WATER AND CARBON DIOXIDE FLUX IN WATER—STRESSED POTATO PLANTS[1] *

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Resumen

Se cultivaron plantas de papa en macetas y se sometieron a potenciales decrecientes suelo/agua (τ) bajo condiciones controladas. Se aplicaron dos tratamientos de intensidad de luz: 1000 y 400 μE/m²s, dos humedades absolutas: 9.30 y 15.40 g/m³ durante el día (16 horas), y 9.64 y 11.79 g/m³ en la noche. El potencial de agua del follaje (ψ) varió con la intensidad de la luz y la humedad del aire y estuvo correlacionado con τ. Sin embargo, las plantas provenientes del tratamiento de aire húmedo mostraron una relación entre ψ y τ siguiendo líneas rectas, en tanto que las provenientes de aire seco siguieron curvas hiperbólicas, para ambas intensidades de luz: las últimas tuvieron una tendencia a llegar a los umbrales de los potenciales de agua del follaje correspondientes al cierre de los estomas (ψ th) con valores de τ más altos que cuando estuvieron bajo condiciones de humedad elevada. Las tasas de transpiración (E) resultaron afectadas por la humedad del aire y la intensidad de la luz, y siguieron curvas hiperbólicas cuando se relacionaron con ψ. Los resultados muestran que se puede aplicar una analogía de la ley de Ohm a las plantas de papa, al menos bajo las condiciones estudiadas. En general, las plantas jóvenes (fase vegetativa) y las maduras (fase de floración) no mostraron diferencias estadísticas significativas para las comparaciones efectuadas, sin embargo, la tasa fotosintética (P) tuvo comportamientos diferentes entre plantas jóvenes y maduras respecto a la conductividad del follaje (Kᶜ), siguiendo curvas hiperbólicas y líneas rectas, respectivamente; por otra parte, P siempre aumentó conforme incrementó Kᶜ. Hubo fuertes diferencias en el ingreso de CO₂ bajo condiciones de una elevada Kᶜ con relación a los dos tratamientos de luz.

Introduction

Physiological characteristics of potato plants have been investigated by many researchers. Potato is a C_3 plant with photorespiration based on its high CO_2 compensation point; yet its productivity is high and even compared to that of some C_4 crops (28). There are proportional hyperbolic increases in transpiration and photosynthesis rates of potato plants with increasing irradiance up to 85μ E/cm^2 s; water use efficiency, when considered at a constant vapour pressure gradient, increased with increasing irradiance.

Soil water movement, water uptake by roots, water movement through the plant, transpiration, and characteristics of the atmospheric environment are necessary data to study water flow in the soil-plant-atmosphere continuum (SPAC). Because of limited knowledge of the water pathway in the plant, the analysis has been based on Ohm's law analogue (10).

Examining the validity of Ohm's law analogue, Hailey et al. (7) showed different responses by different plants and environments, finding conflicting views using the model to describe liquid water flow through plants during transpiration. Other authors (3, 16, 17, 22) continued finding contradictory results later. Therefore, complete interpretation is difficult because of few data involving small numbers of plants. The present report deals with the influence of plant water status on the control of transpiration and photosynthetic rates under different light intensity and air humidity treatments in potato plants grown in drying soil.

Materials and methods

The experimental plants were a commercial variety of potato "King Edward." Single-eye cores of uniform size were sprouted on a moist sand tray after being dipped in Benomyl solution. Ten days later sprouted cores were transferred to plastic pots with 3.5 kg of air-dried Kettering loam soil, 5 g of ammonium nitrate (NH_4NO_3) and 5 g of potassium hydrogen phosphate (K_2HPO_4). Mature plants were planted on March 12, 1976 (60 pots) and young plants on March 26, 1976 (60 pots), and were grown in the glass-house for 11 weeks and 9 weeks respectively, receiving water daily up to pot capacity (–0.05 bars).

Three days before starting the measurements, mature plants initiated flowering, the pots were placed under growth-chamber conditions for acclimatizing. The growth chambers were kept at 15 and $20°C$, night and day, respectively, with photoperiod of 16 hours. Two light intensity treatments were carried out: 1000, and 400μ E/m^2 s (400 – 700 nm Lambda Inst. sensor); two absolute humidities: 9.30 and 15.40 g/m^3 (continuously monitored with an aspirated wet and dry bulb psychrometer) during the day and 6.94 and 11.79 g/m^3 at night.

After reaching a steady state condition the evaporative flux density per unit leaf area (E) was estimated over a period of two hours from the change in weight of the pot and plant. It was assumed that evaporation from the soil surface was negligible because it was covered by polyethylene granules.

The temperature difference between the leaf canopy and ambient air was continuously measured to within $0.05°C$ with four pairs of 40 s.w.g. constant – chromed P differential thermocouples connected in parallel: one junction of each pair was in the air, the other one threaded 4 mm into the lamina of leaves of different ages at different parts of the canopy. Two young expanding leaves and two mature fully expanded leaves (top leaflets) were used for measuring stomatal diffusive resistances (rs) (replicated two times) with a diffusion porometer (13). The same leaves were used for measuring photosynthetic rate (P) and leaf water potential (ψ). Photosynthesis was determined by uptake of radioactive carbon dioxide after feeding 0.75 cm^2 of leaf for 15 s at a flow rate of 100 ml/min with air containing 300 ppm of $^{14}CO_2$ at a specific activity of 0.83 mCi/m mole using a modification of earlier designs made by Shimshi (25). Rates of photosynthesis were calculated from ^{14}C concentrations in the leaves and were expressed as mg CO_2 dm^2 h. Leaf water potential was determined with a pressure bomb (24).

Then the plant was removed from the pot and leaf area was measured through a leaf area meter (Patton Ind, Pty Ltd.) Soil water contents were measured on duplicate samples taken from the top, middle and bottom of the pot. Soil water potentials (τ) were estimated from the relationship between soil-water content and soil-water potential determined with a pressure membrane apparatus. The Fick's first law of diffusion is valid to describe the flux in the gaseous phase from the leaf to the atmosphere:

$$E = \frac{\Delta \bar{x}}{r_a + r_c}$$

where $\Delta \bar{x}$ (g/m^3) is the difference in water vapour content between the ambient air (χ_a) and air at the evaporating surfaces within the leaves (χ_c), which was assumed to be the saturation vapour pressure at the temperature of the canopy; r_a and r_c (s/cm) are resistances to the diffusion of water vapour offered by the canopy boundary layer, and the stomata plus intercellular spaces of the leaves within the canopy, respectively. The air close to the plants was stirred vigorously, therefore r_a was neglected (16).

The relationship between r_s and r_c was:

$$\ln r_c = 1.15 + 0.06 \ (\pm 0.002) \ r_s; \ (r^2 = 0.79**)$$

The model of Ohm's law analogue (10) proposes that the steady state flux of water from the soil to the evaporating surfaces within the leaves can be calculated from:

$$F.R. = \tau_s - \psi_c$$

in which F, the flux of water through the plant, is obtained by E; τ_s and ψ_c are the mean water potentials of the soil and leaf canopy, respectively; R is the sum of R_s (soil water resistance) plus R_p (plant water resistances.)

Results and discussion

Leaf water potential and canopy diffusive conductance

Figure 1 and Table 1 depict the relationship between k_c and ψ. There was higher canopy diffusive conductivity under greater light intensity in both young and mature plants. According to Fisher (6), light stimulates the uptake of potassium ions into the guard cells, and in conjunction with a suitable ion creates turgor changes that cause stomatal opening.
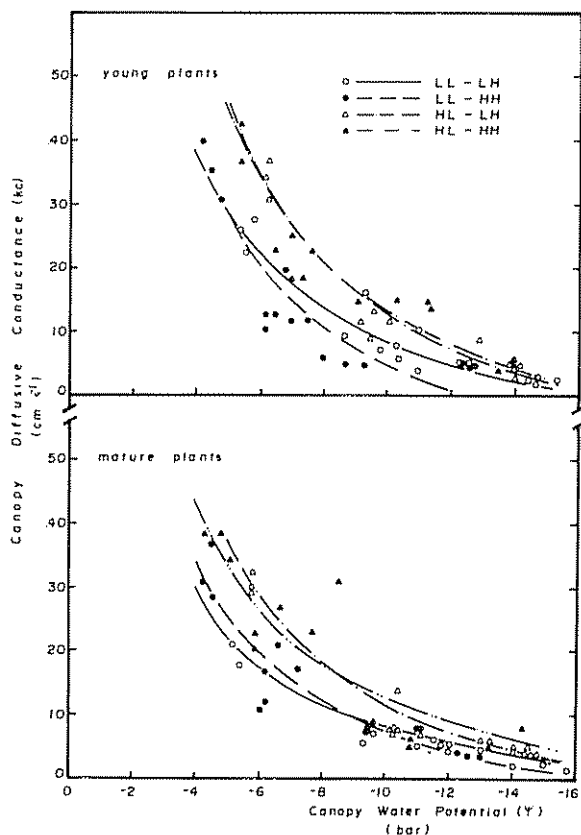
Fig 1.

When water is not limiting, the stomata respond predominantly to light (27), but at low ψ stomata are controlled mainly by plant water stress (26). This last conclusion possibly explains why in Fig. 1, the curves tend to approach. Air humidity did not affect significantly the canopy diffusive conductance in relation to ψ However, at low values of ψ, and under low light intensity, there were tendencies to have larger k_c in the treatment of low humidity in relation to the other one. That means a variation in the threshold canopy water potential for stomatal closure (ψ th) with varying environmental conditions. In young plants, the threshold canopy water potentials were −10 bars at low light and high humidity treatment and −12 bars at low light and low humidity treatment using $k_c = 0.05$ cm/seg for ψ th (14) (while, for mature plants ψ th were −11.2 and −12.5 bars, respectively.) Stomatal closure must be affected by air humidity, because of the dependence on transpiration rate of vapor pressure gradient on leaf surface. Vapor pressure gradient influences transpiration rate, and an increase in E affects ψ that can result in stomatal closure. Different species behave differently under changes in humidity (8); for

instance, potato plants do not show a similar behaviour as sorghum (20), where ψ th is quite evident.

Because of the dependence of k_c on ψ, it is to be expected that ψ and E would also be correlated (Figure 2 and Table 1.).

Photosynthesis, canopy diffusive conductance and canopy water potential

There was similarity in the relationships between P and ψ (Figure 3 and Table 1) and those between k_c and ψ (Figure 1): both followed hyperbolic
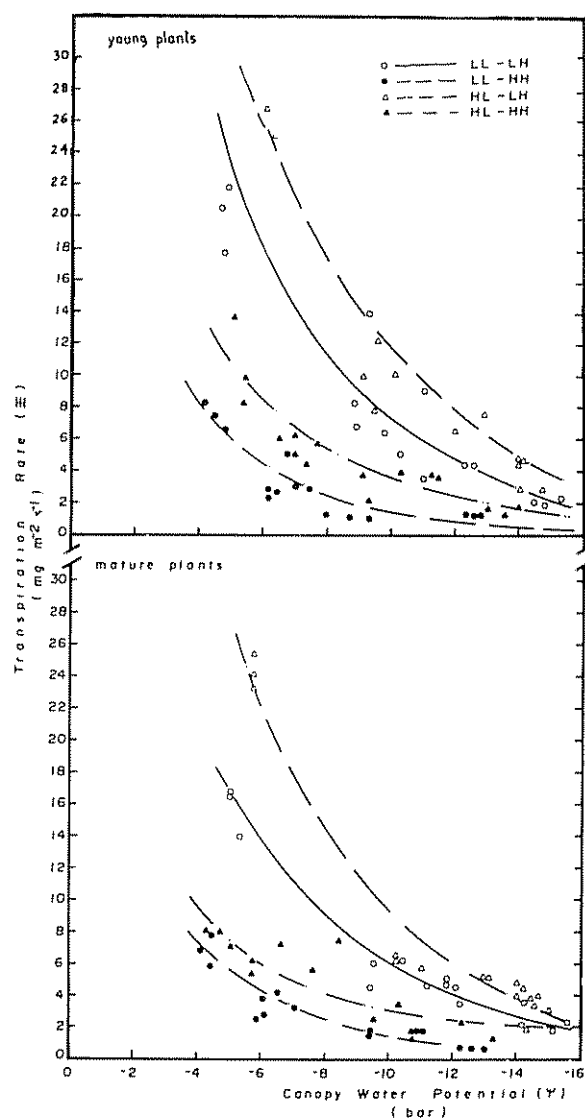

Fig 2.

Table 1.   Equations related to the curves from Fig. 1 to 5 for young and mature plants, high and low light intensities, and high and low humidities.

Young Plants	and	Mature Plants
High Light (HL)	and	**High Humidity (HH)**

$k_c = -0.20 + 3.30/\psi;$ $r = 0.90^{**}$ $k_c = -0.084 + 2.11/\psi;$ $r = 0.89^{**}$
$P = 12.78 + 4.15 \ln k_c;$ $r = 0.89^{**}$ $P = 0.058 + 24.46 k_c;$ $r = 0.96^{**}$
$E = -3.71 + 71.53/\psi;$ $r = 0.92^{**}$ $E = -1.12 + 43.59/\psi;$ $r = 0.86^{**}$
$\psi = 5.81 + 0.67\tau;$ $r = 0.95^{**}$ $\psi = 5.18 + 0.62\tau;$ $r = 0.96^{**}$
$P = -4.14 + 76.92/\psi;$ $r = 0.97^{**}$ $P = -1.91 + 52.46\psi;$ $r = 0.89^{**}$

Low Light (LL)	and	**High Humidity (HH)**

$k_c = -0.17 + 2.19/\psi;$ $r = 0.93^{**}$ $k_c = -0.11 + 1.81/\psi;$ $r = 0.93^{**}$
$P = 7.81 + 2.05 \ln k_c;$ $r = 0.91^{**}$ $P = 0.27 + 17.41 k_c;$ $r = 0.96^{**}$
$E = -3.27 + 45.90/\psi;$ $r = 0.91^{**}$ $E = -2.23 + 38.11/\psi;$ $r = 0.94^{**}$
$\psi = 5.16 + 0.61\tau;$ $r = 0.97^{**}$ $\psi = 4.60 + 0.60\tau;$ $r = 0.97^{**}$
$P = -1.26 + 31.80/\psi;$ $r = 0.94^{**}$ $P = -1.79 + 33.07/\psi;$ $r = 0.94^{**}$

High Light (HL)	and	**Low Humidity (LH)**

$k_c = -0.20 + 3.31/\psi;$ $r = 0.97^{**}$ $k_c = -0.14 + 2.55/\psi;$ $r = 0.99^{**}$
$P = 12.50 + 3.58 \ln k_c;$ $r = 0.91^{**}$ $P = -0.44 + 29.47;$ $r = 0.99^{**}$
$E = -12.47 + 239.02/\psi;$ $r = 0.96^{**}$ $E = -10.27 + 196.98/\psi;$ $r = 0.99^{**}$
$\psi = 10.27\tau + 0.11;$ $r = 0.96^{**}$ $\psi = 10.46\tau + 0.13;$ $r = 0.99^{**}$
$P = -4.95 + 90.10/\psi;$ $r = 0.95^{**}$ $P = -4.60 + 75.56/\psi;$ $r = 0.98^{**}$

Low Light (LL)	and	**Low Humidity (LH)**

$k_c = -0.12 + 2.07/\psi;$ $r = 0.95^{**}$ $k_c = -0.07 + 1.46/\psi;$ $r = 0.98^{**}$
$P = 7.89 + 2.11 k_c;$ $r = 0.92^{**}$ $P = -0.31 + 23.10 k_c;$ $r = 0.97^{**}$
$E = -8.63 + 159.28/\psi;$ $r = 0.94^{**}$ $E = -5.04 + 109.94/\psi;$ $r = 0.99^{**}$
$\psi = 9.19\tau + 0.11;$ $r = 0.92^{**}$ $\psi = 9.65\tau + 0.13;$ $r = 0.98^{**}$
$P = -2.40 + 45.02/\psi;$ $r = 0.93^{**}$ $P = -2.08 + 34.13/\psi;$ $r = 0.98^{**}$

k_c = canopy conductivity
ψ = canopy water potential
P = photosynthetic rate
E = transpiration rate
τ = soil water potential
r = correlation coefficient

curvature. Photosynthesis was higher under high light intensity in both air humidities and four young and mature plants, mainly regarding high ψ. Air humidity influenced slightly photosynthesis at high values of ψ, producing higher[i] values of P under both light intensities for young plants. This influence was not so evident for mature plants.

The decrease of P with ψ is, according to Moorby et al. (21), that there is a gradual decrease in P with increased stress.

The photosynthetic rate had a different behaviour for young and mature plants under the variation of k_c (Figure 4 and Table 1). While the fitted curves were hyperbolic for young plants, they were straight lines for mature ones. P and k_c decrease with leaf age and the decrease of P with leaf age is often associated with a reduction in the activity of photosynthetic enzymes and increase in leaf diffusive resistance (21). Thus, as mature plants have more mature leaves, different curves in young and mature plants are expected.
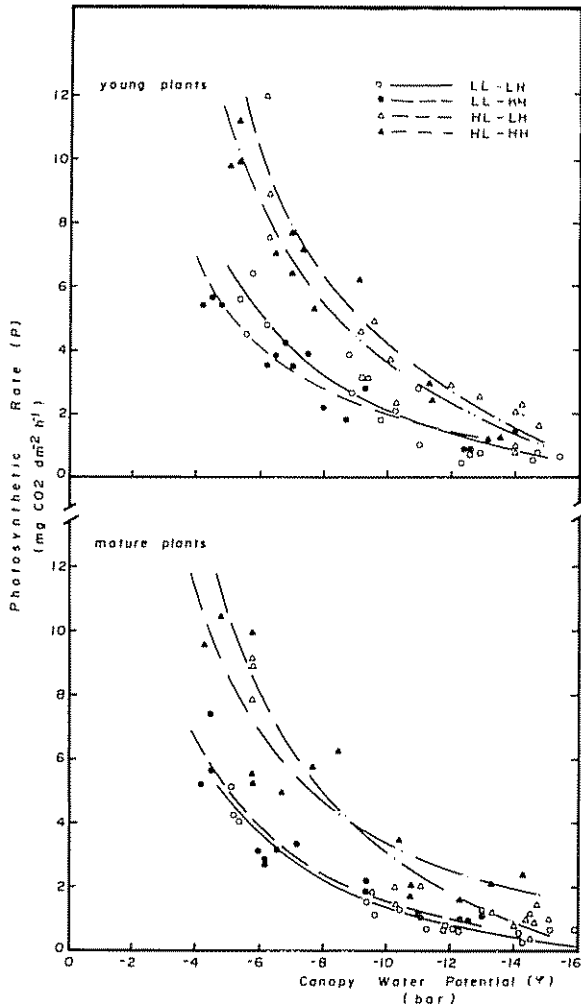
Fig 3

Fig 4

There were strong differences in the CO$_2$ uptake under high k_c, regarding the two light intensity treatments, while at low k_c (or at the threshold water potentials) P was very low, because the stomata were closed. Air humidity did not have significant influence on P as occurred in relation to ψ, (Figures 3 and 4).

Relationships among soil water potentials, leaf water potentials, and transpiration rates

Canopy water potential (ψ) varied with light intensity and air humidity (Figure 5 e and Table 1). Plants subjected to high air humidity had 1 bar ψ difference, approximately, for the young plants and a little less for the mature ones, under the two light intensity treatments. Plants subjected to low
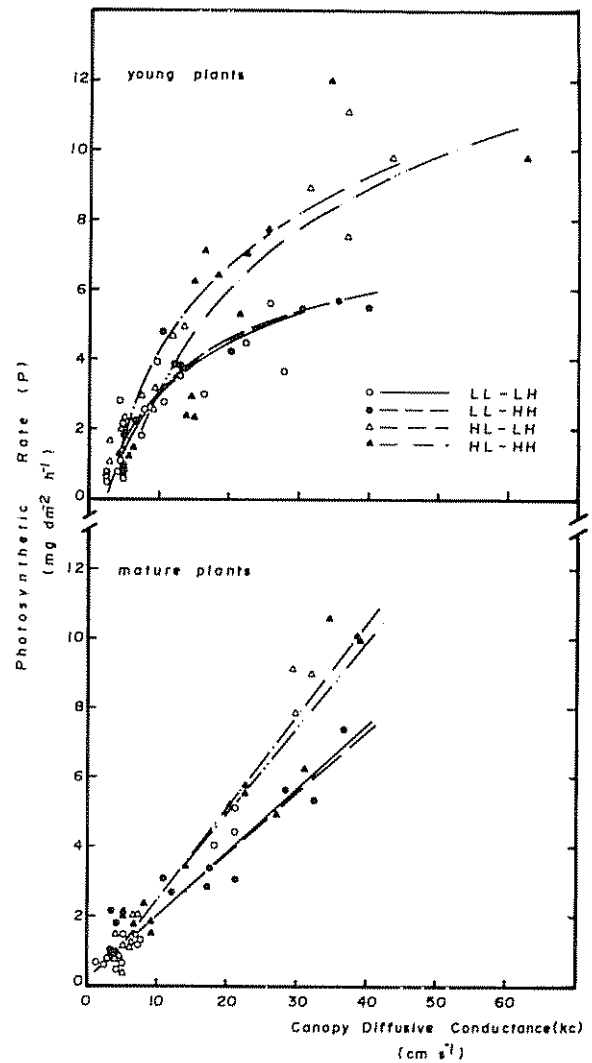
humidity had similar behaviour in relation to the influence of light intensity, the high light treatment presenting the highest ψ; however, there was a tendency to follow a hyperbolic curve instead of a straight line from the wet air treatment. So, plants under high atmospheric evaporative demand were closer to the threshold canopy water potential at high τ, because of the lack of balance between E and water uptake which forced plants to lose water from the tissue and to show visible signs of water stress. According to Epstein and Grant (5), potato plants exhibit water stress when τ drops below —0.25 bars under field conditions. Plant water stress is caused by either excessive loss of water from the plant or an inadequate supply of water to the roots; thus, the internal water equilibrium of the plant is a
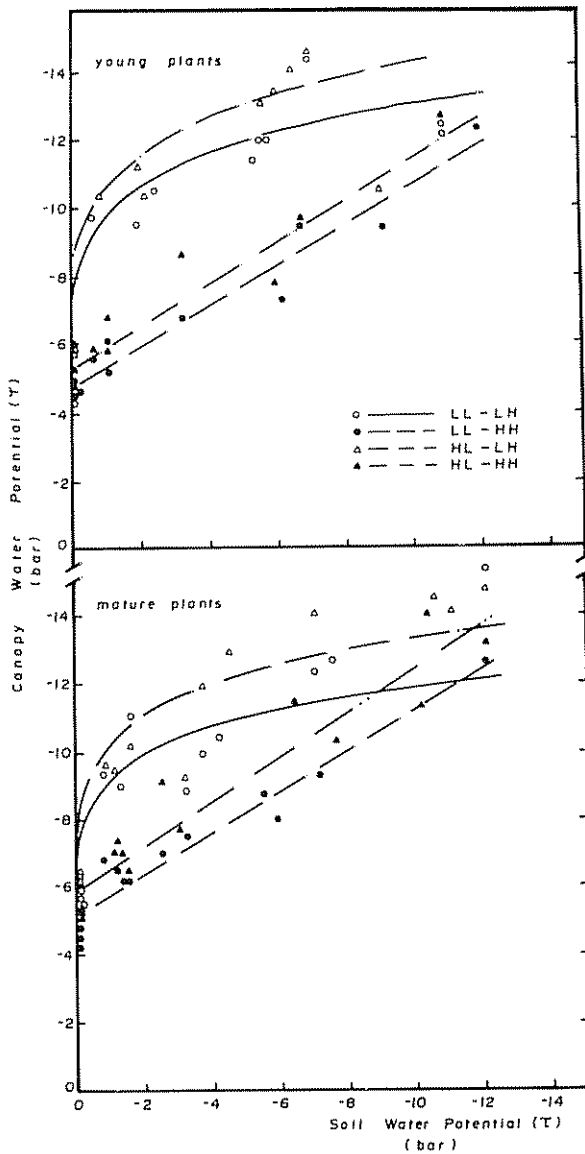
Fig. 5

The nine crops used by Hoffman showed different ranges of variation in water, osmotic and turgor potentials in leaves under air humidity treatments; the difference in ψ under high and low air humidity treatments ranged from 1 bar in onion, radish and wheat to almost 8 bars in corn; the leaf osmotic potential of pepper and the leaf turgor potential of cotton were exceptions comparing the behaviour of the nine crops studied by Hoffman.

Figure 2 depicts the influence of light and humidity treatments on the transpiration rate (E) under variation in ψ. Equal E values had different ψ in relation to different atmospheric evaporative demands; ψ, for young plants and E = 6 mg/m^2 s, was —5.0, —7.5, —11.0 and —13.0 bars under low light — high humidity, high light — high humidity, low light — low humidity and high light — low humidity treatments, respectively. Mature plants had —4.8, —6.0, —10.0 and —12.0 bars for the same E = 6 mg/m^2 s and following for young plants, they were straight other hand, the largest differences in E under the same ψ occurred at high ψ values. The curves were hyperbolic in all cases. Janes (12) found that the relationship between E and water potential gradient from the soil to the leaf ($\Delta\psi$) in pepper plants varied with light intensity. Elfving et al. (4), working with Citrus sinensis, found deviations of the Van den Honert model, when τ was lower than —0.3 bar or soil temperatures were lower than 15°C, with more negative ψ than the predicted transpirational flux. Liu et al. (18) reported that at a given E, $\Delta\psi$ was always higher in the afternoon, when the New York Vineyard plants were rehydrating under field conditions. However, Lawlor and Lake (16) concluded that decreasing E by changing light intensity or humidity had no effect on ψ of Lolium, Trifolium and Lysimachia, this means that flux of water-resistance (R_D) through the plants varied and Ohm's law analogue did not apply. Brower (1) and Macklon and Weatherley (19) suggested that the change in R_D with change in E is due to alterations in number and size of pores that are functioning in the roots. Water stress increases tension in the xylem and some water columns in the vessels break or cavitate and stress can be aggravated by the increased resistance to water flow (11). On the other hand, Dimond (2) reported that only a small Δ ψ is required to maintain flow in large bundles in tomato plants; water flows through primary xylem in accordance to Poiseuilles law. Each plant reacts differently to the environment and possibly Ohm's law analogue does not always apply. The magnitude of flow is governed by resistances (membranous, frictional and diffusive) and the energy gradient imposed across the xylem (12). It is obvious that Ohm's law analogue is an oversimplification of the soil-plant-atmosphere continuum system (23),

function of both soil and atmosphere (15). Sugar beet behaviour was different with straight lines in both air humidity treatments used by Lawlor and Milford (17). Possibly, sugar beet is more resistant to water stress than potato; ψth seems lower for sugar beet than for potato. The same authors did not find significant differences in ψ under the influence of air humidity treatments. This conclusion is opposite to these results and those obtained by Hoffman (9) who worked with nine crops in sunlit climate chambers; he reported that plants grown at low humidity had lower ψ than plants grown at high humidity. However, different species respond differently to the variation of atmospheric humidity.

and cannot always describe adequately the flow in the plant and its environment.

Summary

Potato plants were grown in pots with decreasing soil water potential (τ), under controlled conditions. Two light intensity treatments were carried out: 1000 and 400 ψ E/m² s; two absolute humidities: 9.30 and 15.40 g/m³ during the day (16 hours), and 6.94 and 11.79 g/m³ at night. Canopy water potential (ψ) varied with light intensity and air humidity and was correlated with τ. However, plants from wet air treatment showed a relationship between ψ and τ following straight lines and those from dry, hyperbolic curves, for both light intensities: the latter had a trend to reach threshold canopy water potentials for stomatal closure (ψ th) with higher values of τ than under high humidity. Transpiration rates (E) were affected by air humidity and light intensity and followed hyperbolic curves when related to ψ. The results showed that Ohm's law analogue can be applied for potato plants, at least under the conditions studied. In general, young (vegetative phase) and mature (flowering phase) plants did not show statistically significant differences for the comparisons made; however photosynthetic rate (P) had different behaviour for young and mature plants in relation to canopy conductivity (k_c), following hyperbolic curves and straight lines, respectively; on the other hand, P always increased with k_c. There were strong differences in the CO₂ uptake under high k_c, regarding the two light treatments.

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