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Growth, reproduction, and photosynthesis of ragweed parthenium (*Parthenium hysterophorus*)

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Growth and reproductive potential with respect to season and photosynthetic gas exchange behavior under elevated (short-term) CO₂ at varying temperature, relative humidity (RH), and irradiance levels were investigated in ragweed parthenium (also known as carrot grass and congress grass), a noxious weed in India. Lower values of biomass, relative growth rate, net assimilation rate, crop growth rate, leaf area duration, leaf area index, and numbers of flowers and seeds in winter compared with summer stands showed that ragweed parthenium is greatly suppressed by low temperatures during winter. This was due to constrained vegetative growth, seedling emergence, and seed to flower ratio. The species showed maximum photosynthetic response to temperature at 25 to 35 C, and the net photosynthetic rate was reduced considerably at a low temperature (7 C). These temperatures approximately corresponded to the normal temperatures experienced by summer (25–35 C) and winter (7 C) stands of ragweed parthenium. Elevated CO₂ enhanced leaf net photosynthetic efficiency, maximum photosynthetic rate, and water use efficiency (WUE) but decreased the light compensation point for net photosynthesis, stomatal conductance, and transpiration rate. The interactive effects of elevated CO₂ and temperature resulted in a decrease in light-limited and light-saturated net photosynthetic rates and WUE. The interactive effects also reduced an elevated CO₂-induced decrease in light compensation point relative to elevated CO₂ alone. Stomatal conductance was insensitive to photosynthetic photon flux but was greatly influenced by RH. Leaves of the species may show increasing rates of net photosynthesis with a rise in CO₂ and temperature. However, excessive increase in transpiration with temperature, especially at 47 C (noon temperature during summer in the plains of northern India), appears to be disadvantageous for the leaves when conservation of water is of prime importance.

Nomenclature: Ragweed parthenium, *Parthenium hysterophorus* L. PTNHY.

Key words: Elevated CO₂, growth and reproductive potential, humidity, irradiance, temperature, net photosynthesis, water use efficiency.

Ragweed parthenium is an aggressive herbaceous weed of the Asteraceae with an almost worldwide occurrence (Towers et al. 1977). A few plants of this species were first noticed in Pune (India) in the 1950s (Rao 1956), and since then the species has spread and become widely distributed over India with a variety of implications and growing public concerns (Anonymous 1997; Towers et al. 1977). The species continues to spread to newer areas in India including the central Himalayas (Anonymous 1997). It threatens human and animal health, the environment, agriculture, and natural biodiversity through its prolific growth, copious pollen and seed production, and constituent bioactive and toxic allelochemicals (Das and Das 1995; Kanchan and Jayachandra 1980; Mersie and Singh 1988; Pandey 1996; Towers et al. 1977). It causes allergic contact dermatitis, rhinitis, and respiratory problems in sensitive humans. It also results in allergic contact dermatitis in animals. The weed may cause toxicity, sometimes even death, when consumed by animals, especially during summer, when green forage is scarce. Thus, it has tremendous socioeconomic implications affecting human life in various ways. Unchecked growth and spread of the species may exacerbate the socioeconomic implications more as global climate changes.

In India the species is limited presently to about 2,000 m above mean sea level but continues to spread upward

through human activities (Aneja et al. 1991). It is seed-propagated and is capable of completing several life cycles in a year. It infests almost all field crops, pastures, and abandoned land. Ragweed parthenium has been reported to be a C₃–C₄ intermediate, with leaves on top having C₃ mesophyll with non-Kranz leaf anatomy and leaves at the middle and base having C₄ mesophyll with Kranz leaf anatomy (Rajendrudu and Rama Das 1990). Thus, it exhibits features intermediate between C₃- and C₄-plants. The species' response to seasons is poorly understood. Visual observations indicate that ragweed parthenium grows vigorously during summer compared with winter months, probably reflecting temperature sensitivity. However, comparative information on growth and reproductive characteristics of summer and winter stands of ragweed parthenium is lacking.

A large number of reports indicate that atmospheric CO₂ has risen from a preindustrial concentration of about 270 μmol mol⁻¹ air to its present level of over 355 μmol mol⁻¹ air and is likely to double by the end of the 21st century (Carter 1996; Watson et al. 1990). This potential increase may have substantial direct and indirect effects on various life forms, particularly on vegetation, because CO₂ is a substrate for photosynthetic carbon assimilation of plants and also a major greenhouse gas influencing the radiation budget of the earth (Adams et al. 1990; Rhode 1990). Although

several plants have shown increased photosynthesis and growth in response to CO₂ enrichment (Bowes 1993; Ceulemans and Mousseau 1994; Cure and Acock 1986; Kimball 1983; Parry 1990), the magnitude of enhancement depends on species and interacting effects of CO₂ with other environmental factors (Lee and Jarvis 1995; Long 1991; Sage et al. 1989).

The rising concentrations of CO₂ and other greenhouse gases are predicted to increase mean global air temperature by approximately 3 to 6 C by the end of the 21st century (Watson et al. 1990). According to Bolin et al. (1986), the greenhouse gas-induced global warming will be greater at higher altitudes. This may reduce current temperature constraints on occurrence—and productivity potential—of plant species and would probably facilitate the spread of species whose distribution is currently constrained by low temperatures to higher elevations particularly in the northern parts of the world including those in Asia (Parry 1990). Photosynthetic gas exchange analysis can be used to describe the responses of carbon fixation of single leaves and the canopy to changes in the environment (Beadle 1993). The photosynthetic response of leaves to elevated CO₂ in relation to temperature, moisture, and illumination would play a decisive role in determining the fate of a species in a climate. Adequate information is not available on the photosynthetic gas exchange response of ragweed parthenium leaves to changes in the environment.

The present investigation was designed to study growth and reproductive performance of ragweed parthenium with respect to seasons and photosynthetic gas exchange behavior at different levels of CO₂, temperature, light, and relative humidity (RH) to understand the likely effects of these variables on the adaptation of the species.

Materials and Methods

Climate

Meteorological data collected adjacent to the study site during 1996–1997 are shown in Figure 1.

Plant Material

Ragweed parthenium seeds were collected from the surroundings of the institute at Almora (Uttaranchal) and sown in nursery beds and pots (40 cm diameter, 20 L capacity) in sandy loam soil at Kosi (1,144 m above mean sea level, lat 21°37'30"N, long 79°38'9"E) to obtain suitable stands and plants for experiments. Plants emerged and were allowed to form stands in nursery beds, whereas those in pots were thinned to two per pot. The ragweed parthenium stands and pots were watered daily except when it rained. Care was taken not to allow flow of water out of the beds and pots. Nursery stands facilitated both growth and photosynthetic gas exchange studies, and pots facilitated the gas exchange studies at higher temperatures because the plants could be easily moved to a polyhouse with appropriate temperature control. Growth and photosynthetic response during 1996–1998 did not obviously differ between the two media.

Growth Analysis

Ragweed parthenium seeds were sown in plots (200 seeds m⁻²) in the first week of April and October 1996–1997 for summer and winter stands, respectively. There were three replicate plots each for the summer and winter stands. Fifty days after emergence (just before flowering), 10 representative plants were sampled from each of the three plots, washed to remove soil, and used for the growth studies. Plant height was measured to the apical meristem. Plants were separated into stems, leaves, and roots and weighed. Leaf area was measured immediately using a portable leaf area meter.¹ The plant parts were swiftly cut to small (< 1.0 cm) pieces and uniformly mixed. For determination of dry weights, a representative 100 g each of fresh root, shoot, and stem tissue or the whole mass (if less than 100 g) was oven dried at 80 C to constant weight. Total plant dry weights were calculated by adding up weights of individual components. Using these plant attributes different growth functions, e.g., relative growth rate (RGR) = $(\ln W_2 - \ln W_1)/(t_2 - t_1)$; net assimilation rate (NAR) = $[(W_2 - W_1)/(t_2 - t_1)] \times [(\ln S_2 - \ln S_1)/(S_2 - S_1)]$; crop growth rate (CGR) = $[(S/G) \times (W_2 - W_1)]/[(t_2 - t_1) \times (1/S)]$; leaf area duration (LAD) = $[(L_2 + L_1)] \times [(t_2 - t_1)]/2$; and leaf area index (LAI or *L*) = S/G were calculated (Beadle 1993) using various attributes: whole plant dry weight (*W*), leaf area (*S*), ground area (*G*), and time (*t*), where 1 and 2 denote a time of 10 (emergence completed) and 50 d after sowing of the seeds, respectively.

Flower production was monitored in 10 representative plants in each of three plots in the institute nursery at the end of bloom (about 120 d after sowing) by counting traces of dehiscent seeds and all the flowers. Seed production was calculated by multiplying number of flowers by mean number of seeds per capitulum (flower) for 100 flowers each in triplicate for both summer and winter stands.

Effect of Season on Emergence of Parthenium

Ragweed parthenium seeds (200 m⁻²) were sown in each of three plots in the institute nursery in the first week of April 1996, allowed to grow, flower, and produce and shed seeds through natural death of the plants. Residue of the dead plants was chopped to pieces (< 2 cm) and spread over the same beds. Emergence of parthenium was monitored as normal plants from August 1996 to August 1997. We have found that lemna (*Lemna paucicostata* Hegelm.) was more sensitive to the inhibitory activity of ragweed parthenium residue than were ragweed parthenium seed germination and seedling growth. Aqueous extracts of soil from the plots (prepared by pouring into 50 ml of soil an equal volume of distilled water and stirring for 2 h at 25 C) did not test positive for inhibitory activity in a lemna growth bioassay test (Einhellig et al. 1985), ruling out autotoxicity due to possible leaching of inhibitors from the weed residue (data not shown). Therefore, it was deduced that emergence and growth of ragweed parthenium plants in the plots were a function of temperature.

Effect of Season on Seed to Flower Ratio Index

The effect of low temperature on seed formation was studied by monitoring seed production in relation to num-

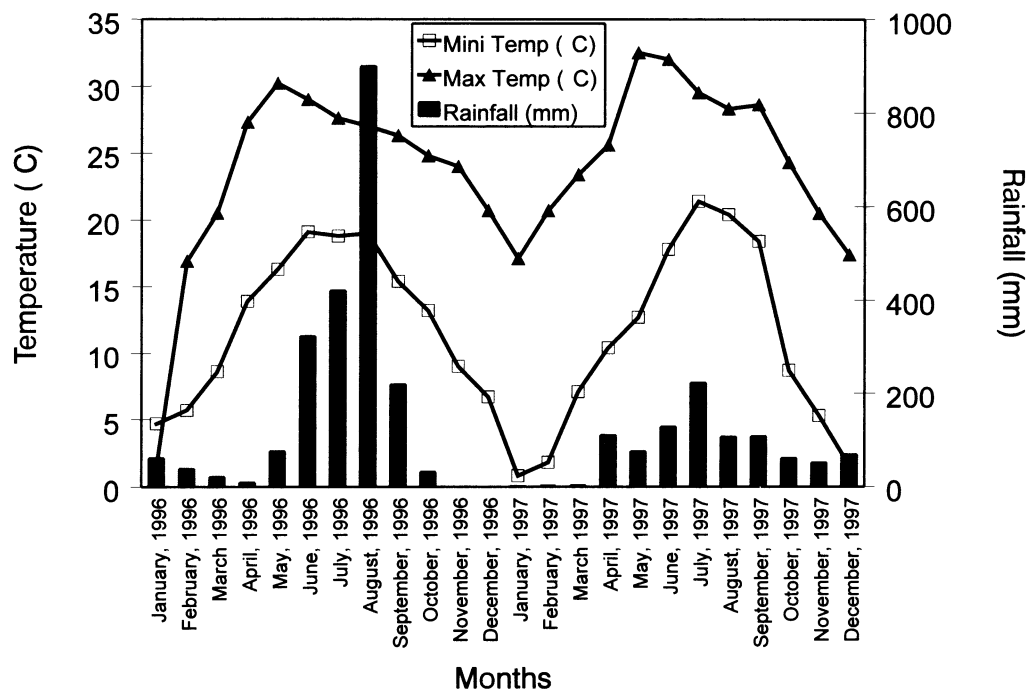


FIGURE 1. The meteorological data of the experimental site during 1996–1997.

ber of flowers borne on the plant. The seed to flower ratio (SFR) = (number of seeds/number of flowers) \times 100. The ragweed parthenium plants were protected from frost by being covered with 500-gauge polyethylene sheets during the night. Seeds and flowers were counted on two plants in five replications at intervals from November 1996 to April 1997 and values of SFR computed. This was done on summer and winter stands.

Field Measurements of Gas Exchange

Gas exchange was measured on 10 single fully grown leaves on each of 10 well watered plants in the pots and in the nursery beds. The measurements were repeated three times on different sets of plants over 3 mo in summer (April to June, 1996–1998) for temperatures of 25, 35, 36, and 44 C. Measurements at lower temperatures of 7 and 20 C were made similarly on plants grown in winter (October to December, 1996–1998). The measurements were made at a time and on a day when the temperature was within ± 5 C of the required temperature, as the LI-6400 leaf chamber had provision for temperature control within this limit only. For temperatures of 34 and 44 C during April through June, pots containing plants were transferred to polythene chambers (polyhouses) maintained at 36 ± 3 C and 44 ± 3 C, using heat convectors, and equilibrated for 30 min. The plants in the pots were kept under these conditions for half an hour before the measurements were made and were removed afterward but not later than after another half an hour. The temperature 47 C was chosen because during summer in northern India the noon temperature is often as high as 47 C, and ragweed parthenium grows at this temperature.

Gas exchange was measured on fully grown leaves between the fifth node down from the tip and the fifth node above the stem base. Effects of CO₂, temperature, photosynthetic photon flux (PPF), and RH on net photosynthesis

and related parameters (e.g., stomatal conductance, internal CO₂ concentration, transpiration, and water use efficiency [WUE]) of ragweed parthenium were measured. Gas exchange measurements were made with an open-flow gas-exchange system² equipped with an LED red-light source³ built onto the top of the leaf chamber for control of light intensity and a CO₂ injection system⁴ for control of CO₂ concentration. The CO₂–H₂O analyzer was calibrated for CO₂ using a cylinder of known CO₂ concentration and for water vapor with a humidity dew point generator⁵ at regular intervals during measurements. Carbon dioxide supply from a cylinder was controlled using a CO₂ scrubbing column. Air was humidified by being bubbled through water at ambient temperature, and humidity was controlled by passing the air flow through a desiccant, dririte⁶.

Effect of temperature on net photosynthesis at 360 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air (corresponding to present ambient CO₂ level) was studied at 7, 25, 35, and 47 C (covering temperatures experienced by ragweed parthenium) and 30% RH (keeping it constant for facilitating comparison). Photosynthetic temperature response at elevated CO₂ (700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air) was determined at 20, 30, 40, and 47 C cuvette air temperature and 30% RH. Net photosynthesis was measured at different concentrations of external CO₂ (360, 700, 1,000, and 2,000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air) at 30 C and 30% RH. The effect of humidity was studied at 30 and 60% RH. Measurements were made over a range of PPF (10 to 2,000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$). Net photosynthesis rate, transpirational water loss, stomatal conductance for water, and internal CO₂ concentration (C_i) were calculated according to Von Caemmerer and Farquhar (1981). WUE was calculated as the ratio of net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). Each observation recorded by the equipment was the mean of 10 measurements.

The experimental data were subjected to analysis of variance (Cochran and Cox 1957), and significant differences

TABLE 1. Relative growth characteristics of ragweed parthenium (*Parthenium hysterophorus* L.) during summer (May–July) and winter (October–December) in 1996–1997 influence of season.

Attribute	Season				LSD at < 0.05	
	Summer (S)		Winter (W)			
	1996 (Y1)	1997 (Y2)	1996 (Y1)	1997 (Y2)	Y1 × Y2	S × W
Growth characteristics						
Leaf area index	5.64	5.89	3.38	3.60	NS ^a	0.931
Mean		5.76		3.49		
Relative growth rate (g g ⁻¹ d ⁻¹)	0.080	0.080	0.053	0.056	NS	0.006
Mean		0.080		0.054		
Net assimilation rate (g m ⁻² d ⁻¹)	4.768	4.806	0.550	0.665	NS	0.530
Mean		4.787		0.607		
Crop growth rate (g m ⁻² d ⁻¹)	15.72	16.00	1.51	1.83	NS	2.209
Mean		15.86		1.67		
Leaf area duration (d)	259.5	365.3	157.1	162.0	NS	41.910
Mean		312.4		159.5		
Plant height (m)	1.779	1.730	0.148	0.157	NS	0.306
Mean		1.755		0.152		
Production (m ⁻²)						
Biomass (kg)	1.414	1.440	0.136	0.165	NS	0.199
Mean		1.427		0.150		
Flowers (in thousands)	42.956	41.686	0.365	0.447	NS	5.471
Mean		42.325		0.406		
Seeds (in thousands)	147.965	116.746	0.365	0.478	NS	18.614
Mean		132.355		0.421		

^a NS = not significant.

between treatments were computed using tables provided by Fisher (1946). The SFR and photosynthetic gas exchange were analyzed by completely randomized block design, and seedling count and growth were analyzed by randomized block design.

Results and Discussion

Weather data during 1996 and 1997 are shown in Figure 1. Low temperatures and spells of frost characterized the winter, especially in December. The summer had comparatively moderate temperatures.

The low winter temperature considerably reduced growth performance, flowering and seed production, and photosynthesis of ragweed parthenium. This was evident from reductions in LAI, RGR, NAR, CGR, and LAD, resulting in significant ($P < 0.05$) reductions in biomass and numbers of flower and seed production (Table 1). The winter plants were stunted, with small leaves and little branching. Winter stands had lower SFR (90.7) than did summer stands (344.4) (LSD at $P < 0.05$ was 51.4).

Subsequent to stand death, fallen seeds continued to emerge and grow, though poorly, into plants until October. Thereafter, in the winter bed the number of normal plants declined, and by January all plants had died, with no ragweed parthenium plants or seedlings observed until near the end of winter in the third week of March 1997, when a few seedlings emerged. The beds were fully covered with ragweed parthenium seedlings by the second week of April (Figure 2), and luxuriant growth followed.

The SFR decreased during December and was nil by January through mid February and started rising by the end of February and continued through April (Figure 3). This appeared to be a function of temperature.

The effect of light and temperature on leaf net photosynthesis and transpiration at ambient CO₂ concentration and 30% RH is shown in Figure 4. Net photosynthesis increased with increasing PPF from 10 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ except at 47 C, where maximum net photosynthesis occurred at 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Net photosynthesis declined at all temperatures when PPF was $> 1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$. Maximum net photosynthetic rates were observed at 25 and 35 C. Though both high and low temperatures were inhibitory to ragweed parthenium, the overall rate of net photosynthesis was lowest at a high temperature (47 C). There was an increase in light compensation value, the PPF at which net photosynthesis is zero, with temperatures above 25 C. The value was maximum at 47 C and minimum at 7 and 25 C. Irrespective of PPF, transpiration doubled with an increase in temperature from 7 to 25 C, and it further doubled at 35 C. Transpiration at 47 C was about three times greater than at 35 C.

The interactive effects of CO₂ concentration and PPF showed that net photosynthesis increased as light levels increased up to 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and declined at higher light levels at all levels of CO₂ from 360 up to 2,000 $\mu\text{mol mol}^{-1}$ air (Figure 5a). The decline was more pronounced at the higher CO₂ concentrations. At the optimum PPF of 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, photosynthesis at 2,000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air was nearly threefold higher than that at 360 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air. The light compensation point decreased with an increase in CO₂ concentration. Stomatal conductance also decreased at elevated CO₂ concentrations, with maximum reduction at 2,000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air, regardless of PPF (Figure 5b). Transpiration decreased at elevated CO₂ concentrations independent of PPF. Transpiration measured at 700, 1,000, and 2,000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air was about 34% of the value obtained at 360 $\mu\text{mol CO}_2$

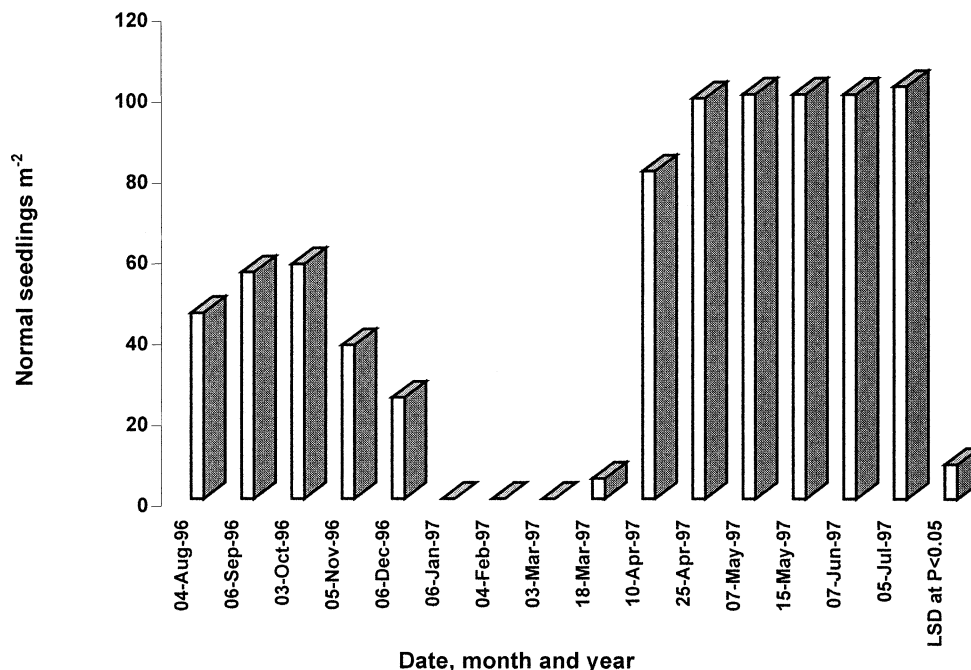


FIGURE 2. Effect of season on ragweed parthenium (*Parthenium hysterophorus* L.) seedlings. Values are means of three replications.

mol⁻¹ air (Figure 5d). WUE also increased with increasing PPF and CO₂ concentration, with a maximum recorded WUE at a PPF between 500 and 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for all CO₂ levels (Figure 5e). Ci increased as external CO₂ increased, and it decreased with increasing PPF (Figure 5c).

The effect of temperature and light on leaf photosynthesis at elevated CO₂ (Figure 6a) indicates that elevated CO₂-induced increases in both light-limited and light-saturated net photosynthetic rates decreased at 47 C. There appeared to be a shift in the irradiance level for optimum net photosynthesis at elevated CO₂. Light saturation of net photosynthesis occurred at 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF at all temperatures at elevated CO₂. Whereas stomatal conductance further decreased with increased temperature at elevated CO₂ (Figure 6b), transpiration increased with increase in temperature regardless of PPF (Figure 6d). Ci decreased sub-

stantially with increase in temperature at higher PPFs (Figure 6c). This decrease was lower at lower PPFs except at the high temperature (47 C), where it increased relative to the value obtained at 40 C despite no apparent differences in stomatal conductance between 40 and 47 C. This suggests an increase in biochemical limitations to net photosynthesis at 47 C. The WUE also decreased substantially with increased temperature (Figure 6e).

The effects of RH and PPF on net photosynthesis and related parameters at 700 $\mu\text{mol CO}_2 \text{mol}^{-1}$ air at 25 C are shown in Figure 7. In general, net photosynthesis, Ci, WUE, and stomatal conductance were considerably higher at 60 than at 30% RH at any given light level. However, there was no obvious effect of RH on transpirational water loss.

Weather data for the study period show marked differences in summer and winter temperatures. This was associated with differences in growth and reproductive potential in summer and winter stands of ragweed parthenium. A significant ($P < 0.05$) reduction in RGR observed in the winter stand was invariably associated with reduced NAR, CGR, LAD, and LAI (Table 1). Plant growth ultimately depends on both photosynthetic area and photosynthetic rate. A low temperature is known to influence leaf photosynthesis by reducing photosynthetic efficiency of the existing leaves, by affecting the development of new leaves, thereby causing a reduced net photosynthetic efficiency at maturity, and by affecting translocation of photosynthate (Beale et al. 1996; Brown 1982). However, predicting plant growth on the basis of photosynthetic response of one leaf is difficult. On the other hand, it has also been demonstrated that an increase in temperature alone could increase growth in several species by providing more optimal temperature conditions for photosynthesis (Mikola 1952). Thus, the poor performance of ragweed parthenium in winter may be attributed to reduced leaf area (Table 1); and reduced pho-

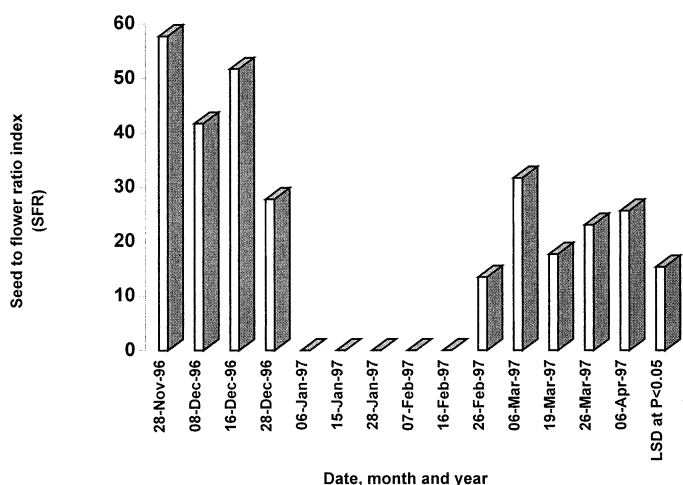


FIGURE 3. Effect of season on seed to flower ratio in ragweed parthenium (*Parthenium hysterophorus* L.) during 1996–1997. Values are means of five replications.

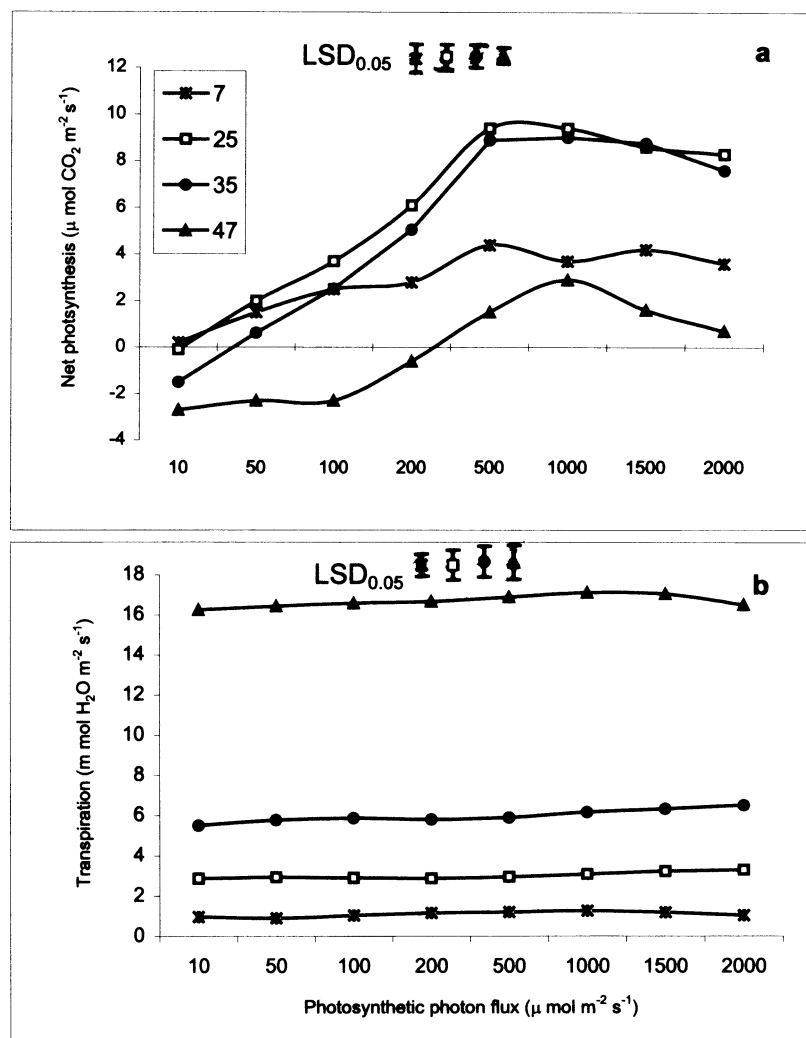


FIGURE 4. The effect of temperature (7, 25, 35, and 47 C) and photosynthetic photon flux on (a) photosynthesis and (b) transpiration at ambient CO₂ concentration and 30% relative humidity. Vertical bars represent LSD at $P < 0.05$.

photosynthetic capacity and reduced photosynthetic efficiency may be due to low temperature. In addition to reduced leaf area and reduced photosynthetic capacity, the poor performance of ragweed parthenium during the winter appears to be due also to lower photosynthetic efficiency, as indicated by the reduced NAR (Table 1) and lower rates of net photosynthesis (Figure 4a)—that is to say, in addition to reduced leaf area and reduced overall growth, the rates of net photosynthesis per unit leaf area were greatly reduced in winter ragweed parthenium, especially under high PPF (Figure 4a). This assumption is partly supported by the net photosynthetic temperature response curve of ragweed parthenium (Figure 4). Ragweed parthenium exhibited maximum net photosynthetic rate between 25 and 35 C, which corresponds roughly to temperatures experienced by the plants during summer, whereas at 7 C, which corresponded to the prevailing low temperature at Kosi during winter, the rate of photosynthesis was considerably reduced. Differences in inherent RGR among species have been attributed to differences in NAR, leaf area ratio, specific leaf area, leaf mass ratio, photosynthesis, and respiration (Lambers and Poorter 1992).

Lack of inhibition of germination or growth of ragweed

parthenium in the beds clearly showed that the species alone or with its residue was not toxic to emergence of its own seeds. This rules out autotoxicity and its possible role in regulating the life cycle of the species under prevailing conditions (Picman and Picman 1984). Apparently, emergence and seedling growth and survival depended on temperature because from January to March there was no emergence of seedlings in the bed and the existing seedlings were killed before the end of December due to low temperatures and night frost. Thus, winter temperatures did not allow growth of ragweed parthenium.

The SFR shows that seed formation was reduced in winter, as shown by lower values in winter than in summer stands, and that seed formation stopped at low winter temperatures and resumed with the onset of warm temperatures. The mechanism of inhibition of seed formation by low temperatures has not been explained. However, the winter temperature at the site facilitated flowering with normal viable pollen (results not presented).

Anatomy of the top leaves of ragweed parthenium was non-Kranz C₃ with C₃-type mesophyll. Leaves in the middle had C₄ Kranz anatomy with C₄-type mesophyll. Leaves at the base had Kranz anatomy with C₄-type mesophyll (results

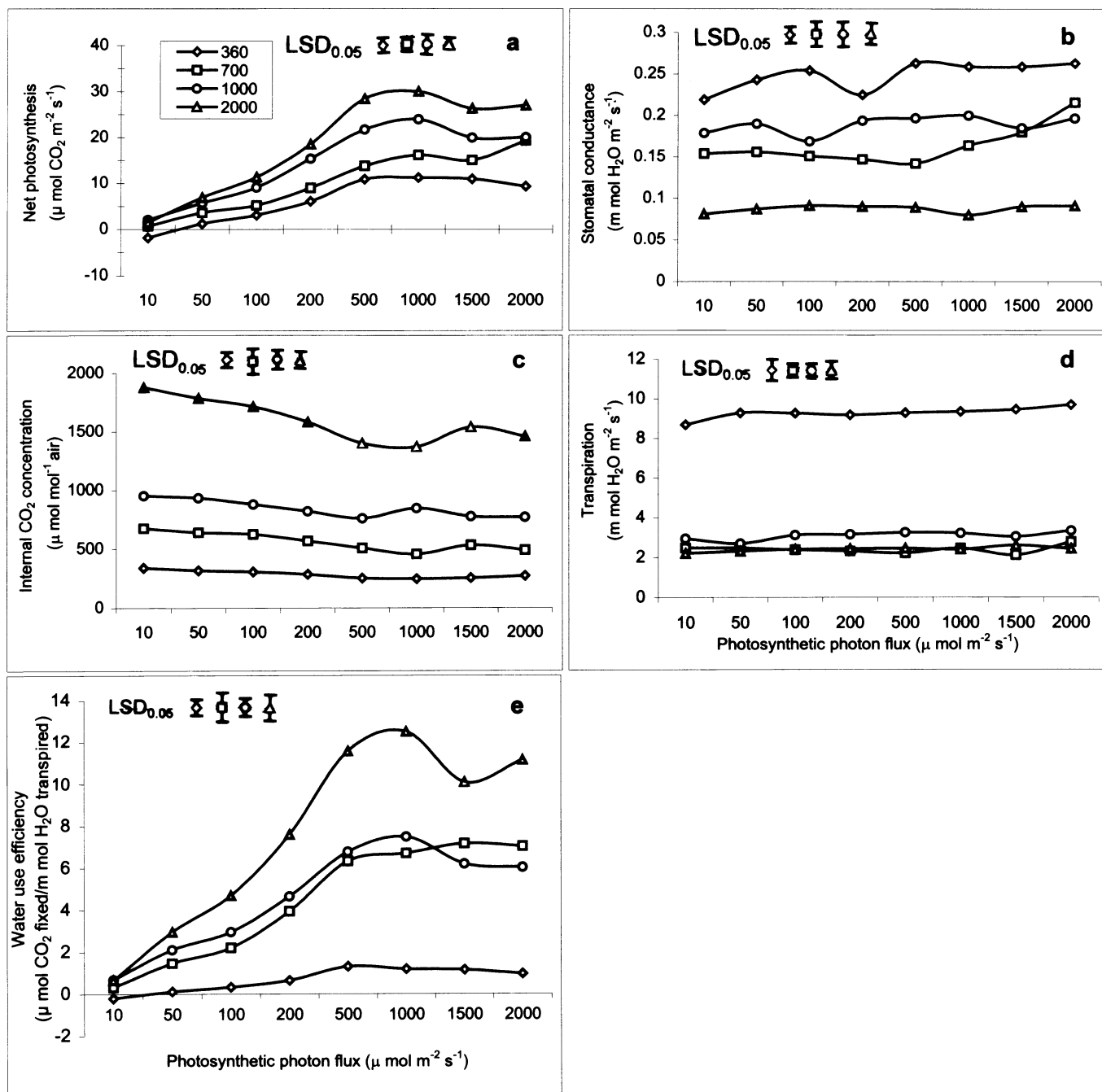


FIGURE 5. The effect of CO₂ concentration and photosynthetic photon flux on (a) photosynthesis, (b) stomatal conductance, (c) internal CO₂ concentration, (d) transpiration, and (e) water use efficiency at 30 C and 30% RH. Vertical bars represent LSD at P < 0.05.

not presented) as has been reported by Rajendrudu and Rama Das (1990). Further, we have found that ragweed parthenium leaves have a chlorophyll a/b ratio of 2.69 (irrespective of leaf position on the stem) compared with 3.2 in bermudagrass [*Cynodon dactylon* (L.) Pers.] and 3.34 for corn (*Zea mays* L.), both C₄ plants. The leaves did not show differentiation into C₃ and C₄ photosynthetic types under starch granule iodine staining in situ (Bolhar-Nordenkamp and Draxler 1993). Earlier reports showed that ragweed parthenium exhibited C₃-like carbon isotope discrimination (Rajendrudu and Rama Das 1990). Photosynthetic gas exchange results in the present study appear to be those typical of C₃ plants. Thus, whole plant response to carbon dioxide

levels in the present case appears to be predominantly that of a C₃ type. It is evident from the effects of light and temperature on net photosynthesis that maximum photosynthetic activity in ragweed parthenium occurred at temperatures of 25 to 35 C and PPF of 500 to 1,000 μmol m⁻² s⁻¹. Though both high and low temperatures markedly reduced net photosynthetic rates in ragweed parthenium, the overall decrease was greater at higher temperatures, probably indicating its greater inclination toward C₃ physiology. It must be noted that photosynthetic measurements in the present study were made on leaves between the fifth node from the shoot tip and above the fifth node from the base of the plant. Thus, this investigation revealed that the pho-

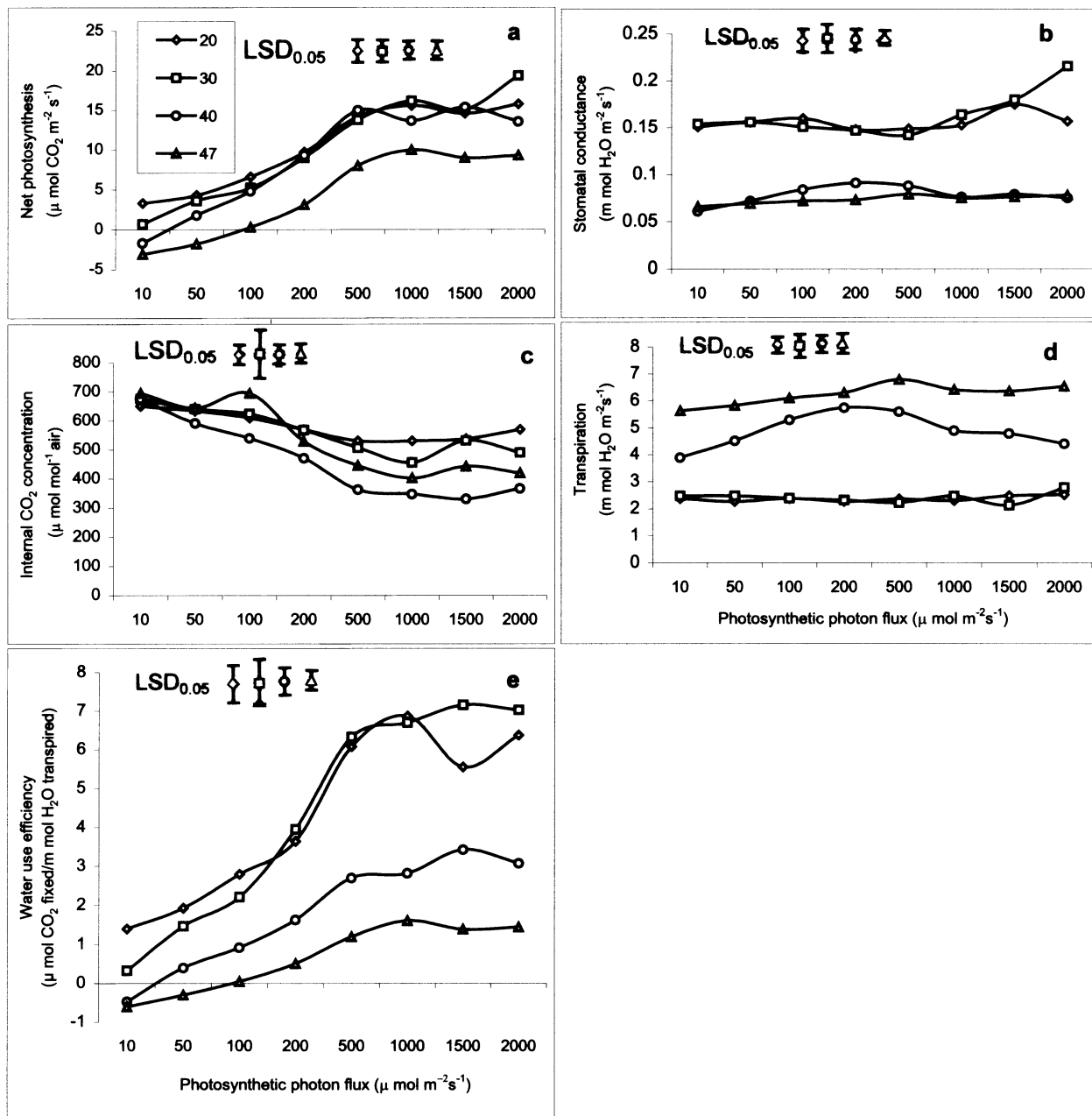


FIGURE 6. The effect of elevated CO₂ (700 μmol mol⁻¹ air) and temperature (20, 30, 40, and 47 C) on (a) photosynthesis, (b) stomatal conductance, (c) internal CO₂ concentration, (d) transpiration, and (e) water use efficiency at 30% relative humidity. Vertical bars represent LSD at P < 0.05.

tosynthetic characteristics of ragweed parthenium resemble those of a representative C₃ plant. Drastic increases and decreases in transpiration and net photosynthesis, respectively, at high temperature (47 C) suggest that high temperature is a disadvantage for the species. Summer stands of ragweed parthenium in the plains of northern India experience brief exposure to temperatures as high as 47 C at noon (D. K. Pandey, unpublished data).

The evidence indicates there is increased growth and photosynthetic rate in plants exposed to elevated CO₂ (Bazzaz 1990; Ceulemans and Mousseau 1994; Eamus and Jarvis 1989; Kimball 1983; Mousseau and Saugier 1992). This is more true in species whose photosynthesis is not saturated by the present CO₂ concentration (Lawlor and Keys 1993; Mooney et al. 1991). Net photosynthetic rate of ragweed

parthenium was greatly enhanced by short-term elevation of CO₂ (Figure 5a). Net photosynthetic rate increased as CO₂ concentrations increased from 360 up to 2,000 μmol mol⁻¹. It has been demonstrated that a short-term increase in atmospheric CO₂ concentration increases net photosynthesis in C₃ plants by increasing the velocity of carboxylation and substrate concentration at the primary carboxylating enzyme (Drake et al. 1997). Though the response of CO₂ assimilation as a function of C_i was not determined, it is evident from Figure 6 that both initial slope, which is an indirect effect of RubP carboxylase (Sage 1994; Von Caemmerer and Farquhar 1981), and maximum net photosynthetic capacity increased with increasing CO₂ concentration in ragweed parthenium.

Many CO₂ enrichment studies have shown that very high

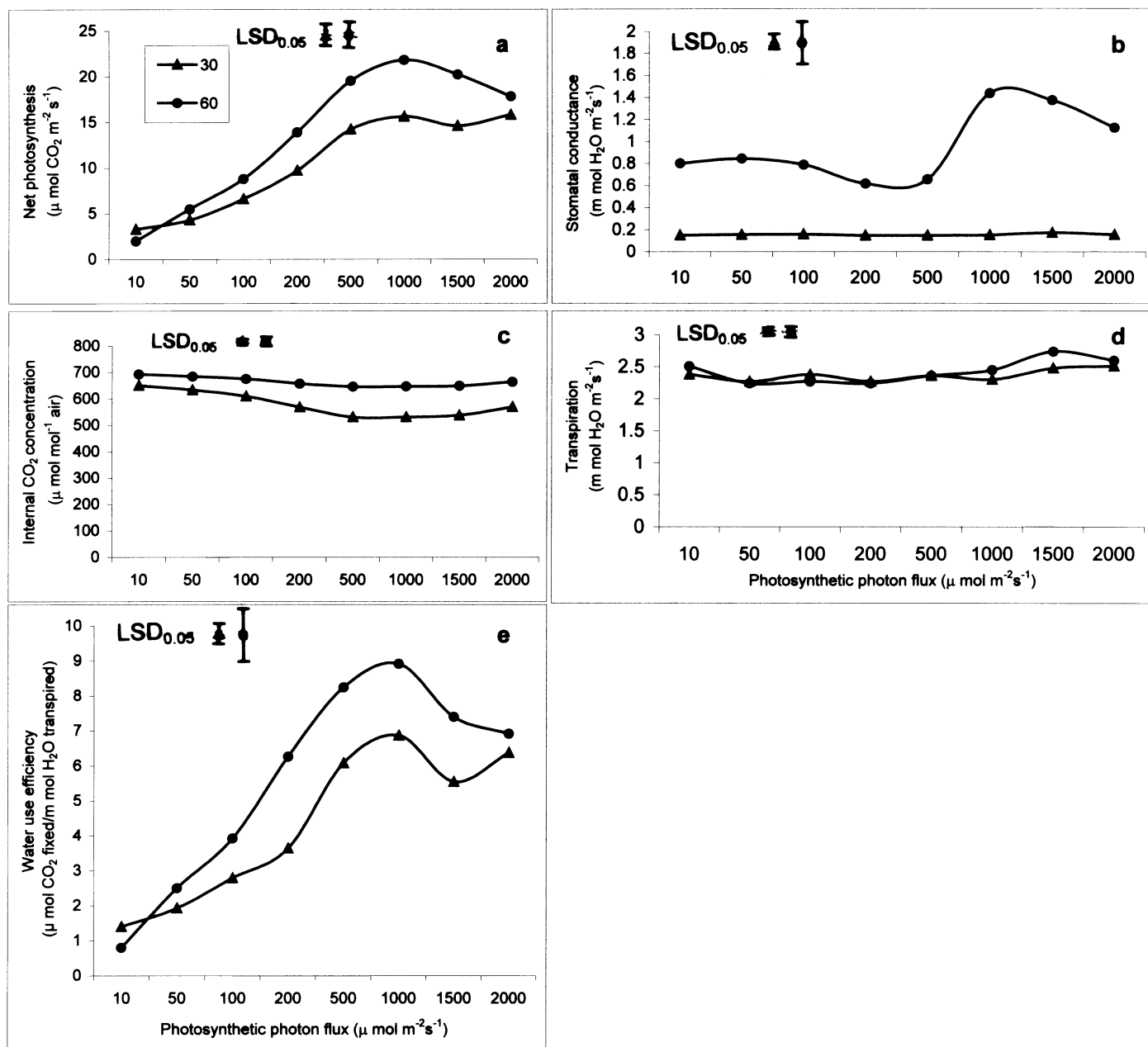


FIGURE 7. The effect of relative humidity (30 and 60%) on (a) photosynthesis, (b) stomatal conductance, (c) internal CO_2 concentration, (d) transpiration, and (e) water use efficiency at elevated CO_2 ($700 \mu\text{mol mol}^{-1}$ air) at 25°C . Vertical bars represent LSD at $P < 0.05$.

CO_2 concentrations ($> 1,200 \mu\text{mol mol}^{-1}$ air) inhibit photosynthesis and growth of plants (Mackowiak and Wheeler 1996; Madson 1974; Reuveni and Bugbee 1997). A twofold increase in net photosynthesis in ragweed parthenium when measurements were made at $2,000 \mu\text{mol CO}_2 \text{mol}^{-1}$ air as compared with measurements made at $700 \mu\text{mol CO}_2 \text{mol}^{-1}$ air at 30°C clearly indicates that elevation of CO_2 concentration to $2,000 \mu\text{mol mol}^{-1}$ air may not be harmful to its net photosynthesis and growth. Though it has been reported that short-term measurement of photosynthetic rate may overestimate the potential for carbon assimilation of plants, particularly in those species which show down-regulation (depression by the accumulation of starch or by reduction of Rubisco [ribulose biphosphate carboxylase oxygenase enzyme]) of photosynthesis (Kalina and Ceulemans

1997; Sage et al. 1989) when subjected to long-term exposure to elevated CO_2 (Oechel and Strain 1985), this short-term study provides an approximation of the potential of ragweed parthenium for long-term high rates of carbon assimilation with elevated CO_2 .

Elevated CO_2 -induced enhancement of leaf net photosynthesis in ragweed parthenium was influenced by light and temperature (Figures 5a and 6a). There was a shift in light optimum for net photosynthesis with elevated CO_2 (Figure 6a). Higher net photosynthesis is attributed to greater supply of CO_2 at the fixation site in the chloroplast as C_i increased with increased external CO_2 concentration. In contrast to light, there was no shift in temperature optima with elevated CO_2 , whereas CO_2 -induced enhancement of quantum yield in ragweed parthenium was decreased by increas-

ing temperature (Figure 6a). This has been observed in many C_3 species (Berry and Bjorkman 1990). However, even at 47 °C, the overall rates of net photosynthetic CO_2 assimilation were high at elevated CO_2 relative to ambient CO_2 at all PPF levels tested (Figures 4a and 5a). There is also evidence that CO_2 enrichment ameliorates the adverse effects of high temperature in plants (Bazzaz 1990).

It has been shown that stomatal conductance generally decreases with increasing atmospheric CO_2 concentration, but the magnitude of stomatal response to elevated CO_2 is quite variable and depends on other environmental factors (Curtis 1996; Field et al. 1995; Morison 1998). Stomatal conductance in the present study decreased at elevated CO_2 and temperature. The extent of reduction increased with CO_2 , and an increase of temperature further enhanced the CO_2 -induced reduction. However, the rate of reduction was little influenced by PPF. Small changes in stomatal conductance due to CO_2 enrichment in response to PPF have been reported for *Eucalyptus pauciflora* Sieb. ex Spreng. (Wong et al. 1978) and five herbaceous species (Sharkey and Raschke 1981). However, at 60% RH, stomatal conductance of ragweed parthenium increased, especially at PPF levels from 500 up to 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The conductance values were much higher than those observed at 30% RH, probably indicating stomatal sensitivity to humidity (Comstock and Ehleringer 1993).

C_i , which is regarded as a set point in gas exchange metabolism for studying how plants respond to environmental changes (Ehleringer and Cerling 1995), provides a means of assessing the relative importance of stomatal and mesophyll processes in limiting photosynthesis (Renburg and Kruger 1993). In the present investigation, C_i values increased with CO_2 concentration despite considerable decreases in stomatal conductance. In contrast, C_i decreased with increasing temperature. However, at a high temperature (47 °C), the C_i value increased relative to that at 40 °C despite no differences in stomatal conductance between 40 and 47 °C. These results suggest that both stomatal and mesophyll components are involved in the regulation of C_i . However, the magnitude of involvement of stomatal and mesophyll components in the regulation of C_i varied with changes in CO_2 and temperature. The rate of transpiration under different temperature and PPF levels clearly indicates that temperature, rather than light, is the major factor controlling transpiration rate. Similar results have been obtained for alpine (Rawat and Purohit 1991) and woody plants (Alexander et al. 1995). Increasing concentration of CO_2 reduced transpiration (Figure 5d), as has been reported for many plants exposed to elevated CO_2 (Bazzaz 1990; Field et al. 1995; Green et al. 1995; Oechel and Strain 1985). Transpiration increased substantially at elevated CO_2 with increasing temperature in cotton (*Gossypium hirsutum* L.) (Reddy et al. 1998).

An increase in instantaneous WUE of ragweed parthenium was observed at elevated CO_2 . Several studies have shown an increase in instantaneous WUE of plants with elevated CO_2 as a consequence of lowered stomatal conductance for water–transpiration rate and enhanced photosynthesis or both (Ceulemans and Mousseau 1994; Kimball 1983). In the present study, a combination of increased net photosynthesis and decreased transpiration was responsible for the increase in WUE. However, the elevated CO_2 -in-

duced increase in WUE was greatly reduced by increasing temperature, primarily as a result of increased transpiration.

The present findings show that ragweed parthenium may perform better with global temperature and atmospheric CO_2 increases. However, higher temperatures drive increased transpiration, especially during warmer summer days and may, depending on the temperature, reduce its invasiveness or even threaten survival. This is so if a species is unable to check excessive loss of water when conservation of water is necessary. Increase in winter temperature due to global warming may facilitate growth, reproduction, and invasiveness of ragweed parthenium during winter months in areas like the central Himalayas of India, where currently the species is constrained due to low temperatures. This might result in increased threats to human and animal health, agriculture, the environment, and natural biodiversity of the region. Increased invasiveness of the species due to atmospheric CO_2 and temperature increases may cease when the temperature rises beyond an undefined limit during the warmer days and months as this may cause an increase in transpiration, threatening the survival of the species. The effect of RH on photosynthesis and related parameters as implied by the present study (Figure 7) reveals that arid conditions may reduce its performance and invasiveness by reducing both net photosynthesis and water economy. Thus, survival at higher temperatures due to excessive transpiration may become more difficult. This may restrict the species from invading and predominating arid areas of India and elsewhere.

Sources of Materials

- ¹ Portable leaf area meter, model LI3000A, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.
- ² Portable photosynthesis system, model LI6400, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.
- ³ LED red-light source, model LI6400-02, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.
- ⁴ CO_2 injection system, model LI6400-01, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.
- ⁵ Dew point generator, model LI610, Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.
- ⁶ Desiccant, dririte, supplied by Li-Cor Corporation, 4421 Superior Street, Lincoln, NE 68504.

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