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Growth responses of potato (*Solanum tuberosum*) grown in a hot tropical lowland to applied paclobutrazol: 1. Shoot attributes, assimilate production and allocation

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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. Regardless of the method of application, PBZ increased chlorophyll *a* and *b* content and net photosynthesis of the leaf tissue, but reduced shoot growth, plant height, stomatal conductance, and rates of transpiration compared with the control. PBZ significantly delayed the onset of leaf senescence and increased the partitioning of assimilates to the tubers while reducing assimilate supply to the leaves, stems, roots, and stolons. PBZ improved the productivity of potatoes grown in a hot tropical climate by reducing shoot growth, increasing leaf chlorophyll content, enhancing the rate of photosynthesis, improving water use, and modifying partitioning of dry matter to the tuber.

Keywords chlorophyll content; paclobutrazol; photosynthesis; stomatal conductance; transpiration

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INTRODUCTION

Lowland tropical regions are characterised by high soil and air temperatures that limit successful potato (*Solanum tuberosum* L.) cultivation (Midmore 1984). In Ethiopia, c. 55% of the available agricultural land is situated in arid and semi-arid parts of the country, where high temperatures throughout the year limit potato production.

Leach et al. (1982) developed a detailed carbon budget for potato, indicating that plant growth rate is strongly related to net photosynthesis and dark respiration. Of the gross carbon fixed in hot tropical growing conditions, up to 50% may be used through respiration (Burton 1972). Respiration increases with temperature and it is estimated to roughly double for each 10°C increase between 10°C and 35°C (Sale 1973). Conversely, above 30°C the rate of net photosynthesis declines rapidly (Leach et al. 1982; Thornton et al. 1996). Hence, reduced photoassimilate production through decreased photosynthesis and its increased utilisation by respiration in hot tropical lowlands are important factors limiting potato productivity.

The most noticeable morphological features of potatoes grown in high temperatures are taller plants with longer internodes, increased leaf and stem growth, decreased leaf:stem ratio, and shorter and narrower leaves with smaller leaflets (Menzel 1985; Manrique 1989; Struik et al. 1989). Although there are genetic differences (Manrique 1989; Hammes & De Jager 1990) high temperatures decrease the partitioning of assimilate to tubers and increase partitioning to other parts of the plant (Wolf et al. 1990; Vandam et al. 1996). Under long photoperiods, high temperatures may shift partitioning of assimilates to the shoots, thereby delaying leaf senescence (Struik et al. 1989); but under short photoperiods, high temperatures favour rapid growth and development that likely shorten the growing season (Vander Zaag et al. 1990). Higher temperatures favour the production of high levels of gibberellin-like compounds in potato (Menzel 1983).

Paclobutrazol ((2R, 3R+2S, 3S)-1-(4-chlorophenyl) 4,4-dimethyl-2-(1,2,4-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 gibberellin (GA) biosynthesis and abscisic acid (ABA) catabolism. In addition, PBZ induces various plant responses such as shoot growth reduction (Terri & Millie 2000; Sebastian et al. 2002), enhanced chlorophyll synthesis (Sebastian et al. 2002), delayed leaf senescence (Davis & Curry 1991), improved water use by reducing transpiration rate (Ritchie et al. 1991; Sankhla et al. 1992; Eliasson et al. 1994) and increased assimilate partitioning to the underground parts (Balamani & Poovaiah 1985; Davis & Curry 1991; Bandara & Tanino 1995).

Previous greenhouse experiments on the effects of PBZ on potato growth suggested that it enhanced the productivity of potatoes grown under non-inductive conditions (Tekalign & Hammes 2004). It is hypothesised that PBZ reduces GA biosynthesis in potatoes grown in lowland tropics and improves productivity. This paper reports the effects of foliar and root- applied PBZ on shoot growth, chlorophyll content, stomatal conductance, rate of transpiration, photosynthetic efficiency as well as biomass production and partitioning in potato grown under hot tropical conditions in the 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, and 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, 0.12% total nitrogen, 14.15 ppm phosphorus, 1.08 meq 100 gm^{-1} exchangeable potassium, 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 nitrogen 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.

Data recorded

Two weeks after treatment application, stomatal conductance, rate of transpiration, and photosynthesis were measured using a portable LCA4 photosynthesis system (ADC Bio Scientific Ltd, United Kingdom) and leaf chlorophyll content was determined. The measurements were made on three randomly selected plants using the 2nd, 3rd, and 4th terminal leaflets of healthy, fully opened and expanded younger compound leaves. To determine the concentrations of chlorophyll (Chl.) *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).

Two, 4, 6, and 8 weeks after treatment, three randomly selected plants were harvested from each treatment category. Samples were separated into leaves (including petioles), stems, tubers, and roots and stolons. Leaf area was measured with a portable CI-202 leaf area meter (CID Inc, Vancouver, Washington, United States) and only photosynthetically active green leaves were considered. Plant tissues were 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 was measured from the base of the stem to shoot apex. Days to physiological plant maturity were recorded when 50% of the leaves turned yellow. 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). Means were compared using 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 interaction. Hence, pooled data are presented for discussion.

There were no significant differences between the foliar spray and soil application for chlorophyll content, stomatal conductance, rate of transpiration, and plant height. Means pooled over methods of application showed that PBZ treatments significantly reduced total plant leaf area (Fig. 1). PBZ treatment resulted in a significant height reduction and application of 3 or 4 kg a.i. PBZ ha^{-1} resulted in a mean reduction of 63% in stem length (Table 1).

The concentrations of Chl. *a* and *b* in leaf tissue were significantly increased with PBZ treatments (Table 1). Compared with the control, application of 3 or 4 kg a.i. PBZ ha^{-1} increased the Chl. *a* content of leaf tissue by an average of 65%. In the same manner, regardless of the concentration, PBZ treatment increased the Chl. *b* content by an average of 55% compared with the control. Total leaf area significantly correlated with Chl. *a* ($r = -0.93$, $P < 0.01$) and Chl. *b* ($r = -0.97$, $P < 0.01$) content. Irrespective of the rate of application, PBZ treatment greatly reduced stomatal conductance and rate of leaf transpiration (Table 1). The lowest stomatal conductance (0.16 mmol m^{-2} s^{-1}) and rate of transpiration (3.78 mmol m^{-2} s^{-1}) values were recorded for plants that received 4 kg a.i. PBZ ha^{-1}. In contrast, PBZ treatment enhanced the rate of leaf net photosynthesis, with the highest value observed in plants treated with 3 or 4 kg a.i. PBZ ha^{-1}.

A significant interaction between method and PBZ application rate was observed for days to physiological maturity (Table 2). Compared with the control, regardless of the concentration, foliar spray of PBZ delayed the onset of senescence by an average of 17 days whereas applying 3 or 4 kg a.i. PBZ ha^{-1} as a soil drench delayed the maturity by c. 15 days.

Paclobutrazol significantly affected total dry matter (DM) production and assimilate allocation to the different plant parts of potato (Table 3). At all harvesting stages, PBZ significantly reduced total biomass production. Compared with the control, at all harvesting stages PBZ treatment greatly reduced the partitioning of assimilate to the leaves, stems, roots, and stolons, and increased assimilation to the tubers. At the first harvest, irrespective of the concentration, PBZ increased assimilate partitioning to tubers compared with the control which had not initiated tubers. At the second and third harvests, of the total carbon fixed c. 31% and 36% was partitioned to the tubers of PBZ-treated plants, whereas 14% and 22% were allocated to tubers of untreated plants. Correspondingly, at the fourth harvest, the plants treated with 3 or 4 kg a.i. PBZ ha^{-1} partitioned c. 40% of the assimilates to the tuber compared with 26% in the control. At the first and second harvests, the method of application did not affect total DM production and partitioning among plant parts. However, during the third and fourth sampling periods, although there was no consistency, method of application significantly influenced total DM production and allocation amongst plant parts.

DISCUSSION

Paclobutrazol is a potent synthetic plant growth regulator and at relatively low concentrations induces physiological, anatomical, and morphological changes in plants. The most striking growth response of potato to PBZ treatment was reduced shoot growth. Treated plants appeared to be short and compact, presumably because of the reduction in total leaf area and stem elongation. In accord with this study, Davis & Curry (1991) reported that depending on the species and cultivar, PBZ reduced shoot growth mainly by reducing internode length. It is speculated that reduced gibberellin synthesis in response to PBZ treatment might have resulted in a

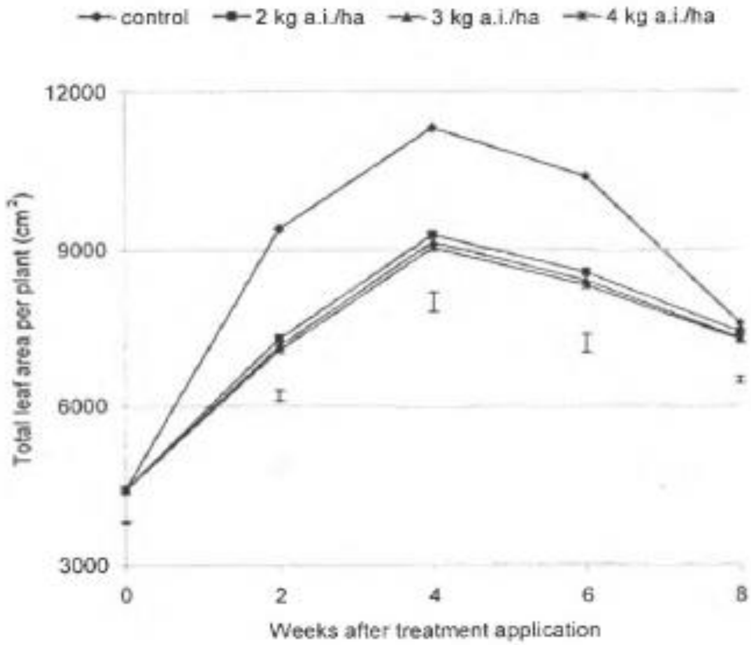


Fig. 1 Total leaf area of potato (*Solanum tuberosum*) grown under hot tropical lowland conditions as influenced by rates of paclobutrazol application. Vertical bars represent least significant differences at $P < 0.01$. (a.i., active ingredient.)

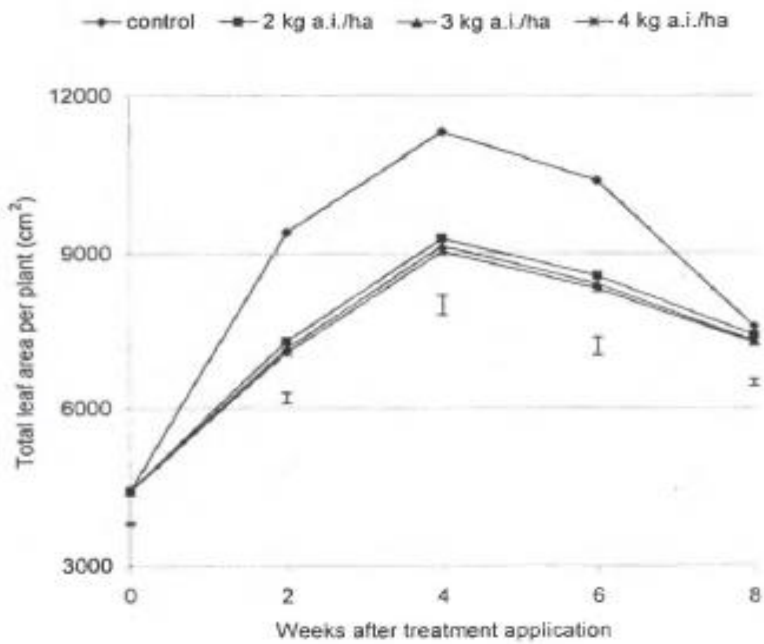
Table 1 Chlolophyll (Chl.) *a* and *b*, stomatal conductance (Gs), rate of transpiration (E), net photosynthesis (Pn) of leaf tissue and potato (*Solanum tuberosum*) plant height as influenced by rates of paclobutrazol application. (a.i., active ingredient; SEM, standard error of the mean; FW, fresh weight.) Means within the same column sharing the same letters are not significantly different ($P < 0.01$).

Rate (a.i. kg ha^{-1})	Chl. *a* (mg g^{-1} FW)	Chl. *b* (mg g^{-1} FW)	Gs (mmol $m^{-2}s^{-1}$)	E (mmo $m^{-2}s^{-1}$)	Pn (μmol $m^{-2}s^{-1}$)	Plant height (cm)
0 (control)	0.50c	0.15b	0.25a	5.00a	6.47b	77.92a
2	0.68b	0.22a	0.19b	3.97b	7.34ab	33.02b
3	0.81a	0.23a	0.18b	4.08b	8.40a	30.03bc
4	0.84a	0.25a	0.16b	3.78b	8.21a	27.63c
SEM	0.03	0.01	0.02	0.26	0.36	0.81

Table 2 Days to physiological maturity for potato (*Solanum tuberosum*) plants grown in a hot tropical climate as influenced by paclobutrazol (PBZ) application method and rate. (a.i., active ingredient; SEM, standard error of the mean.) Means within columns and rows sharing the same letters are not significantly different ($P < 0.01$).

Application method	Rate (a.i. kg PBZ ha^{-1})			
	0 (control)	2	3	4
Foliar spray	83.00e	100.83a	100.83a	100.00ab
Soil drench	83.17e	97.33d	98.00cd	99.17bc
SEM	0.38			

reduction in cell proliferation that apparently leads to a reduction in stem elongation and leaf expansion. In support of this postulate, Haughan et al. (1989) reported the 2R configuration of PBZ conferred great potency in retarding cell proliferation in celery. Previous studies disclosed that PBZ effectivel suppressed growth in a wide range of plant specie and the treated plants tended to be darker, short an more compact in appearance (Kamoutsis et al. 199 Terri & Millie 2000; Sebastian et al. 2002).



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The foliage of PBZ-treated plants typically exhibited dark green colour compared with the control. This may be a result of an increase in chlorophyll content of the leaves either because of enhanced chlorophyll synthesis and/or the presence of more chloroplasts per unit leaf area of treated leaves. The observed negative correlation between total leaf area and chlorophyll content indicated that the reduction in total leaf area in response to PBZ treatment substantially contributed to Chl. *a* and *b* increase. In agreement with these findings, an increased chlorophyll concentration for potato leaves in response to PBZ treatments was reported by Balamani & Poovaiah (1985) and Bandara & Tanino (1995). Increased chlorophyll synthesis as a result of PBZ treatment was reported in *Dianthus caryophyllus* (Sebastian 2002). Investigations undertaken by Khalil (1995) on cereals showed the existence of more densely packed chloroplasts per unit leaf area in response to PBZ treatment.

The higher chlorophyll content and delayed senescence in the treated potato leaves may be related to the influence of PBZ on endogenous cytokinins. It has been proposed that PBZ stimulates cytokinin synthesis which increases chloroplast differentiation and chlorophyll biosynthesis, and prevents chlorophyll degradation (Fletcher et al. 1982). Investigations on rice (Izumi et al. 1988), soybean (Grossmann 1992), and *Dianthus caryophyllus* (Sebastian et al. 2002) showed that exogenous application of GA biosynthesis inhibitors increased the cytokinin content of plant tissues. Previous investigations revealed that the onset of senescence was considerably delayed with the aid of triazoles in several plant species and treated leaves were retained longer than the untreated leaves (Davis & Curry 1991; Binns 1994).

The rate of transpiration in potato leaves was significantly reduced by PBZ treatments. This could be because of the partial closure of stomata in response to PBZ treatment as clearly depicted by the concomitant reduction in stomatal conductance. It is postulated that the reduction in stomatal conductance in response to PBZ treatment may have been mediated through its effect on endogenous ABA content (Rademacher 1997), as ABA is involved in regulating the opening and closing of stomata (Salisbury & Ross 1992). Asare-Boamah et al. (1986) observed reductions in transpiration, increased diffusive resistance, and a transient rise in ABA level in response to triazole treatment. This response may improve the drought tolerance of potato plants. PBZ treatment has been shown to reduce water loss and improve water use efficiency

Table 3 Total dry matter production and distribution amongst different parts of potato (*Solanum tuberosum*) plants grown under a hot tropical condition, as influenced by rate and method of paclobutrazol (PBZ) application. Harvest 1, 2, 3, and 4 were done 2, 4, 6, and 8 weeks after treatment application, respectively. (SEM, standard error of the mean.) Means within the same column sharing the same letters are not significantly different ($P < 0.01$).

Treatment	Leaves (%)	Stems (%)	Roots and stolons (%)	Tubers (%)	Total (g)	Leaves (%)	Stems (%)	Roots and stolons (%)	Tubers (%)	Total (g)
Harvest 1						**Harvest 2**				
Foliar spray	43.3a	27.7a	10.1a	18.8a	48.9a	38.3a	24.5a	10.5a	26.7a	92.5a
Soil drench	44.1a	27.2a	10.1a	18.6a	46.7a	39.9a	23.6a	10.2a	27.2a	89.0a
SEM	0.52	0.44	0.20	0.31	0.50	0.47	0.31	0.20	0.33	0.70
0 (control)	53.6a	34.5a	11.9a	0.0c	51.3a	43.5a	29.2a	13.5a	13.7b	99.0a
2	42.4b	25.6b	9.3b	22.7b	50.5a	37.2b	22.7b	9.8b	30.2a	90.3b
3	38.7c	25.1b	9.3b	26.5a	46.3b	36.7b	22.0b	9.3bc	31.9a	88.6bc
4	40.2bc	25.0b	9.4b	25.4a	43.2c	37.0b	22.3b	8.7c	32.a	85.0c
SEM	0.75	0.62	0.28	0.44	0.71	0.66	0.44	0.28	0.46	0.99
Harvest 3						**Harvest 4**				
Foliar spray	34.1b	23.5a	9.6b	32.4a	129.7a	32.4a	23.2a	9.0b	35.1a	151.9a
Soil drench	35.5a	23.0a	9.0a	32.5a	124.6b	33.1b	22.5a	8.4a	36.0b	146.9b
SEM	0.26	0.33	0.13	0.28	0.78	0.21	0.32	0.13	0.18	0.82
0 (control)	39.8a	26.3a	11.9a	22.0b	138.0a	37.3a	25.8a	11.1a	25.8c	162.2a
2	33.3b	22.4a	8.8b	35.5a	125.1b	31.3b	22.1b	8.2b	38.4b	146.3b
3	33.4b	22.3b	8.4b	35.9a	124.4b	31.2b	21.9b	7.7b	39.0ab	146.3b
4	33.4b	22.0b	8.1b	36.5a	121.2b	31.2b	21.6b	7.6b	39.6a	142.6b
SEM	0.37	0.47	0.19	0.40	1.10	0.30	0.46	0.18	0.35	1.16

in grapevine, chrysanthemum, and beetroot (Ritchie et al. 1991; Smith et al. 1992; Roberts & Mathews 1995).

Unlike its effect on the rate of transpiration, PBZ treatment enhanced the rate of net leaf photosynthesis. This response could be linked to the increase in chlorophyll concentration and earlier tuberisation. Previous studies conducted in carbon fixation and allocation in various crops showed that source:sink balance influenced the rate of photosynthesis in such a way that an increased sink demand could increase the rate of photosynthesis and a decreased sink demand could result in decreased photosynthesis (Geiger 1976; Hall & Milthorpe 1978; Peet & Kramer 1980). A similar interaction has been observed in the potato. Nosberger & Humphries (1965) reported that removal of growing potato tubers reduced the rate of net photosynthesis, whereas an increased rate of net photosynthesis was reported after tuber initiation by Moorby (1968) and Dwelle et al. (1981). Increased net photosynthesis in response to PBZ treatment has been reported in soybean (Sankhla et al. 1985) and rape (Zhou & Xi 1993). Reduced stomatal conductance did not lead to reduced net photosynthesis. This may be related with PBZ-induced cell morphology modification of the photosynthetic tissue (mesophyll) that might have allowed better diffusion of CO_2 from air space to carboxylation sites. In considering leaf anatomy in relation to photosynthesis, De Greef et al. (1979) reported that the rate of photosynthesis increases as the mean cell size increases, because bigger mesophyll cells have larger contact surface-to-volume ratio. Our microscopic observation showed that PBZ increased the size of epidermal, palisade, and spongy mesophyll cells of potato leaves.

Paclobutrazol treatments remarkably affected the overall pattern of carbon fixation and assimilate partitioning to different potato organs. In all harvests, tubers were found to be the dominant sinks that attracted the highest proportion of DM relative to the leaves, stems, roots, and stolons. This dominance may be linked to the presence of low GA concentrations in tubers as a result of PBZ treatment, increasing tuber sink strength. This speculation is supported by Menzel (1980) and Mares et al. (1981) who reported that exogenous GA_3 application inhibited tuber formation, decreased tuber sink strength, and encouraged shoot and stolon growth. Previous investigations have been published indicating that high temperatures decrease tuber growth rate, reduce the partitioning of assimilates to the tubers, and increase assimilation to other parts of the plant (Menzel 1980; Struik et al. 1989; Vandam et al. 1996) which could be associated with high GA synthesis.

The field trials demonstrated that PBZ treatment increased leaf chlorophyll content, improved water use efficiency by reducing the rate of transpiration, and enhanced the rate of net photosynthesis with a direct effect on potato crop productivity. The treatments also reduced shoot growth and increased partitioning of assimilates to the tubers. It was also observed that there were no significant differences between foliar spray and soil drench for most of the parameters considered. Hence, for ease of application and to reduce soil pollution, foliar spray is suggested. In conclusion, from this investigation PBZ is a plant growth regulator with the potential to increase the productivity of potato cropping in the lowland area of eastern Ethiopia where high temperatures are limiting.

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