RELATIONSHIP BETWEEN LEAF GAS EXCHANGE CHARACTERISTICS AND PRODUCTIVITY OF POTATO CLONES GROWN AT DIFFERENT TEMPERATURES [1]

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Abstract

The rate of dark respiration (Rd) and net photosynthesis (Pn) at various leaf temperatures was examined in three potato clones (*Solanum tuberosum* L.) differing in heat tolerance. Plants were grown at low (25/12 C, day/night) and high (35/25 C) greenhouse air temperatures for five weeks, beginning two weeks after tuberization. Gas exchange characteristics were measured by manometric and infrared gas analyzer techniques. Respiration:photosynthesis ratios were calculated as indicators of leaf carbon balance. High greenhouse temperature reduced whole plant and tuber growth rate of all clones, however, the reduction was highest in the cultivar Russet Burbank (heat sensitive). Gas exchange characteristics did not explain differences in heat tolerance. The heat tolerant cultivar Desiree had Rd similar to Russet Burbank, while the clone DTO-28, also heat tolerant, had lower Rd of mature leaves than Russet Burbank or Desiree. However, all clones had similar Rd of immature leaves. There was no apparent relationship between heat tolerance and Pn for the three clones. DTO-28 had lower respiration:photosynthesis ratios of immature and mature leaves than Russet Burbank 4 weeks after the start of the high temperature treatment. Desiree had respiration:photosynthesis ratios as high as Russet Burbank. At different sampling times, Rd increased in a linear and curvilinear manner with increasing leaf temperature up to 40 C. Heat tolerant and sensitive clones had similar rates of increase in Rd with increasing leaf temperature. Simultaneous measurement of Rd and Pn did not help explain differences in heat tolerance among clones. However, determination of respiration:photosynthesis ratios may help explain the physiological basis for heat tolerance of some clones.

Compendio

La tasa de respiración en oscuridad (Ro) y fotosíntesis neta (Fn) a varias temperaturas foliares fue examinada en tres clones de papa (*Solanum*

tuberosum L.) que difieren en su tolerancia al calor. Las plantas fueron desarrolladas en invernaderos de temperaturas bajas (25/12 C día/noche) y altas (35/25 C) por cinco semanas, empezando dos semanas después de la tuberización. Las características de intercambio gaseoso fueron medidas por técnicas manométricas y de análisis infrarrojo de gases. Las proporciones de respiración:fotosíntesis fueron calculadas como indicadoras del balance carbónico de la hoja. La temperatura alta del invernadero redujo la tasa de crecimiento de los tubérculos y de la planta en general en todos los clones, aunque la reducción fue mayor en el cultivar Russet Burbank (sensible al calor). Las características de intercambio gaseoso no explicaron las diferencias en la tolerancia al calor. El cultivar Desiree, tolerante al calor, tuvo una Ro similar a la del cultivar Russet Burbank, mientras que el clon DTO-28, también tolerante al calor, tuvo una Ro menor que la de Russet Burbank o Desiree en las hojas maduras. Sin embargo, todos los clones mostraron una Ro similar en las hojas inmaduras. No hubo una relación aparente entre la tolerancia al calor y la Fn de los tres clones. DTO-28 presentó menores proporciones de respiración:fotosíntesis que Russet Burbank en las hojas maduras e inmaduras, cuatro semanas después de iniciado el tratamiento con temperatura alta. Las proporciones de respiración:fotosíntesis de Desiree fueron tan altas como las de Russet Burbank. La Ro aumentó en forma lineal y curvilínea cuando se incrementó la temperatura foliar hasta 40 C, en diferentes épocas de muestreo. Los clones tolerantes y sensibles al calor mostraron tasas similares de incremento de la Ro cuando se aumentó la temperatura foliar. La medición simultánea de Ro y Fn no ayudó a explicar las diferencias en la tolerancia al calor de los clones. Sin embargo, la determinación de las proporciones de respiración:fotosíntesis puede ayudar a explicar la base fisiológica para la tolerancia al calor de algunos clones.

Introduction

Potatoes have traditionally been considered a cool season crop, and tuber production of most cultivars is greatly reduced at high temperatures (2, 11). However, potato cultivars or clones able to maintain relatively high yields at high temperature have been identified in field trials (10, 12, 15). Efforts to breed progeny with high levels of heat tolerance are hindered by the inefficient nature of field trials (15, 17), a lack of understanding of the physiological basis for heat tolerance (14), and the difficulty in incorporating complex gene combinations for stress tolerance with agronomic performance (14). Identification of physiological traits associated with heat tolerance would greatly enhance efforts to select heat tolerant clones.

Leach, *et al.* (9) developed a detailed carbon budget for potatoes showing that plant growth rate is closely related to the rates of net photosynthesis

(Pn) and dark respiration (Rd). Under field conditions 15 to 40% of carbon assimilated is utilized in Rd (3, 20, 24). Rd increases rapidly with temperature, roughly doubling for each 10 C increase between 10 and 35 C (20, 24). Conversely, Pn shows a broad temperature optimum at 20 to 30 C, but rates fall rapidly at higher temperatures (4, 9, 24). Thus, reduced photoassimilate production through photosynthesis and increased utilization of photoassimilates in respiration are factors that limit productivity of potatoes at high temperature.

Differences in heat tolerance among potato clones have been related to differences in Pn and Rd. Hammes and De Jager (7) reported that a heat sensitive clone exhibited a larger decline in Pn than two heat tolerant clones as leaf temperature was increased from 15 to 40 C to simulate a hot day. Wolf, *et al.* (25) found that Pn of a heat sensitive clone declined when grown at high greenhouse temperatures, but heat tolerant clones were not significantly affected. In the same study, Rd was significantly higher in all clones at high compared to low greenhouse temperatures. However, heat tolerant clones exhibited less increase in Rd than a heat sensitive clone.

Gas exchange characteristics are affected by the tissue used for measurements (8). However, little is known about the changes in carbon exchange rates for different ages of leaf tissue in relationship to heat tolerance. Therefore, it is important to determine if potato clones exhibit differences in gas exchange characteristics in both immature and mature leaves.

The objectives of this study were to: 1) determine if Rd and Pn of immature and mature leaves were related to heat tolerance of potato clones, 2) determine if respiration:photosynthesis ratios can be used as a method to detect differences in carbon balance among clones, and 3) determine if heat tolerant clones exhibit a different rate of increase in Rd with increasing temperature.

Materials and Methods

Three potato clones were selected for study based on their reported tolerance to heat stress. The clone DTO-28 was selected at the International Potato Center and is considered to have a high level of heat tolerance (2, 12). The cultivar Desiree has performed well in hot climates (11, 17), while the cultivar Russet Burbank is considered to be relatively susceptible to heat stress (2). Seed tubers were sprouted in the dark at 10 C, and uniform 12g seed pieces with one sprout were removed with a melon scoop. Seed pieces were planted in flats containing a sand, vermiculite and peat moss soil mixture (2:2:1 by volume). Plants were grown in a greenhouse at 25/12 ± 3 C (day/night) for 28 days, then the most uniform plants were transplanted to 6.6 liter pots containing the same sand, vermiculite and peat moss soil mixture. At transplanting, each plant received 100 ml of 20N/8.7P/16.6K soluble fertilizer solution (400 ppm N). For the remain-

der of the experiments, plants were fertilized based on petiole nutrient concentration. Greenhouse temperatures were maintained at 25/12 C day/night up to the start of the temperature treatments.

Total and tuber dry matter production were measured over a five week period, beginning 58 days after planting. Plants had begun to initiate tubers approximately two weeks prior to the first measurements. Six plants were harvested prior to the start of the temperature treatments, and an additional six plants were harvested from each temperature treatment after five weeks of growth. Plant (vines, roots, and stolons) and tuber dry weights were determined after drying at 105 C for 6h, then at 70 C for 3d. Total plant and tuber growth rates were calculated by subtracting initial dry weight from final dry weight, then dividing by number of days grown at the temperature treatments.

Temperature treatments were begun 58 days after planting. Six uniform plants of each clone were moved to an adjacent greenhouse where air temperatures were $35/25 \pm 3$ C. An additional six plants per clone remained in the cool greenhouse at $25/12 \pm 3$ C. Plants were placed in boxes, and moist sand packed around the pots. Plants were arranged in a randomized complete block design with six replications. Additional plants were placed around the edge of the soil boxes to minimize border effects. Soil temperatures were maintained at 16 ± 2 C by a thermostatically controlled system that circulated water through copper tubing placed next to the pots. The surface between pots was covered with Styrofoam insulation to minimize temperature fluctuation. Soil and air temperatures were monitored at 2 hour intervals with copper constantan thermocouples and CR-5 data recorder (Campbell Sci., Logan, UT). Throughout the experiments photoperiods were kept at 15 hours by supplementing natural light with a mixture of metal halide and fluorescent lights. Midday light levels at the top of the canopy were 1250 ± 250 µE m^{-2}s^{-1} (PAR, 400-700 nm). The supplemental lights provided approximately 500 µE m^{-2}s^{-1} of PAR.

Gas Exchange Measurements

Pn and Rd were measured with an LI-6200 portable infrared gas analyzer (LI- COR, Lincoln, NE). Measurements were conducted immediately before the start of the temperature treatments, and at two and four weeks after the start of the temperature treatments. Gas exchange measurements for each of the six replications were made on each of six consecutive days. Randomization patterns from the greenhouses were maintained during measurements. On measurement dates, plants were moved from greenhouses to a laboratory bench 1 hour before the start of the dark period. Light levels of 1400 ± 200 µE m^{-2}s^{-1} PAR at the top of the canopy were provided by a metal halide light. Air temperature was 22 ± 3 C during the day and night. One immature (3rd from apex) and one mature (7th from apex) leaf on

the main stem of each plant was selected for measurements, and only fully illuminated leaves were used. Rd was measured beginning 1 hour after the start of the dark period and again at 2 hours before the end of the dark period. Entire leaves (leaflets and petiole) were enclosed in a 4 liter Lexan chamber. The petiole base was wrapped in putty to reduce leaks from the closed system. The plant and chamber were wrapped in black plastic to exclude light. The chamber was modified by addition of an aluminum block and thermoelectric coolers (Melcor, Trenton, NJ) to control leaf temperature to ±0.2 C of the desired level (measured at the abaxial surface). Rd was measured at leaf temperatures equaling greenhouse night temperatures (12 C for cool greenhouse, 25 C for hot greenhouse). Leaves were equilibrated for 5 minutes in the dark, then Rd was determined by the rate of increase in chamber CO_2 concentration over two consecutive 1 minute intervals.

Pn was measured 4 to 7 hours after the start of the photoperiod on the same immature and mature leaves used in Rd measurements. Leaves were placed in the chamber and equilibrated for 5 minutes at leaf temperatures equaling the daytime greenhouse temperatures (25 C for cool greenhouse, 35 C for hot greenhouse). Two consecutive measurements were taken, then averaged to provide one observation for each leaf. Carbon dioxide concentration was 325 ± 25 ppm.

After the gas exchange measurements, leaves were detached and area measured with a LI-3000 leaf area meter (LI-COR, Lincoln, NE). Plants were returned to greenhouses after measurements were completed.

Leaf Disk Gas Exchange

Manometric techniques were used to determine the rate of change in Rd with increasing leaf temperature. Rd of leaf disks from plants of one replication were measured on each of six successive days by a modification of the manometric technique of Wilson (23). During measurements the randomization pattern from the greenhouse was maintained. Two hours into the light period, one terminal leaflet from the most recently expanded leaf of each plant (5th from apex) was detached and the petiole placed in a cup of distilled water. Only fully illuminated leaflets were sampled. Leaflets were transported to the laboratory and placed in the dark at 4 C for 30 minutes. Four leaf disks (each 0.5 cm²), were excised with a No. 4 cork borer and placed in the outer well of a sterile 15 ml single sidearm respirometer flask containing 2 ml of sterile distilled water. The four leaf disks were placed with the lower surface facing up. Flasks were wrapped in a double layer of aluminum foil, and attached to a Gilson respirometer (Gilson Medical Electronics, Middleton, WI 53562).

Rd of leaf disks was measured at four leaf temperatures (24, 30, 35, 40 C) at the second and fourth week after the start of the greenhouse temperature treatments. Four new leaf disks were excised and placed in flasks

between each leaf temperature. Leaf disks were equilibrated for 30 minutes at each temperature before measurements were begun. Between measurements, leaflets were held in the dark at 4 C with the petiole submerged in distilled water. Preliminary experiments showed that Rd of leaflet tissue was not affected by up to 3 hours of darkness under the conditions described. After the measurements, leaf disks were removed from flasks and dried at 80 C for 24 hours prior to weighing.

During measurements, a CO_2-free atmosphere was maintained in the respirometer flask by placing 0.8 ml of 20% KOH solution in the center well and sidearm. A filter wick was placed in the center well, and flasks were vigorously shaken during measurements to promote rapid gas exchange. Two thermobarometers, containing all components except leaf tissue, were included to allow corrections for differences in temperature and pressure between flasks and manometers.

The number of O_2 atoms in a given volume changes with temperature, and readings were corrected for this based on the ideal gas law. Mean values were converted to mg CO_2 $dm^{-2}h^{-1}$, based on the assumption that the respiratory quotient was equal to 1.0.

Statistical Analysis

The experiments were repeated twice over a 5 month period. Statistical analysis indicated no significant interactions, so the two runs were combined to provide a total of twelve replications.

Data for each experiment and each date were analyzed separately with the analysis of variance procedure of the MSTAT program (6). Greenhouse temperatures were treated as locations, leaf temperatures as main plots (manometric data only), and clones as subplots. Duncan's Multiple Range Test was used to compare treatment means for each clone. Regression analysis was performed on the manometric data to determine the relationship between leaf temperature and Rd for each clone.

Results and Discussion

Effect of Greenhouse Temperature on Plant Growth

High temperature reduced whole plant growth rate of all clones (Table 1). The reduction was largest in Russet Burbank, a clone previously reported to be sensitive to heat stress (2). DTO-28 was the only clone that did not have significantly lower plant dry weight at high compared to low greenhouse temperatures. In contrast, Ben Khedher and Ewing (2) reported that Desiree, DTO-28 and Russet Burbank exhibited large decreases in plant dry matter production when grown under conditions of high air and soil temperatures. In our study, soil temperatures were maintained at a constant 16 C, which would moderate stress conditions in comparison to those

TABLE 1.—*Dry matter production by three potato clones grown at two temperature regimes.*

Clone	Total[1] Dry Weight (g plant[-1])	Total Growth Rate (g plant[-1] day^{-1})	Tuber Dry Weight (g plant[-1])	Tuber Growth Rate (g plant[-1] day^{-1})
25/12 C				
Russet Burbank	166 a	3.7 a	133 a	3.3 a
Desiree	151 b	3.4 ab	117 b	3.0 a
DTO-28	148 bc	3.3 b	116 b	3.1 a
35/25 C				
Russet Burbank	132 d	2.6 c	90 c	2.1 c
Desiree	136 d	2.9 c	90 c	2.2 bc
DTO-28	139 cd	2.9 c	95 c	2.4 b
High:Low[2]				
Russet Burbank	0.80	0.70	0.68	0.64
Desiree	0.90	0.85	0.77	0.73
DTO-28	0.94	0.88	0.82	0.77

[1]Values are means of twelve replications. Plants were harvested five weeks after the start of the greenhouse temperature treatments.
[2]Ratio of dry weight or growth rate for plants grown under high vs low greenhouse temperature conditions.

employed by Ben Khedher and Ewing. Soil temperatures have been shown to interact with air temperature to affect potato plant growth and dry matter partitioning (19).

Tuber growth rate was more affected by high greenhouse temperature than was whole plant growth (Table 1). All clones exhibited a decline in tuber dry matter production at high compared to low greenhouse temperatures, however, Russet Burbank exhibited the largest decline. Potato clones have been shown to exhibit considerable variation in partitioning of dry matter to tubers at high temperature (2, 12). In selecting for stress tolerance it is important to examine total dry matter production, not just harvestable yield, to avoid discarding germplasm with superior overall productivity (18). To increase tuber productivity at high temperature it will be important to combine high dry matter production and ability to partition dry matter to tubers.

Effect of Greenhouse Temperature on Gas Exchange Rate of Leaves

Rd measured near the end of the dark period was not significantly different than Rd measured after 1 hour of darkness (data not shown), therefore, data are presented for the end of dark period measurements only.

TABLE 2.—*Rates of dark respiration (Rd) of immature (3rd from apex) and mature (7th from apex) leaves of three potato clones grown at two temperature regimes. Values are means of twelve replications and are expressed as mg CO_2 dm^2 h^{-1}.*

Clone	Immature leaves[1]			Mature leaves		
25/12 C	0 wk[2]	2 wk	4 wk	0 wk	2 wk	4 wk
Russet Burbank	0.7 a[3]	0.7 c	0.7 c	0.5 a	0.6 c	0.6 d
Desiree	0.7 a	0.8 c	0.9 c	0.6 a	0.7 c	0.6 d
DTO-28	0.7 a	0.7 c	0.8 c	0.4 b	0.5 c	0.5 e
35/25 C						
Russet Burbank	—	1.5 b	1.8 ab	—	1.2 ab	1.2 b
Desiree	—	1.8 a	1.9 a	—	1.3 a	1.4 a
DTO-28	—	1.6 ab	1.7 b	—	1.1 b	1.0 c

[1]Rd was measured with an infrared gas analyzer at leaf temperatures corresponding to the night greenhouse temperatures.
[2]Rates of dark respiration were measured before the start (0 wk), and at two week intervals after start of greenhouse temperature treatments.
[3]Means within a column followed by the same letter are not significantly different (p=0.05) by Duncan's Multiple Range Test.

Rd of both immature and mature leaves of all clones were higher at 25 C than at 12 C (Table 2). Rd was not closely related to differences in dry matter production among clones. For example, at low greenhouse temperatures Russet Burbank produced the highest total plant growth rates, but had Rd similar to Desiree and higher than DTO-28 on several dates (Table 2). At high greenhouse temperatures all clones had similar total plant growth rates, but Desiree had higher Rd than Russet Burbank or DTO-28 on several dates. Midmore and Prange (16) reported a more than four-fold difference among clones of two potato species in Rd, measured after sixteen hours of darkness. Although Rd in that study was negatively correlated with total dry weight at harvest, Rd alone did not explain all differences in heat tolerance.

Tissue selection is an important factor when trying to detect genotypic differences in Rd. Potato clones exhibited more diversity in Rd of mature leaves than of immature leaves (Table 2). This indicates that gas exchange characteristics of immature leaves may not be as useful as physiological indicators of heat tolerance as gas exchange of mature leaves.

Pn of immature and mature leaves tended to be lower at 35 C than at 25 C, however, the differences were significant in only 2 out of 9 comparisons (Table 3). In contrast, several authors have reported a sharp decline in Pn above 30 C (4, 9, 24). Wolf, et al. (25) also reported that plants acclimated at high growth temperature did not exhibit a large decline in Pn compared to plants grown at lower temperature. They concluded that the

TABLE 3.—*Rates of net photosynthesis (Pn) of immature (3rd from apex) and mature (7th from apex) leaves of three potato clones grown at two temperature regimes. Values are means of twelve replications and are expressed as mg CO_2 dm^2 h^1.*

Clone	Immature leaves[1]			Mature leaves		
	0 wk[2]	2 wk	4 wk	0 wk	2 wk	4 wk
25/12 C						
Russet Burbank	15.7 a[3]	15.8 a	15.8 ab	12.2 a	10.6 a	9.2 b
Desiree	17.9 a	16.6 a	14.6 abc	13.3 a	11.8 a	10.2 ab
DTO-28	16.2 a	17.3 a	18.2 a	12.7 a	13.0 a	11.7 a
35/25 C						
Russet Burbank	—	16.1 a	11.1 c	—	10.6 a	8.4 b
Desiree	—	17.4 a	16.2 ab	—	12.8 a	8.2 b
DTO-28	—	15.5 a	13.3 bc	—	12.1 a	9.6 ab

[1]Pn was measured with an infrared gas analyzer at leaf temperatures corresponding to the day time greenhouse temperatures.

[2]Rates of net photosynthesis were measured before the start (0 wk), and at two week intervals after start of greenhouse temperature treatments.

[3]Means within a column followed by the same letter are not significantly different (p=0.05) by Duncan's Multiple Range Test.

photosynthetic system of potato leaves has the capacity to adapt to high temperatures.

The two heat tolerant clones, DTO-28 and Desiree, tended to have Pn similar to Russet Burbank at both growth temperatures (Table 3). Basu and Minhas (1) reported that although heat tolerant and sensitive potato clones exhibited similar photosynthesis rates, starch accumulated in leaves of heat sensitive clones due to reduced assimilate transport. They speculated that increased starch accumulation in leaves could contribute to higher respiratory losses, which would reduce overall plant dry matter production.

Respiration:photosynthesis ratios were calculated as indicators of the efficiency of fixed carbon utilization. Leaves of heat tolerant and sensitive clones generally had similar respiration:photosynthesis ratios at both greenhouse growth temperatures (Table 4). The exception was at 4 weeks after the start of the high temperature treatment, when DTO-28 had significantly lower ratios in immature and mature leaves than Russet Burbank. Efficient use of fixed carbon would be an important characteristic of heat tolerant clones if tuber yield is source limited at high temperatures. Tuber growth rates of DTO-28 were higher than Russet Burbank at high growth temperatures, although whole plant growth rates were similar (Table 1). In contrast, Desiree and Russet Burbank generally had similar growth rates and respiration:photosynthesis ratios at both growth temperatures. Desiree may be heat tolerant under field conditions because it initiates tubers earlier than sensitive clones, and may escape some of the effects of high temperature (10, 12).

TABLE 4.—*Ratio of dark respiration to net photosynthesis (Rd:Pn) of immature (3rd from apex) and mature (7th from apex) leaves of three potato clones grown at two temperature regimes. Values are means of twelve replications.*

Clone	Immature leaves			Mature leaves		
25/12 C	0 wk[1]	2 wk	4 wk	0 wk	2 wk	4 wk
Russet Burbank	0.046 a[2]	0.048 b	0.048 c	0.044 a	0.055 b	0.066 d
Desiree	0.045 a	0.053 b	0.076 c	0.048 a	0.065 b	0.065 d
DTO-28	0.049 a	0.048 b	0.043 c	0.034 b	0.045 b	0.042 d
35/25 C						
Russet Burbank	—	0.105 a	0.207 a	—	0.119 a	0.165 b
Desiree	—	0.108 a	0.145 b	—	0.104 a	0.205 a
DTO-28	—	0.115 a	0.134 b	—	0.108 a	0.124 c

[1]Gas exchange rates were measured before the start (0 wk), and at two week intervals after start of greenhouse temperature treatments.
[2]Means within a column followed by the same letter are not significantly different (p=0.05) by Duncan's Multiple Range Test.

The lack of relationship between leaf gas exchange rates and whole plant or tuber growth rate of clones in this study indicates that other tissues, or other factors were responsible for the differences in dry matter production observed. The gas exchange rates measured do not account for total plant carbon exchange because the contribution of other photosynthetic and non-photosynthetic tissue was not taken into account. Burton (3) and Sale (20) found that non-photosynthetic tissues, particularly below ground organs, contributed a substantial portion of total potato plant respiration. Leaves at other positions would also contribute substantially to plant carbon balance. Despite the limitations of gas exchange measurements of individual leaves, other authors have reported significant correlations with tuber yield (4).

Carbon assimilation is only one of several plant processes affected by heat stress. Plant hormones, enzymes and cell membranes may all be affected, resulting in reduced dry matter production and partitioning to tubers at high temperatures (5). It is possible that temperature sensitivity of a number of these processes is related to heat tolerance of potato clones.

Effect of Leaf Temperature on Rd of Excised Leaf Disks

Manometric techniques have been widely used for comparative studies of Pn and Rd of plant genotypes (8, 23). This method does not account for contributions to Rd by alternate pathways, and detachment of leaf tissue

(A)

DS: $Y = -15.98 + 1.05X - 0.014X^2$ $R^2 = 0.92$

RB: $Y = -14.31 + 0.96X - 0.013X^2$ $R^2 = 0.98$

DT: $Y = -12.12 + 0.82X - 0.011X^2$ $R^2 = 0.98$

(B)

DS: $Y = -1.14 + 0.15X$ $R^2 = 0.92$

RB: $Y = -1.00 + 0.13X$ $R^2 = 0.98$
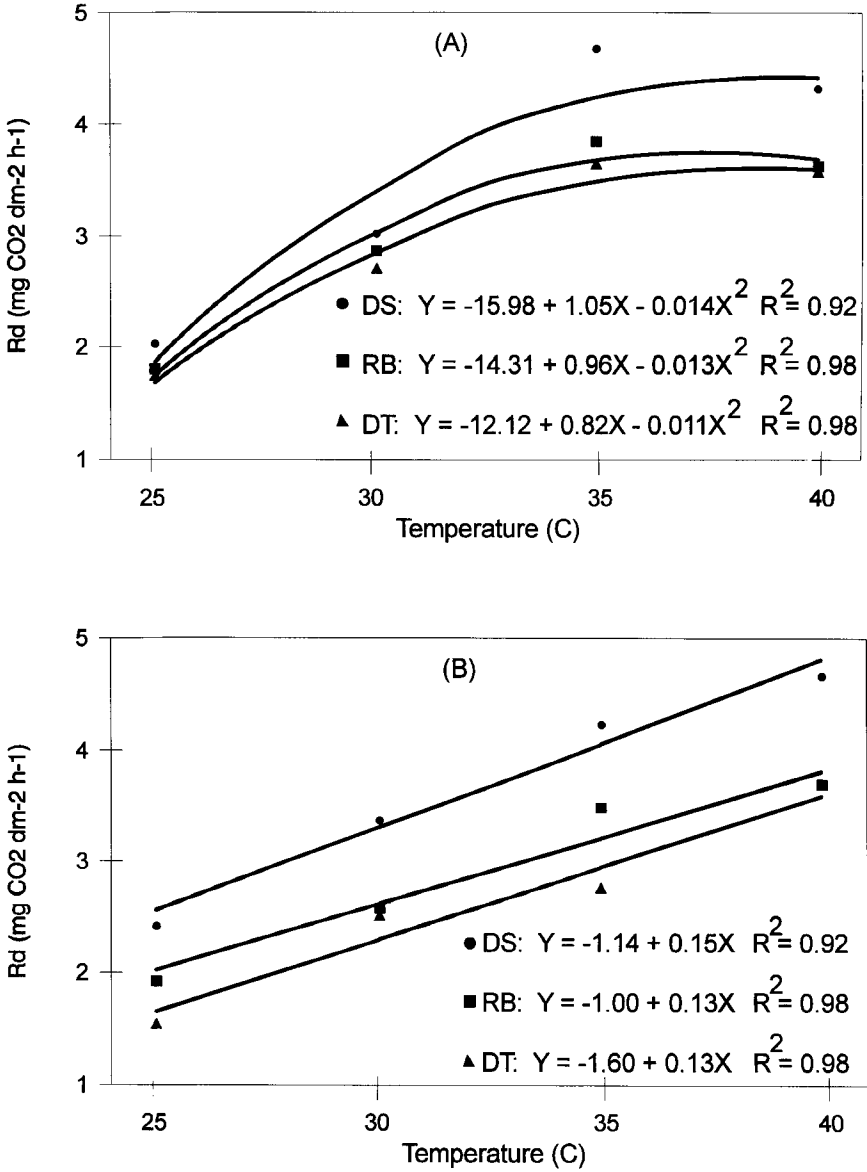
DT: $Y = -1.60 + 0.13X$ $R^2 = 0.98$

FIG. 1. Effect of leaf temperature on rate of dark respiration (Rd) of leaf disks of three potato clones; Desiree (DS), Russet Burbank (RB) and DTO-28 (DT), measured two weeks (A) or four weeks (B) after start of the greenhouse temperature treatments. Values are means of twelve replications and two greenhouse temperatures.

could affect Rd. Despite the limitations of this technique, Rd of leaf disks measured at 25 C in this study were similar to those found for intact leaves of these same clones with an infrared gas analyzer (22).

Rd increased in a curvilinear manner with leaf temperature from 25 to 40 C, two weeks after the start of greenhouse temperature treatments (Fig. 1A). At four weeks, Rd response to leaf temperature was linear (Fig. 1B). The 95% confidence intervals for the slopes of the fitted regression lines overlapped, indicating that the rate of increase in Rd with increasing temperature was similar in all three clones (Fig. 1). Winkler (24) also found no differences among three potato clones in rates of increase in Rd with increasing leaf temperature between 10 and 36 C. In contrast Wolf, *et al.* (25) found that the cultivar Up to Date (heat sensitive) had a greater increase in Rd at high compared to low growth temperature than either Desiree or the clone C1-884 (heat tolerant). Apparently reduced sensitivity of Rd to leaf temperature is not a consistent characteristic of heat tolerant potato clones.

Rd of excised leaf tissue was significantly lower in plants grown at high compared to low greenhouse air temperatures (Fig. 2). The effect of growth temperature on Rd was not altered when the data were expressed on a leaf dry weight basis (data not shown). Therefore, the effect of growth temperature on Rd was not associated with the effect on specific leaf weight. Midmore and Prange (16) also found that high growth temperature reduced Rd of potato leaves. If reduced Rd at high growth temperature is an acclimation process, then heat tolerant and sensitive clones exhibited similar acclimation ability.

High growth temperature could reduce Rd by affecting leaf age and the level of soluble carbohydrates. Rd generally declines throughout leaf development (21). High temperature speeds haulm development, and increases the senescence rate of individual leaves (13). Although leaves sampled in both greenhouses were from the same position on the stem, they may not represent the same chronological or developmental age.

Maximum daily temperatures in the hot greenhouse were above optimum temperatures for Pn (4, 9, 24). Thus, low leaf carbohydrate level could have limited Rd of plants at high temperature. However, leaf carbohydrate levels were not determined in this study.

Conclusions

DTO-28 tended to have relatively low Rd and high Pn compared to Russet Burbank. Consequently, DTO-28 had lower respiration:photosynthesis ratios for immature and mature leaves on one date, indicating more efficient use of fixed carbon. However, Desiree is also reported to be tolerant to heat stress, and it had leaf gas exchange characteristics similar to Russet Burbank.

(A)

Rd (mg CO2 dm-2 h-1)

■ Low: $Y = -13.79 + 0.93X - 0.012X^2$ $R^2 = 0.96$

● High: $Y = -14.49 + 0.96X - 0.013X^2$ $R^2 = 0.94$

Temperature (C)

(B)

Rd (mg CO2 dm-2 h-1)

■ Low: $Y = -1.68 + 0.15X$ $R^2 = 0.96$

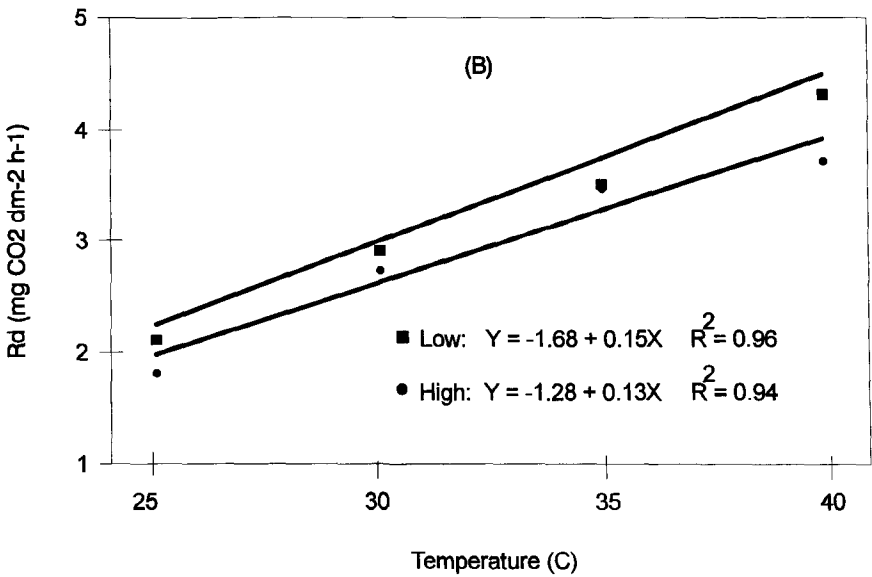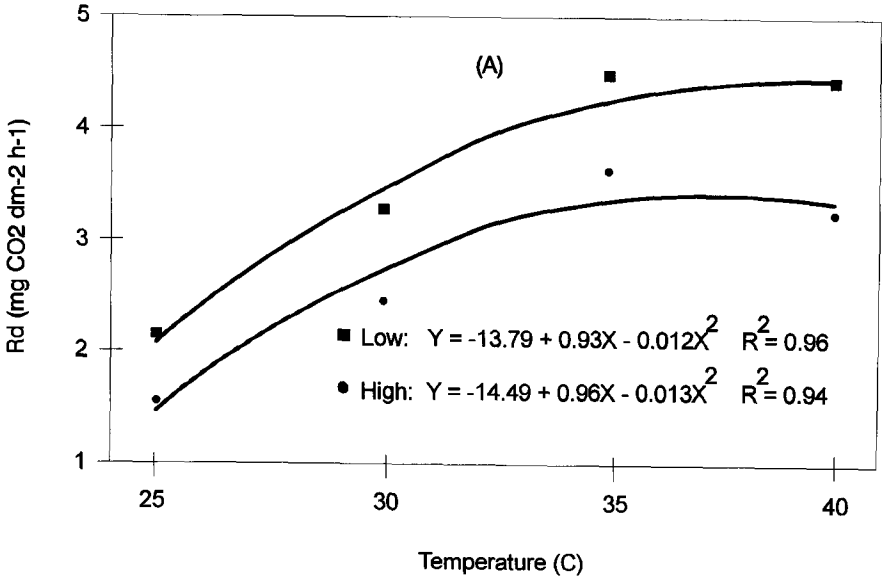● High: $Y = -1.28 + 0.13X$ $R^2 = 0.94$

Temperature (C)

FIG. 2. Effect of leaf temperature on rate of dark respiration (Rd) of leaf disks from potatoes grown at low (25/12 C) and high (35/25 C) greenhouse temperatures measured two weeks (A) or four weeks (B) after start of the greenhouse temperature treatments. Values are means of twelve replications and three clones.

The increase in Rd with increasing leaf temperature was not indicative of heat tolerance because it was similar in heat sensitive and tolerant clones. Growth environment affected Rd, but not sensitivity of gas exchange rates to leaf temperature.

Combining measurements of two physiological traits did not help explain genotypic variation in stress tolerance; this is not surprising because heat stress reduces tuber yields by affecting several plant processes in addition to carbon assimilation via Rd and Pn. Tuber initiation and partitioning of dry matter to tubers are also limiting factors at high temperatures.

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