Photosynthesis and Transpiration Response of Redroot Pigweed (*Amaranthus retroflexus*)[1]

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Abstract. Redroot pigweed is a major weed worldwide. Increasing emphasis on modeling physiological processes of weeds for use in weed control decision support systems requires a knowledge of the response of weeds to resource levels and environmental conditions. The purpose of this study was to determine functional relationships for carbon exchange rate (CER) and transpiration based on photosynthetic photon flux density (PPFD) and temperature from measurements made on field-grown redroot pigweed. Measurements were made using a portable photosynthesis system on four dates. An equation that had the form of a power function on PPFD and a quadratic polynomial on temperature was fit to the data. The equation fit the measured CER data better than the measured transpiration data. The equations should be useful in modeling the physiological processes of pigweed within crop canopies. **Nomenclature:** Redroot pigweed, *Amaranthus retroflexus* L. #[3] AMARE.

Additional index words: Transpiration, stomatal conductance, temperature, carbon exchange rate, models.

INTRODUCTION

Redroot pigweed is a major annual broadleaf weed found throughout the United States and Canada, and throughout other temperate regions of the northern and southern hemispheres (11). Pigweed has the C_4 photosynthetic pathway and exhibits a low CO_2 compensation point and high transpiration efficiency (11).

In recent years, models have been developed to aid in making weed control decisions or to generate insight into weed/crop interactions (7). The development and use of these models is likely to increase in the future. Some of these models require input from process-based models of weed development and growth. These process-based models simulate important processes (e.g., photosynthesis, transpiration) and growth in response to resource levels and environmental conditions and require species-specific photosynthetic-light response data for single leaves of weeds (7). Wilkerson et al. (13) used a weed-specific constant to estimate the maximum photosynthetic rate of common cocklebur (*Xanthium strumarium* L.) under high light conditions from the maximum photosynthetic rate of soybean [*Glycine max* (L.) Merr.] in the weed competition model SOYWEED. Weed photosynthesis, which is affected by light level and temperature, is an important part of this model because it drives the rate of weed dry matter accumulation. The study of plant physiological responses to environmental conditions is also important to ecophysiologists as they relate to weed scientists in studying the physiological mechanisms underlying adaptive traits in weed species that enhance competitive advantage under natural and cropped conditions (6).

Several studies have been done to determine leaf photosynthesis rates under varying light and temperature conditions for both redroot pigweed and a related species, smooth pigweed (*Amaranthus hybridus* L.). The results of these studies are summarized in Table 1. In all but one of the reported studies, plants were grown and measured in a greenhouse or growth chamber. The data of both Chu et al. (2) for redroot pigweed and Patterson (9) for smooth pigweed show photosynthesis rate peaking at a temperature between 30 C and 40 C. The light response data of Singh et al. (10) for redroot pigweed and Patterson (9) for smooth pigweed showed that photosynthetic rates do not light-saturate at high photosynthetic photon flux density (PPFD)[4] levels, i.e., photosynthetic rates continued to increase with increasing PPFD for the entire range of PPFD measured (up to approximately 1925 $\mu mol/m^2/s$. The data of Ahrens and Stoller (1) showed the light response curve for smooth pigweed was nearly saturated at full sun con-

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[3]Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

[4]Abbreviations: CER, carbon exchange rate; PPFD, photosynthetic photon flux density; VPD, vapor pressure deficit.

Table 1. Response of carbon exchange rate (CER) to photosynthetic photon flux density (PPFD) and temperature (T) for redroot pigweed (*A. retroflexus* L.) and smooth pigweed (*A. hybridus* L.).

Species	PPFD	T	CER	Environment	Source
	μmol/m²/s	°C	mg/m²/s		
Redroot pigweed	135/578/1155/1540/1925	30	0.10/1.01/1.53/1.65/1.73[a]	Field[b]	(10)
Redroot pigweed	700	10/20/30/40	0.28/0.97/1.19/0.88	Growth chamber	(2)
Redroot pigweed	1500	33	1.60	Greenhouse	(12)
Redroot pigweed	100/1000	25	0.13/0.76	Greenhouse	(5)
Redroot pigweed	700	28	0.81	Growth chamber	(3)
Smooth pigweed	585/1155/1925	25	0.32/0.67/0.89[c]	Greenhouse	(9)
Smooth pigweed	1500	10/20/30/40/50	0.33/0.83/1.25/1.18/0.71[c]	Greenhouse	(9)
Smooth pigweed	500/1000/2000	30	1.00/1.90/2.25	Greenhouse	(1)

[a]Multiple values of CER correspond to respective multiple values of PPFD or T.
[b]Plants were field-grown, but CER measured under artificial light source.
[c]Whole plant CER.

ditions. Singh et al. (10) showed that redroot pigweed grown under low PPFD had lower maximum photosynthetic rates than plants grown under high PPFD when both were exposed to similar high PPFD. Coleman and Bazzaz (3) found that photosynthetic rates of redroot pigweed leaves were higher for plants that were 30 d old than that of older plants.

Redroot pigweed has an emergence period occurring from early June through early August in the central Great Plains (R. L. Anderson, unpublished data). Under the low plant populations of dryland corn (*Zea mays* L.) production in this area, early season development of corn leaf area is low, and emerging pigweed plants grow under high PPFD conditions (midday values greater than 1500 μmol/m²/s on a majority of days).

In order for light response data to be useful for models of weed growth and development, functional relationships must be developed describing the response. It was the purpose of this study to determine functional relationships that describe the effects of varying level of light and temperature on carbon exchange rate (CER)[4] and transpiration of leaves of field-grown redroot pigweed.

MATERIALS AND METHODS

This study was conducted during the 1989 growing season at the USDA Central Great Plains Research Station, (40°9′ N, 103°9′ W, 1384 m above mean sea level), 6.4 km east of Akron, CO. The soil type at this location was a Rago silt loam (fine montmorillonitic mesic Pachic Argiustoll). Redroot pigweed seed was sown on 2 June, 1989 into three 2.7 m by 2.7 m plots that were covered automatically by a rainout shelter during precipitation events. Plots were thinned to 22 plants per m² on 26 June. Plots were irrigated after planting to stimulate germination and emergence, and at 2-wk intervals to maintain non-water-stressed conditions during growth and development. Additional irrigations of 25 mm were applied on 24 July, 28 July, 4 August, and 15 August to ensure that measurements were made under non-water-stressed conditions.

Leaf CER, transpiration, and PPFD measurements were made on 26 July, 27 July, 2 August, and 17 August using a portable photosynthesis system[5,6] on recently fully expanded, upper-canopy leaves that were fully exposed to the sun. The ranges of PPFD and temperature encountered on the four sampling dates are shown in Table 2. Measurements were made on 26 July and 27 July between 1300 and 1700 Mountain Daylight Time at approximately 45-min intervals on a single leaf of each of six plants in one of the

Table 2. Range of photosynthetic photon flux density (PPFD) and temperature during four sampling periods in 1989.

Date	PPFD range[a]	Temperature range
	μmol/m²/s	C
26 Jul.	0–1801	29.6–31.1
27 Jul.	0–2053	31.8–34.8
2 Aug.	304–2179	25.6–33.1
17 Aug.	545–2053	21.2–28.9

[a]PPFD varied by cheesecloth layers over plants (26 Jul. and 27 Jul.) or by changes in solar elevation angle (2 Aug. and 17 Aug.).

[5]Trade names and company names are included for the benefit of the reader and do not imply any endorsement or preferential treatment of the product by the authors or the USDA.

[6]LI-6000, LI-COR, Inc., Lincoln, NE.

three plots. These same six leaves were measured for all data collected on 26 July, with six different leaves measured on 27 July. Incoming level of PPFD was varied by use of layered cheese cloth, with zero, one, two, four, and eight layers used for the first through fifth set of measurements, respectively. The rainout shelter was closed for the sixth set of measurements (PPFD = 0). Approximately 30 min elapsed between a change in light level by adding cheese cloth and making a set of measurements. An individual leaf measurement required approximately 20 s. Humidity within the leaf chamber was maintained at a nearly constant level by controlling the flow rate of dry air into the chamber. The results from the six leaves measured at each light level were averaged to give single values for CER, transpiration, and PPFD.

For the measurements made on 2 August and 17 August, data were collected at four times between 0900 and 1830 MDT (approximately 3 h between measurement sets), with PPFD levels changing in response to changes in solar elevation angle. Again, only recently fully expanded, upper-canopy leaves, fully exposed to the sun were measured, with six measurements made in each of the three plots. The six measurements from each plot at each sampling time were averaged to give one value each of CER, transpiration, and PPFD for each plot at each measurement time. In total, 144 measurements of CER and transpiration were taken over the four measurement days, with data averaged by similar light level to give a final data set of 33 points to be used in determination of prediction equations.

A function with the form:

$$X = (a + bQ^c)*(d + eT + fT^2) \qquad (1)$$

was fit to the combined data from all four data sets, where X is either CER ($mg/m^2/s$) or transpiration ($mg/m^2/s$); Q is PPFD ($\mu mol/m^2/s$); T is temperature (C); and a, b, c, d, e, and f are curve-fitting constants derived by the iterative curve fitting program in the graphics software package SigmaPlot 5.0[7]. This equation form was chosen because of its simplicity, the general power function shape of the photosynthesis-light response, and evidence in previous research (2) that temperature response has a second order polynomial form. Air temperature was measured with an aspirated psychrometer before each set of six leaf measurements on all four sampling dates.

[7]Jandel Scientific, San Rafael, CA.

RESULTS AND DISCUSSION

Figure 1 shows the response of redroot pigweed CER and transpiration to changes in PPFD at four ambient temperatures as predicted by equation 1 with the coefficients given in Table 3. Table 3 also gives the coefficient of determination (r^2) values as computed by the SigmaPlot transform for computing r^2 for non-linear curve fits (8). The model fit the CER data best ($r^2 = 0.92$), with lower r^2 values for the transpiration data. As a further determination of how well the model fit the data, the measured CER and transpiration values are plotted against the values predicted by equation 1 (Figure 2). The models appear to do well for all data sets with the exception of the transpiration data collected on 26 July. Somewhat drier atmospheric conditions occurred on that date than on subsequent days, and perhaps these conditions had an effect on both transpiration and stomatal conductance, as noted by El-Sharkawy et al. (4) who observed stomatal closure in 19 different warm climate species as vapor pressure deficit (VPD) increased. The consistent performance of the model in accurately predicting CER over four dates indicates that leaf age was a factor that did not need to be accounted for in the model, as a result of our measuring only recently fully expanded leaves.

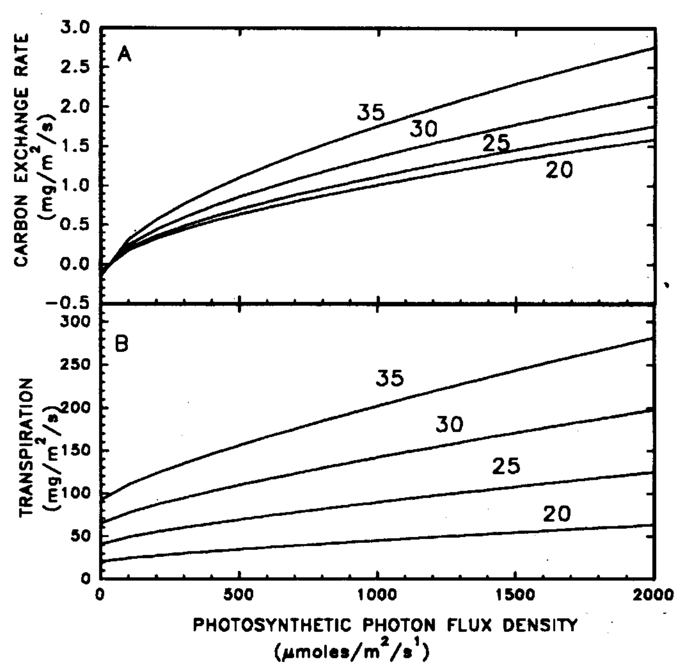

Figure 1. Effect of photosynthetic photon flux density and temperature on A) carbon exchange rate and B) transpiration of redroot pigweed as predicted by equation 1 with constants given in Table 3 (VPD is not held constant, but changes with ambient temperature).

Table 3. Curve-fitting constants and coefficient of determination (r^2) for equation 1 relating redroot pigweed leaf photosynthesis and transpiration to photosynthetic photon flux density and temperature.

X	a	b	c	d	e	f	r^2
CER	–0.1423	0.0265	0.6054	1.273	–0.0678	0.0018	0.92
Transpiration	8.013	0.0428	0.7829	–3.104	0.1066	0.0089	0.80

Equation 1 predicts CER close to values obtained by Singh et al. (10) up to PPFD levels of about 1500 µmol/m²/s. As PPFD increases above this level, CER from equation 1 becomes increasingly greater than observed by Singh et al. (10), e.g., CER at 1925 µmol/m²/s is 1.73 mg/m²/s for the Singh et al. (10) data and 2.09 mg/m²/s for equation 1 data at 30 C. The Patterson (9) CER data are likewise lower than CER from equation 1 at all levels of PPFD, with the largest difference occurring at PPFD of 1925 µmol/m²/s where CER is 0.89 and 1.81 mg/m²/s for the Patterson (9) and equation 1 data, respectively, at 25 C.

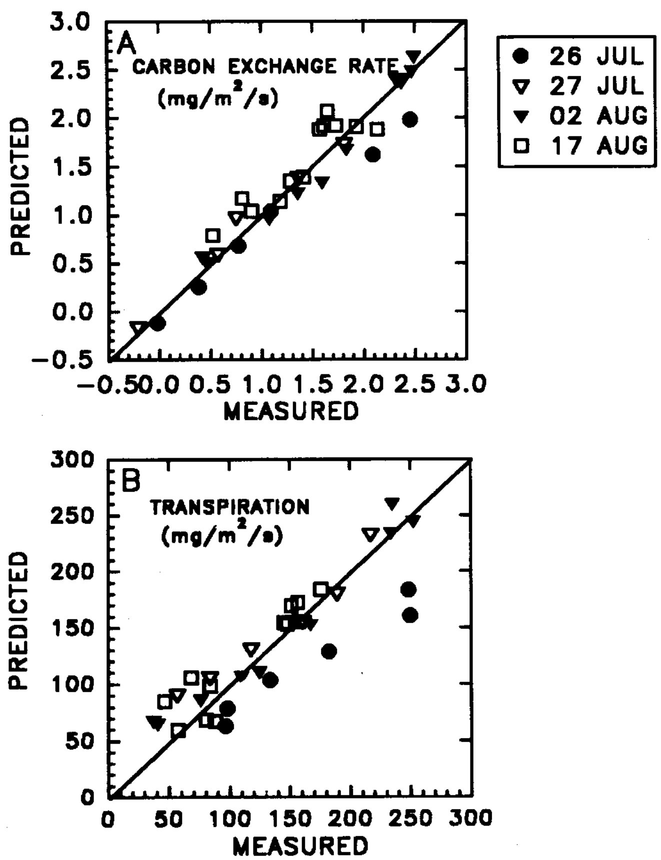

Figure 2. Comparison of field-measured A) carbon exchange rate and B) transpiration of redroot pigweed to values predicted by equation 1 with constants given in Table 3.

The differences in CER could be associated with species differences in photosynthetic capacity, i.e., Patterson (9) studied smooth pigweed, and Singh et al. (10) and equation 1 provide results for redroot pigweed. Another likely explanation for the differences is the observation that redroot pigweed grown under low PPFD had lower maximum photosynthesis rates than plants grown under high PPFD when both were exposed to similar high PPFD (10). The plants measured in our study were grown and measured under the consistently high PPFD conditions found in the field in the central Great Plains during the summer (daily maximum PPFD from 2 June to 21 July averaged 1805 µmol/m²/s). The Singh et al. (10) plants, on the other hand, were field-grown under the more humid and cloudier environment of Illinois, and measurements of CER were made under artificial light conditions in the laboratory. Likewise, the Patterson (9) plants were grown in a controlled-environment greenhouse receiving natural light in the cloudier environment of North Carolina. Also, Patterson (9) measured whole-plant CER which generally will be lower than CER from individual, fully sunlit, upper-canopy leaves.

The temperature response of CER predicted by equation 1 is different than reported by Chu et al. (2) and Patterson (9), probably because of the more limited range of temperature data (Table 2) encountered in the present study. We did not detect CER decreases as temperature rose above 30 C. Equation 1 predicts CER values of 1.46 and 2.29 mg/m²/s at 25 and 35 C, respectively, and 1500 µmol/m²/s.

Kropff and Lotz (7) noted that water use predicted by their crop/weed model was controlled by plant transpiration rates, which was driven by absorbed amount of radiation and vapor pressure deficit (VPD)[4] (VPD is strongly dependent on temperature). Equation 1 predicts similar dependencies of redroot pigweed transpiration on PPFD and temperature (Figure 1B). As temperature rises, the response of transpiration to a given change in PPFD increases. For example, increasing PPFD from 500 to 1500 µmol/m²/s at 25 C increases transpiration rate from 70 to 108 mg/m²/s. At 35 C the same change in PPFD increases transpiration rate from 156 to 244 mg/m^2/s. These predictions are based on data in which VPD was not held constant, but changed with ambient temperature.

Equation 1 and the coefficients presented in Table 3 provide valuable information regarding the interacting influences of temperature and PPFD on CER and transpiration of redroot pigweed that can be used in models of weed growth and competition. This kind of data is essential for developing and validating simulation models of weed growth. Differences between species in equation coefficients, and therefore in plant response to temperature and light conditions, can be important clues as to which species will be more competitive under specific conditions.

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