CANOPY PHOTOSYNTHESIS, STOMATAL CONDUCTANCE AND YIELD OF *SOLANUM TUBEROSUM* GROWN IN A WARM CLIMATE¹

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Abstract

Selected potato *(Solanum tuberosum* L.) genotypes were grown in the field from May to September during 1984 and 1985, to study their growth and gas exchange responses in a warm climate. The parameters measured were leaf area index (LAI), canopy photosynthesis on ground area basis (CPn-Ga), stomatal conductance, dry matter partitioning and yield. The LAI ranged from 1.40 for Dakchip to 6.60 for Pungo during August 1984. The LAI also differed significantly among the potato genotypes for the three samplings during 1985. Atlantic, Chipbelle and DTO-33 showed no decline in their LAI up to 73 days after planting (DAP), indicating a better heat-stress tolerance response than the other genotypes. During both years, CPn-Ga differed significantly among the genotypes and Pungo had higher CPn-Ga than all the other genotypes. Mean CPn-Ga rates were 1.72 and 4.34 g C_2 m⁻²hr⁻¹ during 1984 and 1985, respectively. Mean adaxial and abaxial stomatal conductances were 0.86 and 1.46 cm sec⁻¹, during 1984, and stomatal conductances were similar for both years. Stomatal conductance did not appear to limit gas exchange in potato leaves. Dry matter partitioning to tubers ranged from 8.9% for Pungo to 55.5% for Atlantic 67 DAP during 1984. At final harvest, July 19, 1985, dry matter partitioning to tubers varied from *47.5%* for Pungo to 69.9% for Chipbelle. The tuber yield ranged from 9.6 to 27.8 MT/ha. This study indicated that Atlantic and La Chipper have potential for growing in a warm climate.

Compendio

De mayo a setiembre, durante 1984 y 1985, se cultivaron genotipos selectos de papa *(Solanum tuberosum* L.), para estudiar su crecimiento y la

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respuesta al intercambio de gases en clima cálido. Los parámetros medidos fueron el índice de área de hoja (LAI), la fotosíntesis del follaje expuesto en base al área de terreno (CPn-Ga), la conducción estomática, la repartición de la materia seca, y el rendimiento. Durante agosto de 1984, la LAI varió de 1,40 para "Dakchip" a 6,60 para "Pungo." Durante 1985, la LAI también fue significativamente diferente entre los genotipos de papa para las tres muestras estudiadas. "Atlantic," "Chipbelle" y DTO-33 no mostraron declinación en su LAI hasta los 73 días después de la siembra (DAP), indicando una respuesta mejor para la tolerancia al estrés al calor en comparaci6n con los otros genotipos. Durante ambos afios, la CPn-Ga difiri6 significativamente entre los genotipos y "Pungo" tuvo una CPn-Ga más alta que todos los otros genotipos. Durante 1984 y 1985, las tasas de CPn-Ga fueron 1,72 y 4,34 g $CO₂$ m⁻²hr⁻¹, respectivamente. La conducción estomática media para las caras superior e inferior de las hojas, durante 1984, fue 0.86 y 1.46 cm sec⁻¹, respectivamente, y fue similar para ambos años. La conducción estomática aparentemente no limitó el intercambio gaseoso en las hojas de papa. La repartición de materia seca a los tubérculos varió de 8,9% para "Pungo" a 55,5% para "Atlantic" 67 DAP, durante 1984. A la cosecha final, julio 19, 1985, la repartición de materia seca a los tubérculos vari6 de *47,5%* para "Pungo" a 69,9% para "Chipbelle." El rendimiento en tubérculos varió de 9,6 a $27,8$ t/ha. Este estudio indicó que "Atlantic" y "La Chipper" tienen potencial para ser cultivadas en clima cálido.

Introduction

The pattern of growth and development of potato *(Solanum tuberosum* L.) plants is strongly influenced by environmental factors such as daylength and temperature. The different yield and growth responses of 27 potato cultivars grown during spring and autumn indicated that potato cultivars have critical daylength and thermoperiod requirements for optimum performance (20). Plants grown at high day and night temperatures (40/30 C) as compared with normal spring temperatures reflected decreased percent dry matter and percent dry matter partitioning to tubers (12). Marinus $\&$ Bodlaender (15) tested eight potato cultivars at three temperatures and reported that tuber yields and plant biomass were lower at 27 C than those grown at 16 or 22 C and furthermore, the plants at the higher temperature produced more foliage than tubers. The maximum leaf expansion growth and stem elongation for potato occurred at *25* C and 35 C, respectively (1).

Photosynthate partitioning to potato tubers is also known to be affected by the environment. Ewing (8) reported that high temperatures and long days caused reduction in photosynthate partitioning to tubers, and a significant genetic variability for assimilate partitioning occurred among potato clones. Khedher and Ewing (12) reported that potato genotypes grown under ambient summer greenhouse conditions partitioned more photosynthate to tubers than those grown at higher temperature. Similarly, Victorio *eta/.* (21) reported that photosynthate partitioning to tubers ranged from 73.0 to 85.0% in cool higher elevations and 33.0 to 75.0% in a warm coastal climate. Gawronska, *et al.* (11) reported differences in ¹⁴C-assimilate translocation among four potato genotypes and speculated that high photosynthesis and translocation rates could be useful for increasing potato tuber yield.

Variations in LAI, especially for short duration crops, can strongly influence crop growth rates and productivity. Moll (16) concluded from her studies with 14 potato clones that both large leaf areas and high photosynthetic rates are important for high yields. Khurana and McLaren (13) found a linear relationship between potato tuber yields and interception of photosynthetically active radiation (PAR) which was directly related to LAI. Dwelle, *et al.* (6) reported a positive correlation between potato tuber yield and visual estimation of LAI.

In cool climates, significant genetic variation has been reported in photosynthesis of potato. Dwelle (4) reviewed the research of several scientists and reported significant differences in photosynthetic rates of potato clones. Mean photosynthetic rates for potato were 30.0 and 50.0 mg CO_2 hr⁻¹g⁻¹ leaf dry weight basis at 16 C and 20 C, respectively (22). Dwelle, *et aL* (5), reporting from the data of Kennedy and Dean, indicated that single leaf photosynthetic rates for Russet Burbank, A6948-4 and A66107-51 were 28.0, 40.0 and 50.0 mg C_2 dm⁻²hr⁻¹, respectively. Canopy photosynthetic rates, involving one potato genotype each, ranged from 3.5 to 4.0 (18) and 4.0 to 6.0 (14) g C02hr⁻¹m⁻² ground area. Several studies have suggested that genetic differences in photosynthetic potential and photoassimilate partitioning to economic sinks could be exploited to enhance potato yield (4, 16, 22).

Most of the potato research has been conducted under cool climatic conditions. Potato cultivation is recently being extended to warmer climatic regions (9, 17), but there is lack of information about physiological responses of potatoes grown in warmer climates. The objectives of this study were to examine a range of potato genotypes grown in a warm climate with emphasis upon leaf area index, dry matter partitioning, stomatal conductance, canopy photosynthesis and yield components.

Materials and Methods

This research was conducted during the late spring and summer of 1984 and 1985 at the Agricultural Research Station, Fort Valley State College, Fort Valley, Georgia with selected potato genotypes (Table 1). The experimental design was a randomized complete block with four replications. The seed tubers were obtained from Dr. R.E. Webb, USDA, Beltsville Agricultural Research Center, MD, and stored at 5 C until two weeks before

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 $x =$ Canopy photosynthesis expressed as C0 ₂hr⁻¹g⁻¹ leaf dry weight.

 $W =$ Each value based on four observations.

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planting. Tubers were cut into pieces, each with at least two buds, and stored for two weeks at 25 C before planting May 21, 1984 and May 7, 1985.

During 1984, seed tubers were hand planted in rows 0.60 m wide and 6.0 m long, with 30 cm spacing between plants. During 1985, the beds were $1.20 \text{ m} \times 6.0 \text{ m}$ and planting was done on both sides of the raised center bed 0.60 m wide with 30 cm spacing between plants. The fertilizers were applied at 112.0 kg ha⁻¹ each of N, P and K before planting and an additional 50 kg ha⁻¹ N was applied about 40 days after planting during both years. Manual hoeing, with partial hilling was done three times. No herbicide was applied. Permethrin (3-phenoxyphenyl) methyl 3- (2, 2-dichloroethenyl) -2, 2-dimethylcyclopropanecarboxylate), .05 kg aiha⁻¹, was applied three times to control insects. Starting fifteen days after planting, sprinkle irrigation was applied as needed and plants were also irrigated one day before measuring photosynthesis and stomatal conductance.

For growth analyses plant samples were taken on July 23 and August 6, 1984,and June 13, June 25, and July 19, 1985. Plants were separated into leaves, branches and tubers and were dried at 60 C to a constant weight before weighing. Leaf area was determined with leaf-area meter, Li-Cor 3000. Stomatal conductance was determined with a steady state porometer (Li-1600 Lambda Instruments Corp., Lincoln, Nebraska) on July 8 & 9, 1984, and June 20 & 21 and July 13, 1985. Transpiration on abaxial surfaces was determined June 21, 1985. Stomatal conductance and transpiration were measured on the second or third leaf from the top in full sunlight (above 1500 μ E m⁻² sec⁻¹) between 1100 and 1500 h EST.

Canopy Photosynthesis

Photosynthesis measuring instruments were housed in a trailer at the experimental site and Tygon tubing was used to conduct sample air from the photosynthetic chamber to and from an infrared analyzer (Model 215 B, Beckman). To measure C_0 2 uptake, the canopy was enclosed with a portable plexiglass photosynthetic chamber, 1.26 m \times 1.12 m and 0.68 m high, with an open bottom. A 1.26 m \times 1.12 m rectangular steel frame of 3.7 cm angle iron held the photosynthetic chamber at soil level. The steel frame had a 3.5 cm groove on the top four sides to hold water and a side lip to go in soil to make the system air-tight at soil level. For each measurement, the steel frame was placed around the plants and pushed into the soil to obtain a good seal. The plant canopy was enclosed by placing the photosynthetic chamber on the steel frame groove, which contained water to provide an air-tight seal and C02 depletion was monitored for two to three minutes. Two squirrel cage fans on one side of the photosynthetic chamber provided air turbulance during photosynthesis measurement. A thermocouple placed inside the photosynthetic chamber continuously monitored the temperature.

The infrared analyzer was calibrated in a differential mode with air having 350 and 300 μ L/L of C02. After the calibration, the sample air drawn

from the photosynthetic chamber and the low gas (300 μ L/L of C0₂) from a pressurized cylinder were passed through drierite (CaS04) before entering the infrared analyzer. A continuous sample of ambient air was drawn from the photosynthetic chamber, which was supported on a 1 m high wooden stand when not placed on the canopy, and it passed through the infrared analyzer to establish an ambient C_0 base line. After enclosing the plant canopy, C_2 uptake was monitored for two to three minutes. Photosynthetic measurements were made August 6, 1984 and June 24-26, 1985 on sunny days between 1100 and 1500 h EST under ambient conditions. Photosynthesis rate was determined by calculating C_0 depletion within the chamber for two minutes and photosynthesis was expressed on ground area and leaf dry weight basis.

Temperature During Growth

The mean weekly maximum temperature varied from 25 to 30 C during May 1984 and 1985 but in June, July and August, it ranged from about 28 to 35 C (Figure 1). The mean weekly minimum temperature was below 20 C during May and about 20 C during June, July, August and early part of September for both years.

Results

The leaf area index differed significantly among the potato genotypes during 1984 and 1985 (Table 1). During 1984, 77 days after planting (DAP) LAI ranged from 1.40 to 6.60. The mean LAIs, determined June 13 (37) DAP), June 25 (49 DAP) and July 19 (73 DAP) were 0.69, 1.75 and 1.46, respectively during 1985. The LAI rankings among the potato genotypes changed from 1984 to 1985. During 1985, the LAI declined for most genotypes from 49 to 73 DAP except Atlantic, Chipbelle and DTO-33.

Canopy photosynthesis on ground area basis (CPn-Ga) ranged from 1.03 to 2.60 g $CO₂$ hr⁻¹m⁻² during 1984, 77 DAP (Table 1). The genotypes having higher LAI also had higher photosynthetic rates. During 1985, CPn-Ga among the potato genotypes also differed significantly. The CPn-Ga, determined in June 1985 (49 DAP), ranged from 3.02 to 4.96 g $CO₂$ hr⁻¹m⁻². For both years, Pungo had higher CPn-Ga than all the other genotypes. Photosynthesis expressed on leaf dry weight basis (CPn-Dwt) did not differ significantly among the genotypes.

The abaxial stomatal conductance differed significantly among the genotypes during both years but adaxial stomatal conductance differed significantly only for one out of three dates of determinations (Table 2). The abaxial stomatal conductance ranged from 1.16 cm sec⁻¹ for Ontario to 1.68 cm sec⁻¹ for DTO-33 during 1984. The adaxial and abaxial stomatal conductances for July 1984 and June 1985, determined 44 to 48 DAP, were similar for both years. During 1985, adaxial and abaxial stomatal conduc-

TABLE 2. -- *Stomatal conductance and transpiration of selected fleld-grown potato genotypes dun'ng 1984 and 1985.* TABLE 2. - Stomatal conductance and transpiration of selected field-grown potato genotypes during 1984 and 1985.

Y=Mean adaxial and abaxial stomatal cnductance for each genotype based on 16 observations during 1984 and 1985.

tances peaked at the end of June and in July both conductances in all the genotypes declined probably due to environmental stress. The mean abaxial stomatal conductance was about twice as large as the adaxial stomatal conductance. Abaxial surface transpiration also differed significantly among the potato genotypes. Abaxial stomatal conductance for both years and transpiration for 1985 were lower for Ontario as compared to all the other genotypes.

Percent dry matter partitioning to tubers differed significantly among the potato genotypes for each sampling during both years (Table 3). On July 23, 1984 (63 DAP) five genotypes partitioned less than 10.0% dry matter to tubers but June *25,* 1985 (49 DAP) these genotypes partitioned 10.0 to 26.5% dry matter to tubers. During 1984, Atlantic partitioned more photosynthate to tubers than all the other genotypes. During 1985, mean percent photosynthate partitioning to tubers was 21.2% and 60.0% 49 and 73 DAP, respectively. The higher percent photosynthate partitioning to tubers during 1985 may have been because planting was two weeks earlier than for 1984.

At final harvest, the average number of tubers per plant was higher in 1985 than for 1984 (Table 3). During 1985, DTO-33 had more tubers per plant than all the other genotypes. Mean fresh weight per tuber was similar for both years. The mean fresh tuber weight ranged from 29.6 to 90.3 g during 1984 and 18.7 to 81.5 g during 1985.

The tuber yield ranged from 9.6 to 23.8 MT/ha during 1984 and from 13.6 to 27.8 MT/ha during 1985 (Table 3). Atlantic had higher yield than the other genotypes during both years. With the exception of DTO-33, the potato genotypes having higher per cent photosynthate partitioning to tubers also had higher yields.

Canopy photosynthesis (CPn-Ga) was significantly correlated with LAI of August 6, 1984 ($r = +0.84$) and LAI of June 25, 1985 ($r = +0.88$) (Table 4). Photosynthesis (CPn-Ga) was also significantly correlated with abaxial stomatal conductance ($r = +0.78$) and adaxial stomatal conductance $(r=+0.64)$ during 1985 but not for 1984. During 1984, CPn-Ga also showed a significant positive correlation with tuber yield ($r=+0.76$). During 1984, abaxial stomatal conductance was significantly correlated with dry matter and tuber number/plant. At final harvest, July 19, 1985, tuber yield significantly correlated with fresh weight/tuber and dry matter.

Discussion

Significant genetic variation was observed among the potato genotypes in LAI development in a warm climate. But most of the genotypes, except Pungo in 1984, failed to develop enough foliage to reach the LAI values of 4 to 5 common for potato in cool climates. The optimum leaf area indexes for efficient interception of PAR and maximizing dry matter production for

TABLE *3. -- Dry matter partitioning to tubers and yield of selected fleld-grown potato genotypes dutT"ng 1984 and 1985.* TABLE 3. - Dry matter partitioning to tubers and yield of selected field-grown potato genotypes during 1984 and 1985.

 $Z =$ The values for various parameters for each genotype are based on four observations. \equiv I he values for various parameters for each genotype are based on four observations.

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Characteristics	Year	
	1984	1985
LAI ² Aug. 6 vs. ^y CPn-Ga ^x	$+ 0.84**$	
LAI June 25 vs CPn-Ga		$+0.88**$
LAI June 25 vs. Abaxial SC^{w}		$+0.65*$
LAI June 25 vs. Yield		$+0.65*$
Adaxial SC vs. CPn-Ga	$+0.60$ N.S.	$+0.64*$
Abaxial SC vs. CPn-Ga	$+0.12$ N.S.	$+0.78**$
Tuber vield vs. CPn-Ga	$+0.76*$	$+0.61$ N.S.
Dry matter July 23 vs. Abaxial SC	$+0.69*$	
Tuber no./plant July 23 vs. Abaxial SC	$+0.73*$	
Tuber no./plant Aug 6 vs. Abaxial SC	$+0.75*$	
Fresh wt./tuber July 19 vs. Yield		$+0.83**$
Dry matter July 19 vs. Yield		$+$ 0.65*

TABLE 4. - *Correlation coefficients (r) among selected traits of potato genotypes.*

 $\text{ZLAI} = \text{Leaf area index}.$

 $y_{vs.}$ = versus.

XCpn-Ga=Canopy photosynthesis ground area basis.

wsc=Stomatal conductance.

 $N.S. = Not significant.$

*,**=Significant at the 5% (*) and 1% (**) level of probability.

potato were 2.2 to 4.0 and 3.5 to 4.5, respectively (13). During growth, temperatures greater than 25 C decreased leaf expansion rates (1). Thus, reduction in leaf expansion probably decreased LAI in warm climate where day temperatures were generally higher than 25 C (Figure 1). Thus, the lower LAI and its faster decline in our experiments as compared to those in a cooler environment may have affected the photosynthate supply and subsequently tuber yield.

Transpiration from the abaxial surface and stomatal conductance for both leaf surfaces were similar to other C_3 plants including sweet potato *(Ipomoea batatas* L.) and cassava *(Manihot esculenta* Crantz), (unpublished data of senior author) grown in summer, indicating normal stomatal functioning of the potato genotypes in a warm climate. Potato leaf conductance values are similar to those reported by Stark (19). Thus, stomatal conductance apparently was not limiting C_0 assimilation and dry matter production for potato cultivars grown in a warm environment but some other internal biochemical factors may have limited production.

Variations for carbon assimilation existed among the potato genotypes, representing only a minor fraction of the total potato germplasm pool. Generally differences in CPn-Ga were caused by the differences in LAI development among the genotypes. But most high yielding genotypes developed larger tuber sinks than low yielding genotypes and this may also

have contributed to differences in photosynthetic rates because photosynthesis in potato is affected by the sink demand (18). Since photosynthesis was positively correlated with LAI, the altered ranking in LAI during growth would also indicate that photosynthetic rates and consequently, photosynthate supply to sinks was quite different among the potato genotypes.

During 1984, LAI values were higher than for 1985 but CPn-Ga exhibited the opposite trend. The lower CPn-Ga for 1984 was probably the result of late CPn-Ga measurements made *77* DAP in 1984 versus 49 DAP in 1985. The higher temperature in the photosynthetic chamber at measurement during 1984 (mean 37.2 C) than for 1985 (mean 33.4 C) also may have contributed to the lower CPn-Ga in 1984.

No significant differences in CPn-Dwt were found among these genotypes but on the contrary Winkler (22) reported significant differences in CPn-Dwt among 14 potato cultivars. It appears that higher LAI caused some genotypes to intercept PAR more efficiently than others and that probably led to yield differences among the genotypes even when their leaf photosynthetic efficiencies (Cpn-Dwt) were similar.

Genotypic differences in the initiation of tuberization and allocation of photosynthate to tubers gave more advantage to some genotypes for dry matter accumulation than others. The fresh weight per tuber was also lower than other studies (3, 20) even though plants had attained photosynthetic rates similar to other reports from cool climates, especially in 1985 (14, 18). Canopy respiration rates are reported to increase 2 to 3 times between 25 and 35 C (18). Similar high temperatures were common during the two potato growing seasons of this study (Figure 1). Thus, it is possible that temperature-related increased utilization of photosynthate for respiration decreased photosynthate availability for tuber development and weight gain. It is likely that early initiation of tuberization and faster bulking rates in certain genotypes may have enhanced potato tuber yields as noticed in sweet potato (2).

Mean yield for Atlantic from this study was 61.0% and 69.0% of mean yields for 14 (16) and 19 (6) genotypes grown in cool climates. The growing season for potato in a cool climate lasts for 135 to 150 days $(1, 6, 10)$ and canopy photosynthesis starts declining 85 to 95 DAP (7, 18). The growth period for this potato report was about 90 and 73 days during 1984 and 1985, respectively. This reduction in the growth period coupled with early decline of the physiological activity of leaves caused lower yields in the warm climate as compared to the cooler regions.

The correlation coefficients for the different parameters, over all the genotypes for two years, were determined by excluding data for Red Pontiac (Tables 1, 2, and 3). Tuber yield for 1984 was significantly correlated with tuber yield for 1985 ($P = .02$). The correlation ($r = 0.63$, $P = .06$) between CPn-Ga 1984 and CPn-Ga 1985 was not significant, probably due to age differences of plants at measurement. Abaxial stomatal conductance was

significantly correlated between 1984 and 1985 (P>.01). Tuber number and tuber weight per plant for 1984 were not correlated with those for 1985. On the other hand, dry matter production was significantly $(P>01)$ correlated between years. These two observations indicate that the differences in aerial growth patterns were similar but the partitioning of photosynthate to tubers was confounded by seasonal variation. The correlation coefficients also showed that abaxial stomatal conductance was a better indicator for crop responses than the adaxial surface.

This and other related studies indicated that the mechanisms and strategies employed for organic matter accumulation were different among the genotypes. Canopy photosynthetic rates of Atlantic and La Chipper were similar to many other genotypes but their yields for both years were consistently higher than for all the other genotypes. Further research is needed to evaluate more potato germplasm for adaptation to warm climate.

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