Effect of Soil Temperature on K and Ca Concentrations and on ATPase and Pyruvate Kinase Activity in Potato Roots

Juan M. Ruiz

Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Granada, 18071-Granada, Spain

Joaquín Hernández

Departamento de Biología Vegetal, EUP Ingeniería Técnica Agrícola, Universidad de Almería, 04120-Almería, Spain

Nicolas Castilla

Departamento de Horticultura, CIFA, Camino de Purchil s/n, 18004-Granada, Spain

Luis Romero¹

Departamento de Biología Vegetal, Facultad de Ciencias, Universidad de Granada, 18071-Granada, Spain

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Abstract. Potato (*Solanum tuberosum* L.) ‘Spunta’ plants were grown with the root zone covered by different types of polyethylene plastic mulches. The plastic mulches used were transparent, white, co-extruded black and white, and black. As a control, plants were grown without plastic mulch. The parameters analyzed were soil temperature, root concentration of K and Ca, and enzymatic activities of ATPase and pyruvate kinase (PK), measured as basal and in the presence of K⁺ and Ca²⁺. The physical characteristics of the plastic mulches directly influenced soil and root temperatures in potato plants. In addition, the concentration of cations in the roots (particularly Ca²⁺) and basal ATPase activity were affected by soil temperature, whereas basal PK was not affected by soil temperature. The use of co-extruded black and white plastic mulch improved the nutritional status of Ca in the roots of potato plants. Finally, the basal ATPase and PK activities in the presence of K⁺ and Ca²⁺ were related with the root levels of these cations.

Pyruvate kinase (PK) catalyzes the synthesis of pyruvate and ATP from PEP and ADP. In plants, substantial evidence indicates that PK is the primary control site of glycolytic flux to pyruvate (Huppe and Turpin, 1994). Studies on the kinetics of this enzyme reveal that its activity is dependent on the levels of PEP and ADP, in addition to the presence of cofactors such as K⁺ and Mg²⁺ (Podestá and Plaxton, 1991, 1992). In addition, PK activity may be a good physiological indicator of cation levels (K⁺, Mg²⁺, and Ca²⁺) in plant tissues (Lavon and Goldschmidt, 1999; Ruiz et al., 1999).

ATPase activity in roots, mainly in the plasma membrane, partly reflects ion transport. A direct relationship has been found between ATPase activity and the root concentration of cations. In addition, the activity of ATPase has reportedly been stimulated by cations, K⁺ being regarded as the most effective

(Sklenar et al., 1994; Terry et al., 1989).

Root temperature affects many aspects of plant physiology, mainly water and nutrient uptake (Spiers, 1995). Variations in environmental factors such as moisture and temperature of the root zone influence the absorption and distribution of cations, Ca²⁺ being the most affected (Adams and Holder, 1992). Adams and Ho (1993) reported increased Ca²⁺ absorption with rising root temperatures to a maximum of 26 °C. Similarly, root absorption of Ca²⁺ increased with higher transpiration (Adams and Ho, 1993). Given the impact that the roots exert on yield and quality in potato plants, through the effect of roots on such factors as the concentration of carbohydrates and cations (K⁺ and Ca²⁺), it is important to prevent nutritional imbalances in the roots in relation to these elements (Palta, 1996).

One technique that has strongly boosted agricultural and horticultural output in the last few years in Spain and elsewhere is the use of plastic mulches on the soil surface. The different compositions, thicknesses and colors of the plastic mulches modify various physical-chemical characteristics of the soil, in addition

to improving water use efficiency and soil temperature (Yunasa et al., 1994).

Thus, the objective of this research was to determine how different plastic mulches influence root temperature, and how root temperature in turn affects the concentration of root cations (K⁺ and Ca²⁺). Additionally, the relationship between the cations and their possible bioindicators (ATPase and PK) was also determined.

Materials and Methods

Plant material and culture conditions. The experiment was conducted for 3 years (1993–95) at the experimental station of the Center for Agricultural Research and Training of Granada (Spain). Potato seed pieces were planted on 7 Mar. and the crop cycle was ≈4 months. The climate was semiarid and the area is intensively used for agriculture. The soil used was loamy-sand with the following characteristics: sand (42.8%), silt (39.7%), and clay (17.5%), CaCO₃ equivalent (9%), active CaCO₃ (2.9%), total N (1 g·kg⁻¹), P₂O₅ (49.5 mg·kg⁻¹), cation-exchange capacity (73.9 mmol·kg⁻¹), K⁺ (2.7 mmol·kg⁻¹), Na⁺ (4.1 mmol·kg⁻¹), pH (H₂O, 7.7), and electrical conductivity (EC) (2.76 dS·m⁻¹).

Plastic mulches were applied making a tight seal with the soil and only on the raised beds. The mulches used were transparent polyethylene (25 µm in thickness), white polyethylene (25 µm in thickness), coextruded black and white polyethylene with the white side up (50 µm in thickness), and black polyethylene (25 µm in thickness). No mulch was applied in the control treatment.

The fertilization used was the same as that applied by farmers in the area. In February of each of the 3 years, NH₄NO₃, P₂O₅, and K₂O were each applied at 27 g·m⁻². At the end of April, 25 g·m⁻² was applied as NH₄NO₃.

The experimental design was a randomized complete block with five treatments. Each treatment was replicated four times, for a total of 20 plots. Each plot had an area of 78.4 m² with a planting density of 4.17 plants/m². Plants, grown on slightly raised beds 50 cm wide, were spaced 30 cm apart with a 80-cm separation between rows. The irrigation water had the following properties: pH (7.65), EC (0.91 dS·m⁻¹), Cl⁻ (58.5 mg·L⁻¹), Na⁺ (25 mg·L⁻¹), K⁺ (4 mg·L⁻¹), and H₂CO₃ (369 mg·L⁻¹). The irrigation water was applied constantly using a drip irrigation system, supplying the following micronutrients: Fe (0.5 mg·L⁻¹), B (0.1 mg·L⁻¹), Mn (0.1 mg·L⁻¹), Zn (0.075 mg·L⁻¹), Cu (0.075 mg·L⁻¹), and Mo (0.05 mg·L⁻¹). Iron was applied as FeEDDHA, B as H₃BO₃ and the remaining micronutrients as sulfates.

Plant sampling. Roots were sampled twice yearly, on 27 May and 10 June. These two samplings corresponded to the maturity phase of the plant, the most representative and determinant in the potato crop, given that in this phase the fruits and seeds are produced in addition to the majority of tubers (Manrique, 1995). Ten plants were collected from each replicate per treatment. Roots were rinsed

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¹To whom reprint requests should be addressed. E-mail address: lromero@ugr.es

three times in distilled water after disinfecting with nonionic detergent at 1% (Wolf, 1982), then blotted on filter paper. Fresh tissue was used for the ATPase and PK assays; a subsample was dried in a forced air oven at 70 °C for 24 h, ground in a Wiley mill and then placed in plastic bags for further analyses of total K and Ca.

Measurement of soil temperature. Soil temperature was measured at a depth of 15-cm, using thermocouples (model 107; Campbell Scientific, Logan, Utah). Soil temperature was measured (six times during the day at 4-h intervals) every 3 d during of the crop cycle (March–July). The soil temperatures in Table 1 represent the mean values for each treatment, based on the averages for 1993, 1994, and 1995, from 15 May to 10 June.

Preparation of microsomal fraction. Microsomal fractions were prepared according to the method of Ferrol et al. (1993) with minor modifications. Briefly, 2 g of roots were homogenized with mortar and pestle and then with a glass homogenizer in 5 mL·g⁻¹ fresh weight of grinding medium containing 25 mmol·L⁻¹ 1,3-bis-tris(hydroxymethyl)methylamino]propane-2-(*N*-morpholino)ethanesulfonic acid (BTP-MES) (pH 7.6), 250 mmol·L⁻¹ sucrose, 2 mmol·L⁻¹ dithiothreitol (DTT), 2 mmol·L⁻¹ MgSO₄, 2 mmol·L⁻¹ ATP, 10% glycerol (v/v), 2 mmol·L⁻¹ ethyleneglycol-bis(β -aminoethyl ether)-*N,N,N',N'*-tetraacetic acid (EGTA), 1 mmol·L⁻¹ phenylmethanesulfonyl fluoride (PMSF) and 0.5% albumin from bovine serum (BSA) (w/v). The homogenate was filtered and centrifuged for 10 min at 13,000 g. The supernatant was centrifuged for 35 min at 80,000 g and then the pellet (crude microsomes) was resuspended in a medium containing 2 mmol·L⁻¹ BTP-MES (pH 7), 250 mmol·L⁻¹ sucrose, 1 mmol·L⁻¹ DTT, 10% glycerol (v/v) and 0.2% BSA (w/v) to obtain the microsomal fraction. All these procedures were carried out at 0 to 4 °C.

Plasma membrane ATPase assays. The basal plasma membrane ATPase defined as vanadate-sensitive, molybdate-insensitive, nitrate-insensitive and azide-insensitive Mg-ATP hydrolysis was performed as described by Gibrat et al. (1989). Enzymatic activity was assayed for 30 min at 30 °C in a basal reaction medium containing 3 mmol·L⁻¹ ATP-BTP (pH 6.5), 2 mmol·L⁻¹ BTP-HCl (pH 6.5), 0.1 mmol·L⁻¹ sodium molybdate, 0.25 mmol·L⁻¹ sodium orthovanadate, 100 mmol·L⁻¹ KNO₃ and 1 mmol·L⁻¹ NaNO₃ in a final volume of 1 mL. The amount of membrane protein routinely used was 10–15 µg per assay.

The corresponding inhibitor-sensitive ATPase activities were calculated as differences of activities measured in the presence and in the absence of the corresponding inhibitor. The ATPase activity was determined as the release of inorganic phosphate (Pi), this being quantified by the formation of the phosphomolybdic colored complex (Widell and Larsson, 1990). Protein was determined by the method of Bradford (1976). Triplicate assays were performed for each extract.

Assay of plasma membrane ATPase in the presence of K⁺ and Ca²⁺ followed the same

Table 1. Effect of plastic mulch on soil temperature and root concentration of the total K and Ca. Data are means $\pm$ SD (n = 24).

Mulch	Soil temp (°C)	(g·kg ⁻¹ dry wt)	
		Total K	Total Ca
None	18.1 $\pm$ 1.3	7.50 $\pm$ 0.26	9.31 $\pm$ 0.43
Transparent	20.3 $\pm$ 2.0	8.90 $\pm$ 0.28	9.69 $\pm$ 0.39
White	23.5 $\pm$ 1.8	10.02 $\pm$ 0.28	9.97 $\pm$ 0.41
Co-extruded black and white	27.2 $\pm$ 2.3	6.30 $\pm$ 0.27	20.22 $\pm$ 0.46
Black	30.7 $\pm$ 2.2	6.70 $\pm$ 0.27	18.62 $\pm$ 0.51
LSD _{0.05}	2.0	0.48	1.03
Significance	***	**	**

***, **Significant at $P < 0.01$ and 0.001 , respectively.

method as for basal ATPase, with the difference of adding to the reaction mixture either 0.1 mL of K⁺ in the form of KCl (50 mmol·L⁻¹) and 0.1 mL of Ca²⁺ in the form of CaCl₂ (50 mmol·L⁻¹). The processes of measuring, incubation, centrifugation, and activity were the same as described for basal ATPase.

Pyruvate-kinase assays. The activity of basal PK was determined by the method of Ruiz et al. (1999). A total of 0.5 g of fresh root samples was ground with a mortar and pestle (at 0–4 °C) in 50 mmol·L⁻¹ of Tris-HCl buffer (pH 7.5), 50% glycerol (v/v) and 10 mmol·L⁻¹ 2-mercaptoethanol. The homogenate was centrifuged at 3,000 g for 5 min at 0 °C and then the supernatant was centrifuged again at 24,000 g for 15 min resulting in the enzymatic extract. To prepare the reaction mixture, 0.1 mL of the desalted extract was combined with 0.5 mL of 50 mmol·L⁻¹ Tris-HCl buffer (pH 7.4) together with 0.25 mmol·L⁻¹ sodium molybdate, 25 mmol·L⁻¹ phosphoenolpyruvic acid (PEP), 5 mmol·L⁻¹ ADP, 5 mmol·L⁻¹ MgCl₂ and 0.2 mL of H₂O. The mixture was incubated at 37 °C for 10 min, and the reaction was stopped by adding 0.5 mL of 2,4-dinitrophenylhydrazine 0.0125% (w/v) to 2 mol·L⁻¹ HCl and 0.5 mL 2 mol·L⁻¹ NaOH to avoid possible absorbance changes from altering the pH of the reaction mixture. After centrifugation for 5 min at 3,000 g, the absorbance at 510 nm was measured and compared against a standard curve of pyruvate. Triplicate assays were performed for each extract. To ascertain whether pyruvate was formed exclusively by PK, we determined the activity of acid phosphatase by the method of Besford (1979).

Assay of PK in the presence of K⁺ and Ca²⁺ followed the same method as for basal PK, with the difference of adding to the reaction mixture either 0.1 mL of K⁺ in the form of KCl (50 mmol·L⁻¹), or 0.1 mL of Ca²⁺ in the form of CaCl₂ (50 mmol·L⁻¹). The processes of incubation, centrifugation, and activity measurement were the same as described for basal PK. The soluble proteins from the supernatants or crude enzyme extracts were determined by Bradford's method (1976), with BSA as the standard.

Cation determination. Root dry matter was digested with 96% H₂SO₄ in the presence of hydrogen peroxide (H₂O₂). Total potassium (K) was determined by the flame photometer method (Lachica et al., 1973) and total calcium (Ca) was analyzed by atomic-absorption spectrophotometry (Hocking and Pate, 1977).

Statistical analysis. Analysis of variance

(ANOVA) was used to assess the significance of treatment means. ANOVAs were performed on pooled data for the three years. Only the mean value for each treatment is reported in the tables, since the ANOVA showed no significant differences either between means in the same year or among means for different years. The data shown are mean values $\pm$ SD. Treatment means were compared using LSD at the 0.05 probability level. Finally, when necessary, regression analyses were done using raw data.

Results and Discussion

Plastic mulches increase soil temperature by increasing energy interception and preventing heat loss from the soil. The overall result is less fluctuation between day and night soil temperatures (Manrique, 1995; Schmidt and Worthington, 1998). Different mulch colors cause changes in soil temperature (Decoteau et al., 1989; Yunasa et al., 1994). In our experiment, the application of mulches raised the temperature in the root zone in relation to the control ($P < 0.001$; Table 1). The warmest soil was found under black plastic mulch (30.7 °C) and the coolest under transparent plastic mulch (20.3 °C). Black plastic mulch absorbs roughly 96% of the shortwave radiation (Ham et al., 1993), and this absorbed radiation warms the soil (Teasdale and Abdul-Baki, 1995). For transparent mulch, our results proved similar to those reported by Ghawi and Batikh (1988), who also indicate that soil temperatures under transparent mulch are lower than under other mulches. These authors attribute the reduced soil temperature to a shading effect created by a more vigorous growth of the plants under transparent mulch. In our experiment, during early growth stages above-ground biomass production was highest in plants grown under transparent mulch (data not shown). White plastic mulch resulted in cooler soils (23.5 °C) than did the black mulch (Table 1) because white surfaces reflect most wavelengths of solar radiation (Decoteau et al., 1989; Hatt et al., 1993).

Co-extruded black and white and black plastic mulch treatments resulted in the lowest total K concentrations in roots, while plants under white mulch had the highest (Table 1). Opposite results were found for Ca, which presented the highest levels of total root Ca in co-extruded black and white and black plastic mulch, and the lowest in the control treatment (Table 1).

Root temperature is related to cation absorption, as reflected in the root content of these cations (Spiers, 1995). Our experiment revealed two opposing trends on K: 1) in the control and transparent and white plastic mulch, the concentration of K increased with the temperature; while 2) in co-extruded black and white and black plastic mulch, the concentration of K declined when the temperatures rose ($r = -0.61$, $P < 0.05$). The concentration of Ca was directly related with soil temperature ($r = 0.89$, $P < 0.001$). Previous researchers have described Ca^{2+} as the most sensitive cation to high root temperatures, showing an increased absorption and increases in root concentration (Adams and Ho, 1993). In addition, the antagonistic relationship of Ca^{2+} with the rest of the cations (Ruiz et al., 1999; Song and Fujiyama, 1996) could explain the fall in the K concentration with a rise in root temperature in co-extruded black and white and black plastic mulch (Table 1).

Root cation content is predetermined by the passage of the ions through the plasma membrane, and this requires the participation of ATPase (Dunlop and Gardiner, 1993; Serrano, 1989). In our experiment, the basal activity of ATPase in the plasma membrane was >25% higher in plants under co-extruded black or white and black mulch compared to the lowest activity of plants under transparent mulch (Table 2). It has been demonstrated that basal ATPase activity in the roots reflects ion transport, in some cases showing a direct relationship of the activity of the enzyme with the cation concentration in the roots (Sklenar et al., 1994). We found a direct relationship of the basal ATPase activity with the Ca concentration in the roots ($r = 0.93$, $P < 0.001$), and an inverse relationship of the activity of this enzyme with the K concentration in the roots ($r = -0.86$, $P < 0.01$). Under high Ca^{2+} levels, Ca^{2+} has been found to stimulate ATPase activity (Pomeroy and McMurchie, 1982).

Sommarin et al. (1995) found that higher root temperatures boosted ATPase activity. In our experiment, increased soil temperatures under the mulch were correlated with a high ATPase activity plants under co-extruded black and white and black plastic mulch, those with the highest soil temperatures (Table 1), consistently showed increased enzymatic activity (Table 2) (soil temperature vs. basal ATPase activity, $r = 0.97$, $P < 0.001$).

With respect to ATPase activity of the plasma membrane in the presence of K^+ , the lowest activity was shown in transparent plastic mulch and the highest in co-extruded black and white and black plastic mulch (Table 2), coinciding with the lowest root concentrations of total K (Table 1). In addition, independently of the treatments applied, the activities of ATPase in the presence of K^+ were greater than the activities of basal ATPase (Table 2). ATPase activity is stimulated principally by monovalent cations, K^+ being the most effective (Terry et al., 1989), mainly because this cation increases ATPase affinity for ATP (Gonzalez de la Vara et al., 1992). However, Lindberg and Yahya (1994) found that K^+ stimulated ATPase activity under limiting or

Table 2. Effect of plastic mulches and the presence of K^+ (50 mM) and Ca^{2+} (50 mM) on the ATPase activity. Basal ATPase = ATPase activity in the absence of K^+ and Ca^{2+} . ATPase- K^+ = ATPase activity in the presence of K^+ . ATPase- Ca^{2+} = ATPase activity in the presence of Ca^{2+} . Values in brackets indicate the percent increase (+) or decreases (–) in the presence of K^+ or Ca^{2+} relative to basal ATPase activity. Data are means $\pm$ SD ($n = 24$).

Mulch	(mmol·kg ⁻¹ ·s ⁻¹)		
	basal ATPase	ATPase- K^+	ATPase- Ca^{2+}
None	4.91 $\pm$ 0.11	6.36 $\pm$ 0.14 (+30)	4.96 $\pm$ 0.11 (+1)
Transparent	4.56 $\pm$ 0.08	5.91 $\pm$ 0.11 (+29)	5.21 $\pm$ 0.11 (+14)
White	5.24 $\pm$ 0.08	6.41 $\pm$ 0.11 (+22)	5.43 $\pm$ 0.08 (+4)
Co-extruded black and white	6.55 $\pm$ 0.14	10.20 $\pm$ 0.14 (+56)	6.36 $\pm$ 0.11 (–3)
Black	5.71 $\pm$ 0.11	9.63 $\pm$ 0.14 (+69)	5.82 $\pm$ 0.11 (+2)
LSD _{0.05}	0.36	0.50	0.45
Significance	***	**	**

, *Significant at $P < 0.01$ and 0.001 , respectively.

inadequate nutrient conditions, particularly with respect to K. These conclusions could explain the stimulation of the ATPase activity in the presence of K^+ with respect to the basal activity, in all the treatments and specifically in co-extruded black and white and black plastic mulch. Finally, our results could indicate an inadequate nutrient status in terms of K in the roots of the potato plants grown under our experimental conditions.

The highest ATPase activity in the presence of Ca^{2+} was observed in plants under co-extruded black and white and black plastic mulch, with increases of 28% with respect to the control plants. However, the ATPase did not significantly increase in the presence of Ca^{2+} in relation to the basal activity (Table 2). These results agree with those of Terry et al. (1989), who reported that the ATPase activity is stimulated less by Ca^{2+} than by K^+ , with some cases even registering an inhibition of enzymatic activity. However, these results could be explained by the adequate nutritional status of Ca in potato roots in our experiment.

One widely used physiological indicator of cation levels in different tissues is PK activity. Increased enzymatic activity in the presence of a cation with respect to basal activity indicates a possible deficiency or need for this cation (Lavon and Goldschmidt, 1999; Ruiz et al., 1999). The use of PK as an indicator of the cation level is based on the fact that the activation of PK depends on the presence of cations, primarily K^+ and Mg^{2+} (Podestá and Plaxton, 1991). In our experiment, the highest PK basal activities were found in the control plants and on plants under transparent and white plastic mulch, with

increases >59% with respect to the lowest activities in co-extruded black and white and black plastic mulch (Table 3). Given the dependence of PK activity on K^+ , enzyme activity may be due mainly to the root concentration of total K ($r = 0.97$, $P < 0.001$), since the relationship between enzymatic activity and soil temperature was nonsignificant ($r = 0.58$, $P > 0.05$).

Independent of the plastic mulch treatment, PK activity in the presence of K^+ increased with respect to the basal activity, and most in plants under co-extruded black and white and black plastic mulch (Table 3), which were the two treatments with the lowest root concentrations of total K (Table 1). That is, in all the treatments there appears to be a deficiency of K, which was accentuated in plants under the co-extruded black and white and black plastic treatments.

Similar results has been reported by other authors working with different species and analyzing other organs (Lavon and Goldschmidt, 1999; Ruiz et al., 1999). The deficiency of K in the roots of plants under co-extruded black and white and black plastic mulch, may have arisen because of the negative effect of increased temperature on the uptake and accumulation of K^+ , or because of the antagonism between Ca^{2+} and K^+ , which was intensified under co-extruded black and white and black plastic mulches (Table 1).

PK activity in the presence of Ca^{2+} decreased in comparison to the basal values in all treatments, and was lowest in the co-extruded black and white plastic mulches treatment (Table 3). These results confirm those of Ruiz et al. (1999), who showed that when Ca^{2+} is

Table 3. Effect of plastic mulches and the presence of K^+ (50 mM) and Ca^{2+} (50 mM) on the PK activity. Basal PK = PK activity in the absence of K^+ and Ca^{2+} . PK- K^+ = PK activity in the presence of K^+ . PK- Ca^{2+} = PK activity in the presence of Ca^{2+} . Values in brackets indicate the percent increase (+) or decreases (–) in the presence of K^+ or Ca^{2+} relative to basal PK activity. Data are means $\pm$ SD ($n = 24$).

Mulch	(mmol·kg ⁻¹ ·s ⁻¹)		
	basal PK	PK- K^+	PK- Ca^{2+}
None	0.76 $\pm$ 0.02	1.11 $\pm$ 0.03 (+46)	0.54 $\pm$ 0.01 (–29)
Transparent	0.81 $\pm$ 0.02	1.06 $\pm$ 0.04 (+30)	0.57 $\pm$ 0.01 (–30)
White	0.88 $\pm$ 0.03	1.06 $\pm$ 0.04 (+20)	0.63 $\pm$ 0.02 (–28)
Co-extruded black and white	0.48 $\pm$ 0.15	1.16 $\pm$ 0.07 (+144)	0.24 $\pm$ 0.01 (–50)
Black	0.66 $\pm$ 0.05	1.11 $\pm$ 0.05 (+68)	0.42 $\pm$ 0.01 (–37)
LSD _{0.05}	0.04	0.03	0.06
Significance	***	**	**

, *Significant at $P < 0.01$ and 0.001 , respectively.

present in adequate or excessive amounts, further Ca^{2+} application in the enzymatic extract depresses PK activity due to increased formation of complexes between Ca^{2+} and the PK substrates (Ca^{2+} -PEP and Ca^{2+} -ADP), diminishing the affinity of the substrate with the enzyme and therefore reducing its activity (Ruiz et al., 2000).

In conclusion, the physical characteristics of the plastic mulches directly influenced soil and root temperatures in potato plants. In addition, the concentration of cations in the roots (particularly Ca^{2+}) and basal ATPase activity were affected by soil temperature, whereas basal PK was not affected by soil temperature. The use of co-extruded black and white plastic mulch improved the nutritional status of Ca in the roots of potato plants. Finally, the basal ATPase and PK activities in the presence of K^{+} and Ca^{2+} were related with the root levels of these cations.

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