a	34.60a	24.58b	12.98a	27.84a
	Soil drench	33.20b	27.76a	15.54b	23.51a	32.93a	26.95a	12.93a	27.20a
	SEM	0.29	0.36	0.14	0.22	0.30	0.33	0.19	0.22
Rate	0 (control)	40.30a	28.72a	18.53a	12.44c	41.07a	28.74a	15.50a	14.82c
	45.0 (mg)	31.90b	27.49a	14.59b	26.02b	31.00b	26.24b	12.20b	30.29b
	67.5 (mg)	31.78b	25.48b	14.16b	28.58a	30.80b	24.24c	12.75b	32.52a
	90.0 (mg)	33.45c	25.25b	13.22c	28.08a	32.18b	23.85c	11.47b	32.44a
	SEM	0.40	0.50	0.21	0.32	0.42	0.47	0.26	0.32

SEM, standard error of the mean.
Harvest I, II, III and IV were done 2, 4, 6, and 8 weeks after treatment application, respectively.
Means of the same main effect within the same column sharing the same letters are not significantly different ($p < 0.01$).

Table 4. Tuber fresh mass, number, dry matter, specific gravity, and dormancy period as influenced by rates of PBZ application.

Rate (mg a.i. PBZ plant^{-1})	Tuber fresh mass (g pot^{-1})	Tuber number (count pot^{-1})	Dry matter (%)	Specific gravity	Dormancy period (days)
0 (control)	71.9c	10.47a	16.00b	1.048b	13.84b
45.0	151.5b	8.05b	18.90a	1.061a	42.30a
67.5	155.6a	7.00c	19.82a	1.065a	43.92a
90.0	141.2a	6.01d	18.90a	1.061a	44.08a
SEM	5.0	0.20	0.26	0.001	0.53

SEM, standard error of the mean.
Means within the same column sharing the same letters are not significantly different ($p < 0.01$).

Table 5. Tuber crude protein content as influenced by rate and method of PBZ application.

Rate (mg a.i. PBZ plant^{-1})	Crude protein (%)	
	Foliar	Soil drench
0 (control)	2.09de	1.96e
45.0	2.35bc	2.22cd
67.5	2.28bc	2.24ab
90.0	2.08de	2.54a
SEM	0.04	

SEM, standard error of the mean.
Means within column and row sharing the same letters are not significantly different ($p < 0.01$).

effectively suppresses growth in a wide range of plant species and the treated plants tend to be darker, shorter and more compact in appearance (Kamoutsis et al. 1999; Terri and Millie 2000; Sebastian et al. 2002). Shoot growth reduction occurs primarily due to decreased internode length, and the effective dose varies with species and cultivars (Davis and Curry 1991). The most noticeable potato growth response to PBZ treatment is reduction in shoot growth. As a result, treated plants are short and compact. This response could be attributed to reduction in total leaf area and stem elongation (height). Haughan et al. (1989) reported reduced cell proliferation due to PBZ treatment that may probably be responsible for restricted shoot growth.

Previous investigations on different crops showed that the foliage of PBZ treated plants typically exhibits an intense dark green color due to enhanced chlorophyll synthesis (Belakbir 1998;

Sebastian et al. 2002) or/and more densely packed chloroplasts per unit leaf area (Khalil 1995). A similar explanation has been suggested for the increased chlorophyll *a* and *b* contents in the current investigation. The observed negative correlations between total leaf area and chlorophyll *a* content ($r = -0.91^{*}$) as well as total leaf area and chlorophyll *b* content ($r = -0.65$) indicate that reduction in leaf area was ascribed with the higher chlorophyll *a* and chlorophyll *b* increment. In agreement with the current finding Balamani and Poovaiah (1985) and Bandara and Tanino (1995) observed an increase in chlorophyll content of potato leaf in response to PBZ treatment.

The higher chlorophyll content and delayed senescence of PBZ treated potato leaves may be related to its influence on the endogenous cytokinin content. It has been proposed that PBZ stimulates cytokinin synthesis that enhances chloroplast differentiation and chlorophyll biosynthesis, and prevents chlorophyll degradation (Fletcher et al. 1982). The use of gibberellins biosynthesis inhibitors increased cytokinin content in rice (Izumi et al. 1988), soybean (Grossmann 1992) and *Dianthus caryophyllus* (Sebastian et al. 2002). Previous investigations revealed that the onset of senescence in several plant species is considerably delayed by triazoles (Davis and Curry 1991; Binns 1994).

PBZ increased rate of net leaf photosynthesis. This could be attributed to the higher chlorophyll content and earlier tuberization (data not shown) in response to the PBZ treatment. Increased net photosynthesis in response to PBZ treatment has been reported in soybean (Sankhla et al. 1985) and rape (Zhou and Xi 1993). Compelling evidence exists that application of GA reduces tuberization in potato, and GA biosynthesis inhibitors promote tuberization (Balamani and Poovaiah 1985; Simko 1991; Langille and Helper 1992; Bandara and Tanino 1995). Although it is difficult to examine the rate of photosynthesis as a separate phenomenon, numerous reports in various crops have shown that increased sink demand results in increased source output (net CO_2 fixation); and decreased sink demand decreased source output (Geiger 1976; Hall and Milthorpe 1978; Peet and Kramer 1980). An increased rate of net photosynthesis (Dwelle et al. 1981) and enhanced translocation of photosynthates to the extent of about 90% of the total carbon fixed (Moorby 1968) reported in potato in response to rapid tubers growth. Alternatively, removal of rapidly growing tuber sinks led to a marked depression in net photosynthesis rates due to an imbalance between source and sink (Nosberger and Humphries 1965).

Dry matter accumulation and partitioning were affected by PBZ treatment at all harvesting stages. Of the total carbon fixed, about 22, 29, 29 and 32% were partitioned to the tubers at the 1st, 2nd, 3rd and 4th harvesting period in response to 67.5 or 90 mg a.i. PBZ treatment indicating that tubers are the dominant sinks. This dominance might be associated with the presence of PBZ stimulated low gibberellins content in the tuber tissue that increases tuber sink activity. Elevated temperatures and long day growing conditions stimulate gibberellins biosynthesis that encourages excessive top growth (Menzel 1981; Vreugdenhil and Sergeeva 1999). Exogenous GA application inhibited tuber formation; decreases sink strength of tubers and encouraged shoot and stolon growth (Menzel 1980; Mares et al. 1981; Vreugdenhil and Struik 1989). Similar, reports have been published indicating that high temperatures decrease tuber growth rate, decrease the partitioning of assimilates to the tubers and increase the amount allocated to other parts of the plant (Menzel 1980; Struik et al. 1989; Vandam et al. 1996).

The PBZ treatments considerably boosted tuber yield and this may be due the interplay of early tuberization, increased chlorophyll content, enhanced rate of net photosynthesis, and retaining photosynthetically active leaves longer in response to PBZ treatment. Reduction in tuber number could be linked to the decline in stolon number as result of a decrease in gibberellin activity that may be associated with stolon initiation (Kumar and Wareing 1972). A strong negative correlation ($r = -0.86^{*}$) was observed between tuber fresh mass and number signifying that the substantial increase in individual tuber size was responsible for the yield increment. In agreement with our study PBZ treatment increased tuber yield per plant in the trials of Balamani and Poovaiah (1985) and Simko (1994). However, it is not clear whether the observed yield increment was a consequence of an increase in tuber size or number. On the contrary, Bandara and 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 prob-

ably be explained by the cooler growing conditions in their experiment since they used 23 ± 2 °C/18 ± 2 °C day/night temperature and 16 h day length. Krauss (1978) reported that GA:ABA ratio controls tuberization and subsequent tuber growth; relatively higher GA level reduces or stops tuber growth while higher ABA level promotes tuber growth.

The observed increase in specific gravity and dry matter content of the tubers in response to PBZ may be attributed to reduced gibberellin accumulation in tuber tissue that in turn increased sink strength to divert more assimilates and enhance starch synthesis. Accumulation of GA_3 in tuber tissue reduces sink strength (Booth and Lovell 1972). Under inductive growing conditions the activities of enzymes involved in potato tuber starch biosynthesis such as ADPG-pyrophosphorylase, starch phosphorylase and starch synthase increase (Visser et al. 1994; Appeldoorn et al. 1997). Exogenous application of GA_3 on growing tubers substantially reduced the activity of ADPG-pyrophosphorylase, while the activity of starch phosphorylase remained more or less constant (Mares et al. 1981). Similarly, Booth and Lovell (1972) observed that application of GA_3 to potato shoots reduced export of photosynthates to the tubers, decreased starch accumulation, increased sugar levels and resulted in cessation of tuber growth. A highly significant positive correlation ($r = 0.99^{**}$) was observed between specific gravity and percent dry matter, confirming that specific gravity is an excellent indicator of the dry matter content of the tubers. Tsegaw and Zelleke (2002) have also reported a positive correlation between specific gravity and dry matter content of the tubers. Improving the dry matter content of potato tubers with the aid of PBZ treatment would be useful in the production of tubers having high specific gravity that are suitable for processing.

It has been postulated that PBZ increases tuber crude protein content by counteracting the activity of gibberellins that are known to prevent the induction of tuber protein synthesis. GA_3 treatment inhibits the accumulation of patatin, a glycoprotein associated with tuberization, and other tuber specific proteins (Park 1990; Vreugdenhil and Sergeeva 1999). The increase in crude protein content was closely associated with dry matter content ($r = 0.98^{**}$) probably reflecting increased tuber dry matter content substantially contributed for crude protein increment. Paiva et al. (1983) reported that starch and patatin accumulations were regulated by GA_3 and a close correlation was observed between them.

PBZ treatment significantly extended tuber dormancy. This is in agreement with the results of Harvey et al. (1991), Simko (1994), and Bandara and Tanino (1995). This may be associated with inhibition of gibberellin biosynthesis and ABA catabolism in response to PBZ treatment (Rademacher 1997). This could result in low GA and high ABA concentrations in tubers. It has been reported that GA_3 shorten tuber dormancy (Dogonadze et al. 2000) while ABA inhibited sprouting by hindering DNA and RNA synthesis (Hemberg 1970). It is suggested that the ratio of GA and ABA in the tuber is the most probable control mechanism of potato dormancy. Prolonging the dormancy period of the tubers with PBZ may be useful for the potato seed industry particularly to reduce unnecessary sprouting of potato cultivars having short dormancy period.

It is concluded that PBZ is an effective plant growth regulator to increase tuber yield and quality under high temperatures and long photoperiods by increasing photosynthetic capacity (net photosynthesis) and assimilate partitioning to the tubers. The results are of specific importance to increase the productivity of potato in the hot lowland tropics. There was no significant difference between foliar spray and drench application. Hence, for easy of application and to reduce the risk of soil pollution foliar spray is suggested. Using the information as a springboard further detail field investigation will be undertaken in the lowland tropic where potato cultivation is restricted due to the existence of high temperature.

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