STOMATAL BEHAVIOR OF POTATOES UNDER NONLIMITING SOIL WATER CONDITIONS[1]

J.C. Stark[2]

Abstract

Field studies were conducted to examine the relative effects of net irradiance (R_n), air vapor pressure deficit (VPD) and leaf water potential (Ψ_l), on leaf conductance, (C_l) of well-watered potatoes. Conductances of sunlit, surface-layer leaves for the cultivars Russet Burbank, Kennebec and Lemhi Russet were positively correlated with R_n (r^2=0.79, 0.83 and 0.62, respectively) for R_n between 100 and 650 Wm^{-2}. Leaf conductance (cm s^{-1}) for all three cultivars was described by the linear relation: $C_l = 0.871 + 0.0028 R_n$ (r^2=0.73). Mean C_l for a full Russet Burbank canopy, comprised of measurements from both sunlit and shaded leaves, was also linearly related to R_n. Although VPD and Ψ_l were significantly correlated with C_l (r^2=0.44 and 0.46, respectively), the results of multiple regression analysis showed that they had no additional effect on C_l beyond that attributed to R_n. These results indicate that potato leaf conductance is primarily related to irradiance under nonlimiting soil water conditions.

Resumen

Se condujeron estudios de campo para determinar los efectos relativos de la irradiación (R_n), del déficit de presión de vapor del aire (VPD) y del potencial de agua en la hoja (I_l), sobre la conductancia foliar (C_l) de papas debidamente irrigadas. Las conductancias de las capas superficiales de las hojas iluminadas por el sol, para los cultivares Russet Burbank, Kennebec y Lemhi Russet, estuvieron positivamente correlacionadas con R_n (r^2=0,79, 0,83 y 0,62 respectivamente) para R_n entre 100 y 650 Wm^{-2}. La conductancia de la hoja (cm s^{-1}) para los tres cultivares estuvo representada por la relación lineal: C_l=0,871 + 0,0028 R_n (r^2=0,73). La C_l media para el follaje completo de Russet Burbank, comprendió mediciones tanto de hojas iluminadas por sel sol como de hojas en la sombra y estuvo también correlacionada linealmente con R_n. No obstante que el VPD y el I_l estuvieron significativamente correlacionados con C_l (r^2=0,44 y 0,46 respectivamente), los resultados

[1]Approved for publication by the Director of the Idaho Agric. Expt. Station as research paper No. 86741.

[2]Assistant Research Professor, Dept. of Plant, Soil and Entomological Sciences, University of Idaho Research and Extension Center, Aberdeen, Idaho 83210.

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del análisis de regresión múltiple mostraron que ellos no tuvieron efecto adicional sobre C_l más allá del atribuído a R_n. Estos resultados indican que, bajo condiciones de humedad ilimitada del suelo, la conductancia de las hojas de papa está principalmente correlacionada con la irradiación.

Introduction

Stomata of field-grown plants respond to a number of environmental and plant factors, including light, humidity and plant water status (1, 3, 4, 5, 6, 9, 13, 14, 20). Leaf conductance (C_l) has been commonly reported to be positively correlated with irradiance (4, 5, 6, 7, 11, 23). Dwelle, *et al.*, (6) reported that potato C_l increased linearly as photosynthetic photon flux density (PPFD) increased from 400 to 2000 $\mu E\ m^{-2}\ s^{-1}$. Denmead and Millar (5) and Choudhury and Idso (4) observed that wheat C_l was linearly related to net radiation as long as the plants were well-watered.

Leaf conductance often decreases in response to decreasing leaf water potential (Ψ_l) when Ψ_l falls below so-called "critical" levels (5, 9). For example, stomata of the adaxial and abaxial surfaces of potato leaves begin closing when Ψ_l falls below -0.8 and -1.2 MPa, respectively (1). However, Ψ_l of well-watered potatoes usually remains above -1.0 to -1.1 MPa (8, 19. 22), even under hot, dry conditions (18).

It has also been demonstrated that stomata of a number of plant species close in response to increased leaf-to-air vapor pressure difference (9, 10, 14, 17). This response to humidity appears to be independent of effects caused by changes in bulk leaf water status (2, 9), although exceptions have been reported (12).

Although previous work has shown that microclimate and plant water status can affect stomatal response (1, 6, 7), a determination of the primary factor(s) responsible for controlling potato C_l in irrigated cropping systems has not been made. This study was conducted to determine the relative extent to which net irradiance (R_n), air vapor pressure deficit (VPD) and Ψ_l influence C_l of field-grown potatoes under nonlimiting soil water conditions.

Materials and Methods

The potato cultivars Russet Burbank, Kennebec and Lemhi Russet were grown on a Declo silt loam at the University of Idaho Research and Extension Center, Aberdeen in 1983. Prior to planting, 120 kg N/ha (as ammonium nitrate) and 80 kg P/ha (as triple superphosphate) were broadcast and incorporated with a disk. All other nutrients were present in adequate amounts.

The three cultivars were planted 16 May at 23 cm intervals in 91-cm wide rows. Individual plots were 5.5 m (6 rows) by 15 m and were arranged in a randomized complete block design with four replications. Aldicarb [(2-methyl-2-(methylthio)-proprionaldehyde 0-(methylcarbamoyl)oxime)] insecticide was applied with the seedpiece at 3.0 kg a.i./ha. Metribuzin [(4-amino-6-tert-butyl-3-(methylthio)-as-triazin-5(4HO-one)] was applied at 0.45 kg/ha on 2 June.

Sprinkler irrigation was applied to maintain tensiometer measurements of soil matric potential at the 20 cm depth above -50 kPa thoughout the growing season. The optimal soil matric potential for potatoes has been reported to be between -20 and -60 kPa (21). Supplementary applications of urea ammonium-nitrate were applied via the sprinkler system at the rate of 30 kg N/ha on 29 June, 13 July and 27 July.

Concurrent measurements of stomatal resistance, Ψ_l, R_n and wet and dry bulb temperature were taken from the plots at various times between 0800 and 1800 h (MST) on 28, 29 July and 1, 2, 3, 9 and 10 August. Stomatal resistance was measured with a LI-COR model 1600 steady-state porometer. Measurements, taken from the adaxial and abaxial surfaces of three sunlit leaves at the top of the canopy, were averaged to determine the mean stomatal resistance for each leaf surface at each sample time. Leaf conductance was determined as follows:

$$C_l = \frac{1}{r_{ad}} + \frac{1}{r_{ab}}$$

where r_{ad} and r_{ab} are the mean adaxial and abaxial resistances, respectively.

Leaf water potentials of the three leaves were measured with a pressure chamber immediately after taking the stomatal resistance measurements. Leaves were excised, wrapped in damp cheesecloth and placed in the chamber for pressurization (8). This procedure was usually completed within 90 s from the time of leaf excision.

Net radiation was measured with a Fritschen-type net radiometer and mean R_n values were recorded automatically at 10 min intervals. Wet and dry bulb temperatures were also measured at 10 min intervals with an aspirated psychrometer positioned 1 m above the crop canopy.

Additional data were collected in 1986 from a 2.1 ha field of irrigated Russet Burbank potatoes located at the Aberdeen Research and Extension Center. Cultural practices were similar to those previously described for the 1983 study. Stomatal resistance measurements were taken at various times between 0830 and 1800 h on 7, 8, 19 and 20 August. Measurements were taken from the adaxial and abaxial surfaces of three leaves in the top middle, and bottom third of the potato canopy (nine leaves per sample). Mean leaf conductances for the three canopy layers were then averaged to estimate the mean leaf conductance for the full canopy. Net radiation was measured as previously described.

Results and Discussion

Linear regression analysis was used to evaluate relationships between C_l of sunlit, surface layer leaves for the three cultivars and R_n, VPD, and Ψ_l (Table 1). Leaf conductance increased with increasing R_n and VPD, and with decreasing Ψ_l. However, C_l was more closely related to R_n than to either VPD or Ψ_l, as evidenced by the higher coefficients of determination and lower standard errors for the R_n regression models.

Slopes of the C_l vs R_n regression models for the three cultivars were not significantly different ($P=0.05$) but the intercept for Lemhi was higher ($P=0.05$) than those for Russet Burbank and Kennebec. Dwelle, *et al.*, (6) also reported higher conductances for Lemhi Russet than for Russet Burbank.

Data from all three cultivars were combined to develop a general relationship between C_l and R_n (Figure 1). Conductances ranged from approximately 0.6 to 1.2 cm s^{-1}, during the early morning and evening hours, to about 2.2 to 3.0 cm s^{-1} at maximum irradiance.

The relative effects of R_n, VPD and Ψ_l on C_l were evaluated using multiple regression analysis (Table 2). Only results for Russet Burbank are presented since the other two cultivars responded similarly. Comparisons were made by first considering the total effects of either VPD or Ψ_l on C_l and then considering the additional effects of R_n (15). By adding the variables in this order it appears that all three variables make significant contributions to models of C_l. However, when R_n was considered first, there was no significant additional regression due to either VPD or Ψ_l. These results show that VPD and Ψ_l had no additional effect on C_l beyond that attributable to R_n. Similar results have been reported for comparisons of the effects of R_n and VPD on wheat leaf conductance (4).

TABLE 1. — *Linear regression equations describing stomatal conductance (C_l) of three potato cultivars as a function of net radiation (R_n), air vapor pressure deficit (VPD) or leaf water potential (Ψ_l).*

Model	Cultivar	Regression coefficients a	b	r^2	S.E.
$C_l=a+b\ R_n$[1]	Russet Burbank	0.637	0.0031	0.79	0.241
	Kennebec	0.878	0.0028	0.83	0.215
	Lemhi Russet	1.247	0.0024	0.62	0.336
$C_l=a+b$ VPD	Russet Burbank	1.529	0.359	0.36	0.424
	Kennebec	1.508	0.402	0.54	0.351
	Lemhi Russet	1.797	0.378	0.40	0.417
$C_l=a+b\ \Psi_l$	Russet Burbank	1.070	-1.270	0.36	0.425
	Kennebec	1.016	-1.458	0.51	0.325
	Lemhi Russet	1.409	-1.240	0.41	0.411

[1] $R_n=Wm^{-2}$, $C_l=cm\ s^{-1}$ and $\Psi_l=MPa$.

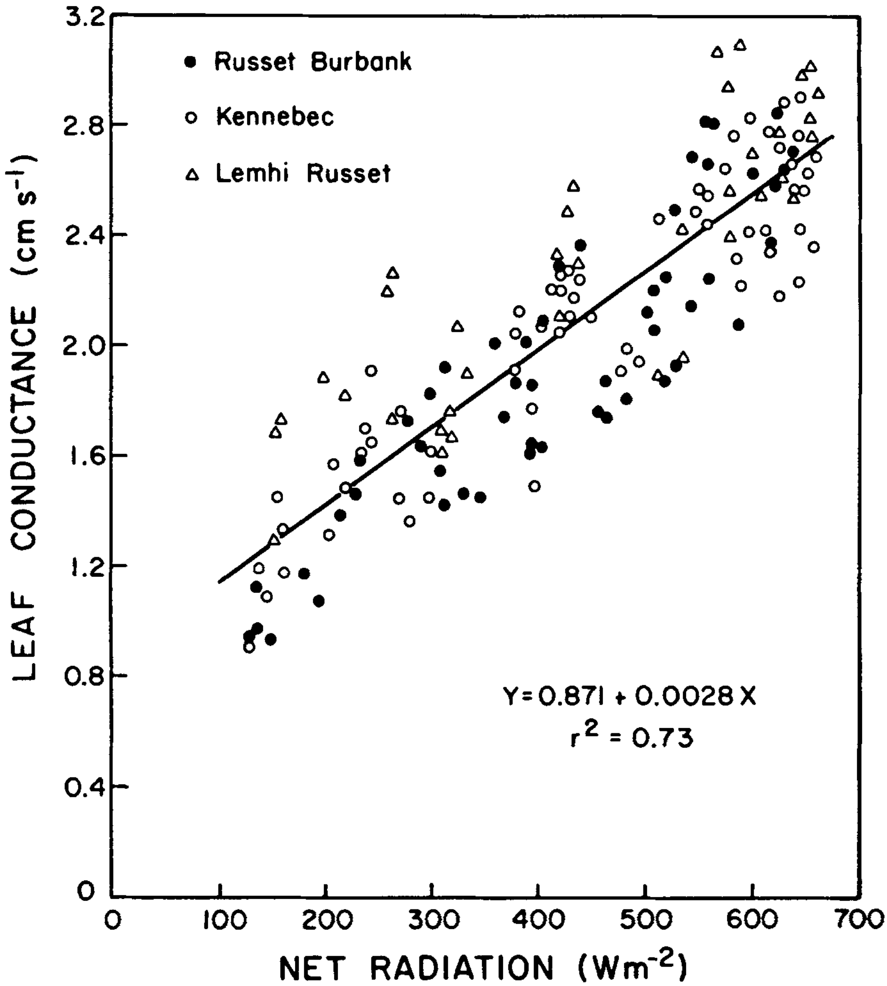

FIG. 1. Leaf conductance of three potato cultivars as related to net radiation.

Measured Ψ_l values in this study were generally greater than -1.0 MPa. Thus, the lack of a significant contribution by Ψ_l to the R_n regression models is consistent with the observation of Ackerson, *et al.*, (1), who found that stomatal resistance of the adaxial and abaxial surfaces of potato leaves did not change appreciably until Ψ_l dropped below -0.8 and -1.2 MPa, respectively. However, the apparent negligible effect of VPD on C_l contrasts with the results of other studies in which irradiance was held constant while humidity was varied independently (9, 10, 12, 16). Under such conditions,

TABLE 2. — *Multiple regression models describing leaf conductance (C_l) of Russet Burbank potatoes as a function of net radiation (R_n), air vapor pressure deficit (VPD) and leaf water potential (Ψ_l).*

Source of variation	df	SS	MS	F
$C_l = f(R_n, VPD)$				
VPD considered first				
Total	51	14.089		
Regression due to VPD	1	5.099	5.099	28.4**
Deviation from simple regression	50	8.990	0.180	
Additional regression due to R_n	1	6.095	6.095	103.2**
Deviation from multiple regression	49	2.895	0.059	
R_n considered first				
Total	51	14.089		
Regression due to R_n	1	11.181	11.181	192.3**
Deviation from simple regression	50	2.908	0.058	
Additional regression due to VPD	1	0.012	0.012	0.21 ns
Deviation from multiple regression	49	2.895	0.059	
$C_l = f(R_n, \Psi_l)$				
Ψ_l considered first				
Total	51	14.089		
Regression due to Ψ_l	1	5.038	5.038	27.8**
Deviation from simple regression	50	9.051	0.181	
Additional regression due to R_n	1	6.144	6.144	103.6**
Deviation from multiple regression	49	2.907	0.059	
R_n considered first				
Total	51	14.089		
Regression due to R_n	1	11.181	11.181	192.3**
Deviation from simple regression	50	2.908	0.058	
Additional regression due to Ψ_l	1	0.0004	0.0004	0.01 ns
Deviation from multiple regression	49	2.907	0.059	

**Significant at the 1% level. ns=not significant.

C_l has been shown to decrease in response to increasing VPD. Conversely, the data from this study show an increase in C_l with increasing VPD. However, the variability of the data is such that effects of VPD on C_l may be masked by the predominant effect of R_n. Large humidity gradients between leaf and air may, in fact, cause partial stomatal closure, but these effects on C_l are evidently smaller than those induced by irradiance.

Other investigators have reported a strong dependence of potato C_l on irradiance. Dwelle, *et al.*, (7) reported that C_l of differentially-shaded Russet Burbank potatoes increased as PPFD increased from 400 to 1700 $\mu E\ m^{-2}\ s^{-1}$. Similar relationships were later reported by Dwelle, *et al.*, (6) for Russet Burbank, Lemhi Russet and two numbered clones, A6948-4 and A66107-51.

Idso (11) used energy balance, heat and water vapor transport equations for cropped surfaces to show that C_l should be a linear function of R_n under well-watered conditions. To support this reasoning, he collected concurrent measurements of R_n and C_l from an aggregate of sunlit and shaded surface layer leaves for wheat, lettuce and fig. Although there were large differences in the magnitude of stomatal response to changes in irradiance, C_l for all three crops increased with increasing R_n. Regression analyses of these data were not presented but all Y-intercepts appeared to be near zero. Similar results for wheat have been reported by Denmead and Millar (5) and Choudhury and Idso (4).

To examine the effects of R_n on C_l of the full potato canopy, additional measurements were taken from the top, middle and bottom of well-watered Russet Burbank potato plants during August, 1986. Mean conductances for the full canopy were related to concurrent measurements of R_n (Figure 2).

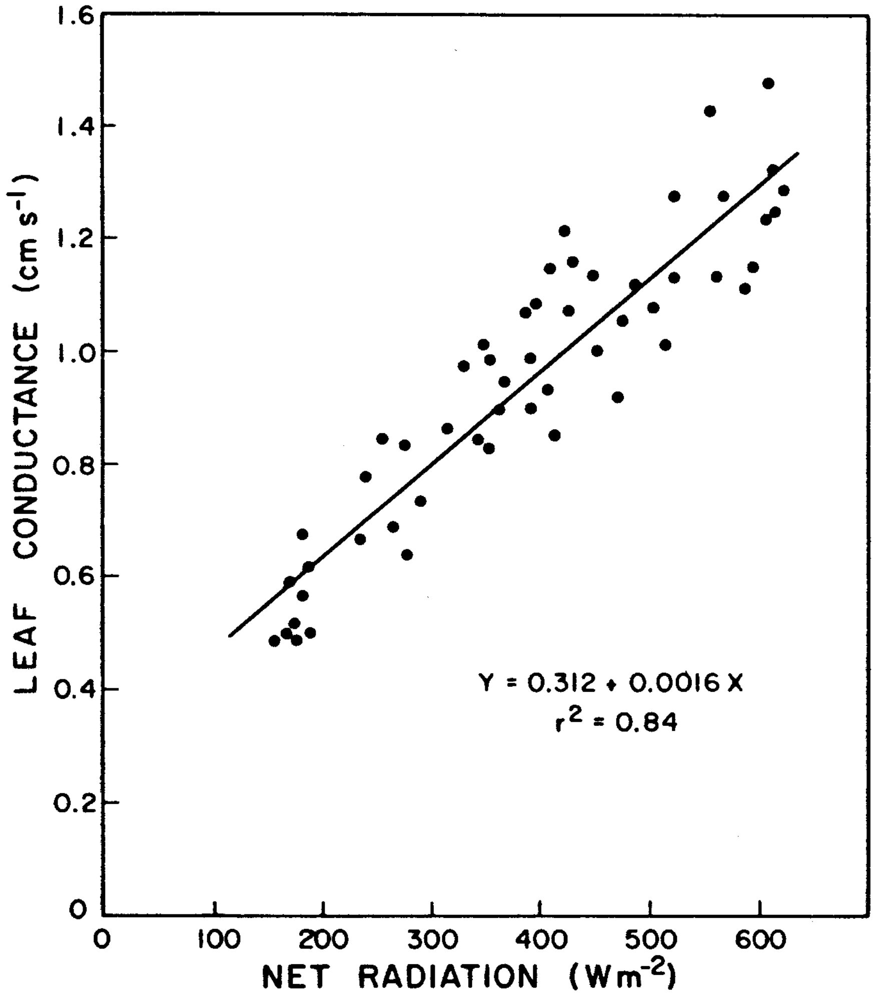

FIG. 2. Leaf conductance of an aggregate of leaves from the top, middle and bottom of a Russet Burbank potato canopy as related to net radiation.

Leaf conductances for the full canopy were considerably lower than those obtained for sunlit leaves in the upper part of the canopy (Figure 1). This result was primarily due to lower conductances in the older, shaded leaves. However, C_l again increased linearly with increasing R_n. The slope of this relationship is slightly lower than those reported for wheat (5, 11), but is similar to that reported for lettuce (11).

Summary

Based on the results of this study, it appears that C_l of field-grown potatoes, under nonlimiting soil water conditions, is primarily related to irradiance. Neither VPD nor Ψ_l had an appreciable effect on C_l beyond that which can be attributed to R_n.

It should be noted, however, that these relationships only apply to nonlimiting soil water conditions such as that obtained with full-season irrigation. When moderate crop water stress is induced by reduced soil water availability, C_l decreases to the extent necessary to prevent Ψ_l from falling below critical levels (5). Therefore, as plant water stress increases, C_l becomes less dependent on irradiance and more dependent on Ψ_l (3, 4). Additional work is required to develop quantitative relationships between C_l of stressed potato plants and the crop environment.

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