CHAPTER 3

RESPONSE OF POTATO GROWN UNDER NON-INDUCTIVE GREENHOUSE CONDITIONS TO PACLOBUTRAZOL: SHOOT GROWTH, CHLOROPHYLL CONTENT, NET PHOTOSYNTHESIS, ASSIMILATE PARTITIONING, TUBER YIELD, QUALITY AND DORMANCY

3.1 ABSTRACT

The effect of foliar and soil applied PBZ on potato were examined under non-inductive conditions in a greenhouse. Single stemmed plants of the cultivar BP1 were grown at 35 (±2)/20 (±2) ºC day/night temperatures, relative humidity of 60%, and a 16h photoperiod. Twenty-eight days after transplanting PBZ was applied as a foliar spray or soil drench at rates of 0, 45.0, 67.5, and 90.0 mg active ingredient PBZ per plant. Regardless of the method of application, PBZ increased chlorophyll *a* and *b* content of the leaf tissue, delayed physiological maturity, and increased tuber fresh mass, dry matter content, specific gravity, and dormancy period of the tubers. PBZ reduced the number of tubers per plant. A significant interaction between rates and methods of PBZ application were observed with respect to plant height and tuber crude protein content. Foliar application resulted in a higher rate of photosynthesis than the soil drench. PBZ significantly reduced total leaf area and increased assimilate partitioning to the tubers. The study clearly showed that PBZ is effective to suppress excessive vegetative growth, favour assimilation to the tubers, increase tuber yield, improve tuber quality and extend tuber dormancy of potato grown in high temperatures and long photoperiods.

Keywords: Crude protein; gibberellin; high temperature; long photoperiod; paclobutrazol

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3.2 INTRODUCTION

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

The carbon budget for potatoes developed by Leach *et al*. (1982) indicates 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 ºC, above which point the carbohydrate consumed by respiration exceeds that produced by photosynthesis according to Levy (1992). Like high temperatures, long photoperiods also decrease partitioning of assimilates to the tubers and increase partitioning to other parts of the plant (Wolf *et al*., 1990).

Potatoes grown under high temperatures or long photoperiods are characterized by taller plants with longer internodes, increased leaf and stem growth, lower leaf: stem ratio, shorter and narrower leaves with smaller leaflets, and less assimilates partitioned to the tubers (Ben Khedher & 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 stolons 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 GA (Van den Berg *et al*., 1995; Jackson & Prat, 1996).

Amador *et al*. (2001) reported that endogenous GA 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 & Wareing, 1973). Under short day conditions GA biosynthesis is reduced (Amador *et al*., 2001). Van den Berg *et al*. (1995) reported that a dwarf potato mutant tuberized under long days due to the incorporation of a gene that partially blocks the conversion of 13-hydroxylation of GA_{12}-aldahyde to $GA_{53,}$ and treatment with GA biosynthesis inhibitors enhance tuberization in *andigena* spp. under long day conditions (Jackson & Prat, 1996).

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

The hormonal balance controlling potato tuberization can be altered using GA biosynthesis inhibitors such as 2-chloroethyl trimethyl ammonium chloride (CCC) (Menzel, 1980), B 995 (Bodlaender & Algra, 1966), and PBZ (Simko, 1994). 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 & Millie, 2000; Sebastian *et al*., 2002), enhances chlorophyll synthesis (Sebastian *et al*., 2002), delays leaf senescence (Davis & Curry, 1991) and increases assimilate partitioning to the underground parts (Balamani & Poovaiah, 1985; Davis & Curry, 1991; Bandara & Tanino, 1995; De Resende & De Souza, 2002).

It is postulated that PBZ blocks GA biosynthesis in potato plants grown under non-inductive growing conditions and modifies its growth to increase the productivity of the crop. Accordingly, the effects of foliar and soil applied PBZ on shoot growth, leaf chlorophyll content, assimilate production and allocation, tuber yield, and quality, and tuber dormancy period of potato grown under conditions of high temperatures and long photoperiod were investigated. The ultimate objective being to generate information to improve potato production in marginal areas where high temperatures and/or long photoperiods are limiting factors.

3.3 MATERIALS AND METHODS

3.3.1 Plant culture

Two experiments with similar procedures and treatments were conducted in 2002 on the experimental farm of the University of Pretoria, South Africa. Potato tubers of a 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 ^{o}C day/night temperatures and a 16h photoperiod. A week after emergence, uniform plants were transplanted to 5-liter plastic pots filled with sand and coconut coir (50:50 by volume) and grown in a greenhouse at 35 (±2)/20 (±2) ^{o}C day/night temperatures, an average relative humidity of 60%, and a 16h 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 randomised complete block design with three replications and each replicate contained seven pots per treatment. Plants were fertilized with a standard Hoagland solution and watered regularly to avoid water stress.

3.3.2 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 the Cultar formulation (250 g a.i. PBZ 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.

3.3.3. Data recorded

Net photosynthesis and chlorophyll content

Two weeks after treatment the rate of photosynthesis was measured using a portable photosynthesis system (CIRAS-1, 1998, UK), and leaf chlorophyll content was determined. From each treatment, three plants were randomly selected and rate of photosynthesis was

measured on the terminal leaflet of three fully expanded younger leaves. The photon flux density incident at the level of the leaf in the cuvette was 1050-1220 $\mu molm^{-2}s^{-1}$ (PAR). Average saturated vapour pressure of water at cuvette temperature was 34.5 mbar and vapour 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 per treatment 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 had senesced. Tuber fresh mass and numbers represent the average tuber mass and count of three plants at the time of final harvest.

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 (Murphy & Goven, 1959). For dry matter content determination, the samples were chopped and dried at a

temperature of 60 ºC for 15h, and followed by 105 ºC for 3h. Dry matter content of the tubers is the ratio between dry and fresh mass. Samples dried at 60 ºC were analysed for total nitrogen (Macro-Kjeldahl method, AOAC, 1984), and tuber crude protein content estimated by multiplying total nitrogen content by a conversion factor of 6.25 (Van Gelder, 1981).

Dormancy

To determine the effect of PBZ on dormancy, six healthy tubers per treatment were selected at the final harvest and labelled. Each treatment was replicated three times and samples were randomly distributed on shelves in a dark room. The dormancy of a particular tuber was deemed to have ended when at least one 2mm long sprout was present (Bandara & Tanino, 1995).

3.3.4 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 interactions. Hence, for all of the parameters considered, the data of the two experiments were combined. Means were compared using the least significant difference (LSD) test at 1% probability level. Correlations between parameters were computed when applicable.

3.4 RESULTS

PBZ treatment considerably reduced leaf area per plant. Irrespective of the rate of application the leaf area of PBZ treated plants were typically 50% smaller than the control at two, four, and six weeks after application (Figure 3.1). Plant height was influenced by the interaction effect of rate and method of PBZ application (Table 3.1). Foliar spray of 45 and 67.5 or 90 mg a.i. PBZ per

plant reduced plant height by about 35 and 46 % while soil drenching of the same concentration brought about 54 and 63% height reduction compared to the control, respectively.

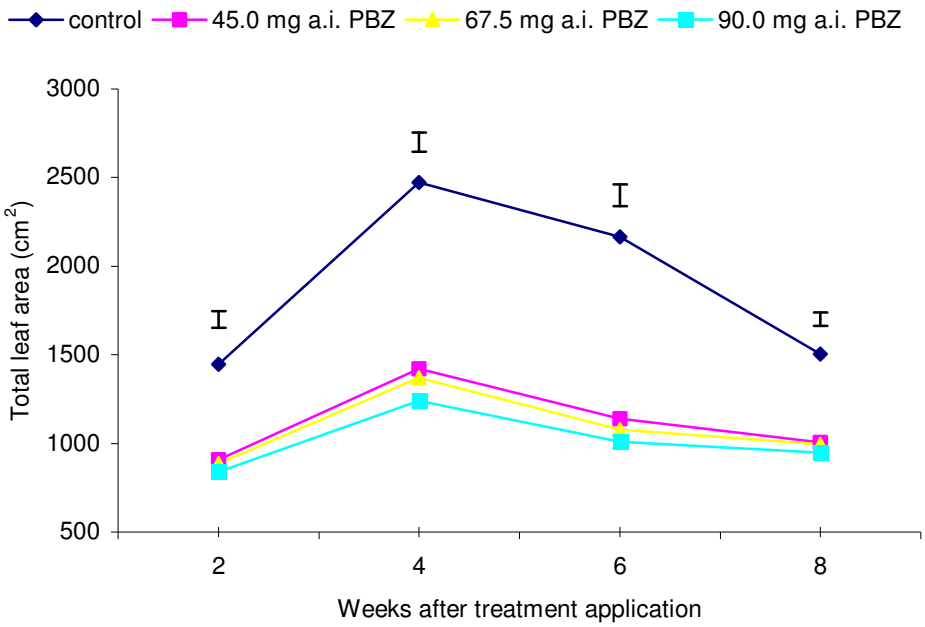

Figure 3.1 Total leaf area per plant as influenced by different rates of PBZ. The vertical bars represent least significant differences at P < 0.01

Table 3.1 Plant height of potato as affected by method and rate of PBZ application

PBZ rate (mg a.i. 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 columns and rows sharing the same letters are not significantly different (P < 0.01).

Regardless of the method of application, PBZ increased chlorophyll *a* and *b* content of the leaf tissue (Table 3.2). 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.

Physiological maturity was influenced by the rate of PBZ application (Table 3.2). The treated plants retained photosynthetically active leaves longer and delayed the date to 50% senescence by approximately 20 days compared to the control.

Table 3.2 Chlorophyll *a* and *b* contents of leaf tissue, leaf net photosynthesis and days to physiological maturity as influenced by method and rate of PBZ application

Treatment	Chlorophyll *a* (mg g^{-1} FW)	Chlorophyll *b* (mg g^{-1} FW)	Leaf net photosynthesis ($\mu molm^{-2}s^{-1}$)	Days to physiological maturity
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
0 (control)	0.50c	0.14b	6.79b	81.48c
45.0 (mg a.i. $plant^{-1}$)	0.67b	0.15b	10.74a	99.71b
67.5 (mg a.i. $plant^{-1}$)	0.78ab	0.23ab	11.65a	100.70ab
90.0 (mg a.i. $plant^{-1}$)	0.86a	0.31a	10.91a	102.39a
SEM	0.03	0.03	0.41	0.58

SEM: standard error of the mean.

FW: Fresh weight.

Means of the same main effect within the same column sharing the same letters are not significantly different ($P < 0.01$).

Leaf net photosynthesis was significantly affected by rate and method of PBZ application (Table 3.2). The highest net photosynthetic rate was observed in plants treated with 67.5 mg a.i. PBZ per plant. Foliar treated plants showed higher net photosynthetic rate than soil drench treated plants.

PBZ affected the pattern of assimilate allocation to the different plant parts (Table 3.3). PBZ greatly reduced the partitioning of assimilate to the leaves, stems, and roots and stolons, and increased the partitioning to the tubers compared to the control, at all harvesting stages. There was no consistency in the effects of methods of application on the pattern of assimilate production and allocation.

Table 3.3 Dry matter distribution (% of the total dry mass) among plant organs 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	8.93 c
	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.

Harvests I, II, III and IV done two, four, six and eight weeks after treatment application.

Means of the same main effect within the same column sharing the same letters are not significantly different ($P < 0.01$).

Regardless of the method of application, PBZ treatment increased tuber fresh mass, dry matter content, and specific gravity but reduced tuber numbers (Table 3.4). Tuber fresh mass per plant increased from 71.9 g (control) to 155.6 g in response to application of 67.5 mg a.i. PBZ per plant. Increasing the rate of PBZ resulted in a concomitant reduction in tuber number. Averaged 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 boosted dry matter content and specific gravity by an average 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 PBZ application.

Table 3.4 Tuber fresh mass, number, dry matter, specific gravity, and dormancy period as influenced by rates of PBZ application

PBZ rate (mg a.i. plant^{-1})	Tuber fresh mass (g pot $^{-1}$)	Tuber number pot $^{-1}$	Dry matter (%)	Specific gravity (g cm^{-3})	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 ($P < 0.01$).

PBZ extended the tuber dormancy period (Table 3.4, Figure 3.2). As the plants were grown under constant high day and night temperatures the tubers had a relatively short dormancy period. Irrespective of the concentration, PBZ extended the dormancy period by nearly a month as compared to the control.

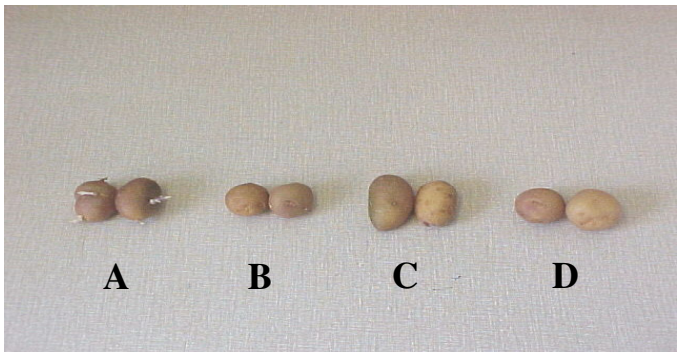

Figure 3.2 Dormancy characteristics of the control and PBZ treated potato tubers stored in a dark room, a month after harvesting. A = tubers from untreated plants (control), B = tubers from plants treated with 45 mg a.i. PBZ, C = tubers from plant treated with 67.5 mg a.i. PBZ, and D = tubers from plant treated with 90 mg a.i. PBZ

A significant interaction between rate and method of application was observed for tuber crude protein content (Table 3.5). Applying 45.0 or 67.5 mg a.i PBZ as a foliar spray gave the highest crude protein content, while drench application of 67.5 or 90.0 mg a.i. PBZ resulted in the highest crude protein content.

Table 3.5 Tuber crude protein content as influenced by rate and method of PBZ application

PBZ rate (mg a.i. 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 ($P < 0.01$).

3.5 DISCUSSION

Triazoles are potent plant growth regulators that inhibit shoot growth at low concentrations. PBZ effectively suppresses growth in a wide range of plant species and the treated plants tend to be darker green, shorter and more compact in appearance (Kamoutsis *et al.,* 1999; Terri & Millie, 2000; Sebastian *et al*., 2002). Shoot growth reduction occurs primarily due to decreased internode length, and the effective dose varies with species and cultivar (Davis & Curry, 1991). The most noticeable potato growth response to PBZ treatment was the reduction in shoot growth. As a result, treated plants were 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 colour due to enhanced chlorophyll synthesis (Sebastian *et al*., 2002) and/or more densely packed chloroplasts per unit leaf area (Khalil, 1995). A similar explanation is suggested for the increased chlorophyll *a* and *b* contents reflected in Table 3.2. 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 associated with the higher chlorophyll *a* and chlorophyll *b* concentrations. Balamani & Poovaiah (1985) and Bandara & Tanino (1995) also observed an increase in chlorophyll content of potato leaves in response to PBZ treatment. The higher chlorophyll content and delayed senescence of PBZ treated potato leaves may be related to the influence of PBZ 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 GA biosynthesis inhibitors increased cytokinin

content in rice (Izumi *et al*., 1988), soybean (Grossman, 1992) and *Dianthus caryophyllus* (Sebastian *et al*., 2002). Previous investigations revealed that the onset of senescence in several plant species was considerably delayed by triazoles (Davis & Curry, 1991; Binns, 1994).

PBZ increased the rate of net leaf photosynthesis (Table 3.2). This could be attributed to the higher chlorophyll content and earlier tuberization in response to the PBZ treatment. Increased net photosynthesis in response to PBZ has been reported in soybean (Sankhla *et al*., 1985) and rape (Zhou & Xi, 1993). Compelling evidence exists that application of GA reduces tuberization in potato, and GA biosynthesis inhibitors promote tuberization (Balamani & Poovaiah, 1985; Simko, 1991; Langille & Helper, 1992; Bandara & 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 & Milthorpe, 1978; Peet & Kramer, 1980). Rapid tuber growth increased the rate of net photosynthesis and enhanced translocation of photosynthates to the tubers (Dwelle *et al*., 1981a, Moorby, 1968). Alternatively, removal of rapidly growing tuber sinks led to a marked depression in photosynthetic efficiency due to an imbalance between source and sink (Nosberger & Humphries, 1965).

Dry matter partitioning was affected by PBZ treatment and at all harvesting stages tubers were the dominant sinks. This dominance might be associated with PBZ stimulated low GA level in the tuber tissue that increases tuber sink activity. Elevated temperatures and/or long days stimulate GA biosynthesis and thereby encourage top growth (Menzel, 1981; Vreugdenhil & Sergeeva, 1999). Exogenous GA application inhibited tuber formation; decreased sink strength of tubers and encouraged shoot and stolon growth (Menzel, 1980; Mares *et al*., 1981; Vreugdenhil & 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 increased tuber yield (Table 3.4) and this may be due to the interplay of early tuberization, increased chlorophyll content, enhanced rate of photosynthesis, and retaining photosynthetically active leaves longer in response to the treatment. Reduction in tuber number could be linked to the decline in stolon number as result of a decrease in GA activity that may be associated with stolon initiation (Kumar & 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 the current finding, PBZ treatment increased tuber yield per plant in the trials of Balamani & Poovaiah (1985) and Simko (1994). However, it is not clear whether the reported yield increments were a consequence of an increase in tuber size or number. On the contrary, 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 probably be explained by the cooler growing conditions in their experiment, namely 23 ± 2°C/18 ± 2°C day/night temperature and a 16h day length.

An increase in specific gravity and dry matter content of the tubers in response to PBZ may be attributed to reduced GA activity in the tuber tissue that in turn increased sink strength to attract more assimilates and enhance starch synthesis. Accumulation of GA_3 in tuber tissue reduced sink strength (Booth & 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 the 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 & 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 tuber dry matter content. Tsegaw & Zelleke (2002) have also reported a positive correlation between dry matter content and specific gravity of the tubers. Improving the dry matter content of potato tubers with the aid of PBZ treatment may ultimately 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 GA that is 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 & Sergeeva, 1999). The increase in crude protein content was strongly associated with dry matter content (r = 0.98**) indicating that an increase in tuber dry matter content might have substantially contributed for crude protein gain. Paiva *et al*. (1983) reported that GA regulates starch and patatin accumulations and a close correlation was observed between starch and patatin content.

PBZ treatment significantly extended tuber dormancy. This is in agreement with the results of Harvey *et al*. (1991), Simko (1994), and Bandara & Tanino (1995). This may be associated

with inhibition of GA biosynthesis and prevention of ABA catabolism in response to PBZ treatment (Rademacher 1997). This could result in low GA and high ABA concentrations in the tubers. It has been reported that GA_3 shortens tuber dormancy (Dogonadze *et al*., 2000) while ABA inhibited sprouting by hindering DNA and RNA synthesis (Hemberg, 1970). Prolonging the dormancy period of the tubers with PBZ may be useful for the potato industry to reduce untimely sprouting of potato cultivars with a short dormancy period.

3.6 CONCLUSION

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 efficiency and assimilate partitioning to the tubers. The results are of specific importance to increase the productivity of potato in the hot lowland tropics. Using the information as springboard field investigations will be undertaken in the lowland tropics where potato cultivation is restricted due to high temperatures.