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GAS EXCHANGE, $\delta^{13}C$, AND HETEROTROPHY FOR *CASTILLEJA LINARIIFOLIA* AND *ORTHOCARPUS TOLMIEI*, FACULTATIVE ROOT HEMIPARASITES ON *ARTEMISIA TRIDENTATA*

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ABSTRACT.—Gas exchange and carbon isotope ratios were measured on 2 facultative hemiparasites, *Castilleja linariifolia* Benth. (Indian paintbrush; Scrophulariaceae) and *Orthocarpus tolmiei* H. & A. (Tolmie owl clover; Scrophulariaceae), and their *Artemisia tridentata* L. (big sagebrush; Asteraceae) hosts. Photosynthetic rates differed greatly between years; rates in 1995 were more than double those in 1994, likely due to more precipitation and less water stress during 1995. Despite this difference in precipitation, photosynthetic rates for *C. linariifolia* were not different from those of their hosts for either year. However, carbon isotope ratios of *C. linariifolia* and *O. tolmiei* were up to 3‰ more negative than those of their *A. tridentata* hosts. Using measured $\delta^{13}C$ ratios in conjunction with $\delta^{13}C$ ratios predicted from gas-exchange measurements, we calculated that *C. linariifolia* derived, on average, 40% of its leaf carbon heterotrophically. Contrary to current suggestions that high photosynthetic rates of hemiparasites are an indication of reduced heterotrophy, *C. linariifolia* exhibited photosynthetic rates similar to autotrophic plants and used a substantial amount of host-derived carbon. Moreover, this evidence shows that manipulation of a heterotrophic carbon supply transcends obligate hemiparasites to include those plants whose parasitism is facultative.

Key words: heterotrophy, hemiparasite, photosynthesis, carbon isotope ratios, shrub ecology.

Hemiparasites, chlorophyllous parasitic plants, form an apoplastic continuum with host xylem (Raven 1983). It has been assumed that these plants are largely autotrophic plants, being parasitic only for water and minerals (Smith et al. 1969). However, hemiparasites may also gain carbon through the passive uptake of dilute concentrations of organic carbon contained within host xylem sap (Raven 1983). Early studies using radiocarbon labeling demonstrated the transfer of solutes from host to parasite (Hull and Leonard 1964, Govier et al. 1967), although it was not possible to quantify this flux. Experiments of Govier et al. (1967), in which [^{14}C]urea or $^{14}CO_2$ was fed to hosts, showed the movement of ^{14}C labeled compounds to all parts of the hemiparasite *Odontites verna* (Scrophulariaceae). More recent studies used a carbon budget model and/or a $\delta^{13}C$ method to quantify the extent of heterotrophy (Press et al. 1987a, Graves et al. 1989, Marshall and Ehleringer 1990, Schulze et al. 1991, Marshall et al. 1994, Richter et al. 1995). Using the latter method, Press et al. (1987a) calculated that 28–35% of total carbon in *Striga hermonthica* and *Striga asiatica* (Scrophulariaceae) is host-derived carbon. There is also ample evidence that hemiparasitic mistletoes utilize host-derived carbon, although the values vary greatly, from 5% to over 60% (Marshall and Ehleringer 1990, Schulze et al. 1991, Marshall et al. 1994, Richter et al. 1995). Despite the potential importance of heterotrophy to carbon acquisition in parasitic plants, relatively few studies have addressed this aspect of parasite-host interactions. Moreover, none have evaluated the exploitation of this carbon source by facultative root hemiparasites.

Photosynthetic rates of hemiparasites fall within the lower range reported for C_3 plants and are generally much lower than photosynthetic rates of the host. *S. hermonthica* has a poorly developed palisade mesophyll, contributing, in part, to photosynthetic rates as low as 2.5 μmol m^{-2} s^{-1} (Shah et al. 1987). Moreover, these rates are half those reported for their *Sorghum* hosts (Press et al. 1987b). *Striga* species are the most extensively studied root hemiparasites because of their importance as agricultural weeds in semiarid Africa, and as obligate hemiparasites they require host attachment for survival. Similarly, low photosynthetic rates were found in facultative root hemiparasites. Press et al. (1988) measured

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light-saturated photosynthetic rates of 2.1 to 7.5 μmol m^{-2} s^{-1} for 8 facultative species of Scrophulariaceae. However, 1 exception to this trend of low photosynthetic rates is the Mediterranean facultative hemiparasite *Bartsia trixago* (Scrophulariaceae), which has CO_2 assimilation rates ranging from 12.4 to 18.8 μmol m^{-2} s^{-1}, well within the range measured for potential hosts (Press et al. 1993).

Castilleja and *Orthocarpus* are facultative hemiparasites, those with the ability to survive in the absence of a host. It is this facultative parasitism that distinguishes them from *Striga*. The majority of *Castilleja* species are perennial, while *Orthocarpus* are annuals. Both occur throughout the Intermountain West most commonly in the pinyon-juniper, mountain brush, and aspen-conifer zones (1140–3140 m elevation), with *Orthocarpus tolmiei* occurring only at the higher elevations (2195–3265 m; Welsh et al. 1987). *Castilleja linariifolia* and *Orthocarpus tolmiei* parasitize a variety of host species (Heckard 1962, Atsatt and Strong 1970). *Artemisia tridentata* is the common host for both hemiparasites at the sites studied in the paper.

Our overall objective was to investigate gas exchange and heterotrophy characteristics for facultative hemiparasites. We focused primarily on the facultative root hemiparasite *Castilleja linariifolia* infecting *Artemisia tridentata* hosts. A secondary focus of this study was *Orthocarpus tolmiei*, a closely related annual facultative root hemiparasite, also infecting *A. tridentata* hosts. We asked the following questions: Do *C. linariifolia* and *O. tolmiei* exhibit gas-exchange activities similar to those of their hosts? Does *C. linariifolia* utilize heterotrophic carbon? Does hemiparasite infection impact water availability and gas-exchange rates of *A. tridentata* hosts? To evaluate these questions, we measured gas exchange and analyzed carbon isotope composition for *C. linariifolia*, *O. tolmiei*, infected and uninfected *A. tridentata*. In addition, predawn water potentials (Ψ_{pd}) were measured for infected and uninfected *A. tridentata* to examine the impact of hemiparasite infection on host water availability.

MATERIALS AND METHODS

Study Sites

This study was conducted at 2 sites in Utah where the hemiparasites have different growing seasons. The first site, Tintic, is located just off McIntyre Road, approximately 12 km south of Eureka, Utah (Juab Co.), at the Desert Range Experimental Station operated by Utah State University (latitude 39°51′N, longitude 112°12′W). The area is a sagebrush steppe habitat at about 1525 m elevation where sagebrush is interspersed with herbaceous species such as *Erigeron*, *Castilleja*, *Astragalus*, and *Phlox*. The growing season for *Castilleja* at this site begins in late April and ends in late June to early July. The second site, Strawberry Reservoir (Wasatch Co.), is about 130 km southeast of Salt Lake City and approximately 800 m north of Highway 40 along Coop Creek Road (latitude 40°15′N, longitude 111°8′W). This site lies in the southern tip of the Uinta National Forest at about 2280 m elevation. Sagebrush is the dominant shrub mixed with a few herbaceous species such as *Castilleja*, *Orthocarpus*, and *Malva*. The growing season for *C. linariifolia* at Strawberry Reservoir begins in early June and extends through August; *O. tolmiei* begins a few weeks later and extends into September.

Twenty pairs of *C. linariifolia* and *A. tridentata* hosts were selected at each site. At Strawberry Reservoir an additional 20 pairs of *O. tolmiei* and *A. tridentata* hosts were selected. In addition, 5 uninfected *A. tridentata* were selected at both sites as hemiparasite-free controls.

Gas Exchange

Photosynthesis and stomatal conductance were measured with a portable gas-exchange system (LI-6200, Licor Instruments, Lincoln, NE, USA) twice during the *C. linariifolia* growing season at the Tintic and Strawberry Reservoir sites. Specific dates were chosen to correspond with the early and late parts of the parasite growing season. At both sites data were collected during diurnal peak photosynthesis (1000–1300 h MST) on 20 pairs of *C. linariifolia* and infected *A. tridentata*, and on an additional 5 uninfected *A. tridentata*. During the late season at Strawberry Reservoir, measurements were taken on an additional 20 pairs of *O. tolmiei* and infected *A. tridentata*. After gas-exchange measurements were completed, foliage was removed for leaf-area measurements using a leaf-area meter (LI-3100, Licor Instruments, Lincoln, NE, USA).

Water Potentials

Stems of approximately equal length and diameter were selected for predawn water-potential (Ψ_{pd}) measurements using a pressure bomb (PMS Instruments, Corvallis, OR, USA) for 20 infected and 5 uninfected *A. tridentata* at both sites. These measurements were taken approximately every 2 wk from May through early July at the Tintic site and late June through the end of August at the Strawberry Reservoir site.

Carbon Isotope Composition

Carbon isotope ratios ($\delta^{13}C$) were analyzed for the same plants used to measure gas exchange. The foliage was dried for 24 h and then finely ground with a mortar and pestle to homogenize the tissue (Ehleringer and Osmond 1989). Subsamples of 1–2 mg were combusted to produce CO_2, which was measured using an isotope ratio mass spectrometer (delta-S, Finnigan MAT, Bremen, Germany). Results are expressed using the $\delta^{13}C$ notation (‰), which relates the isotopic composition of the sample to the PDB standard as follows:

$$\delta^{13}C = \left[\frac{R_{sample}}{R_{standard}} - 1\right] * 1000‰, \quad (1)$$

where R represents the ratio of $^{13}CO_2/^{12}CO_2$ of the sample and standard, respectively (Ehleringer and Osmond 1989). All isotope ratio analyses were conducted at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah, Salt Lake City, Utah, USA.

Calculation of Heterotrophy

Heterotrophy was calculated using measured and predicted $\delta^{13}C$ ratios. The predicted $\delta^{13}C$ ratio (δ_{pp}), the carbon isotope composition of a leaf provided that all carbon is autotrophic, was estimated with intercellular CO_2 concentrations (c_i) from gas-exchange measurements. Equation 2 relates c_i to the leaf carbon isotope ratio as modeled by Farquhar et al. (1982):

$$\delta_p = \delta_a - a - (b-a)(c_i/c_a), \quad (2)$$

where δ_p is the $\delta^{13}C$ of the plant (= δ_{pp} in this study), δ_a is the approximate $\delta^{13}C$ of the air (–7.8‰), a and b are discrimination factors due to diffusion (4.4‰) and carboxylation via RuBP carboxylase (27‰), respectively. c_a is the concentration of CO_2 in air (ppm) and c_i was calculated from gas-exchange measurements described above. Heterotrophy (H) was calculated for the 1994 data (9 *C. linariifolia*, 5 infected and 5 uninfected *A. tridentata*) using Equation 3:

$$H = \frac{\delta_{pp} - \delta_m}{\delta_{pp} - \delta_h}, \quad (3)$$

where δ_{pp} is the predicted $\delta^{13}C$ for the parasite, δ_m is the $\delta^{13}C$ measured in the parasite tissue, and δ_h is the $\delta^{13}C$ measured in the host tissue (Press et al. 1987a).

Statistical Analysis

Analysis of variance was used to compare yearly, seasonal, and plant means within a site for all photosynthetic data, and yearly and seasonal means for carbon isotope ratios (JMP, Version 3, SAS Institute Inc., Cary, NC, USA). The Tukey-Kramer Honestly Significant Difference test (HSD) was used to make specific comparisons. In addition, for each hemiparasite, carbon isotope ratios were compiled for all seasons and sites, and differences between hemiparasites and hosts were compared using a *t* test. A paired *t* test was used to determine differences between predicted and measured $\delta^{13}C$ for each *C. linariifolia*, uninfected and infected *A. tridentata*. Differences in Ψ_{pd} water potential between infected and uninfected *A. tridentata* were determined by *t* tests within each date.

RESULTS

Analysis of annual trends in photosynthetic rates for Strawberry Reservoir (Fig. 1) revealed that plants had significantly higher rates in 1995 than in 1994 for both parasite and host (Tukey-Kramer, $\alpha = 0.05$). For example, in 1995 photosynthetic rates for *C. linariifolia* and infected *A. tridentata* were 18.3 ± 2.1 and 16.0 ± 0.6 μmol m^{-2} s^{-1}, respectively, more than double those during the 1994 season. We also found seasonal differences in photosynthetic rates at Strawberry Reservoir. Both *C. linariifolia* and infected *A. tridentata* at Strawberry Reservoir experienced a significant decline in photosynthetic rates late in the season, with rates falling ~6.7 and 8.6 μmol m^{-2} s^{-1}, respectively (Tukey-Kramer, $\alpha = 0.05$). However,

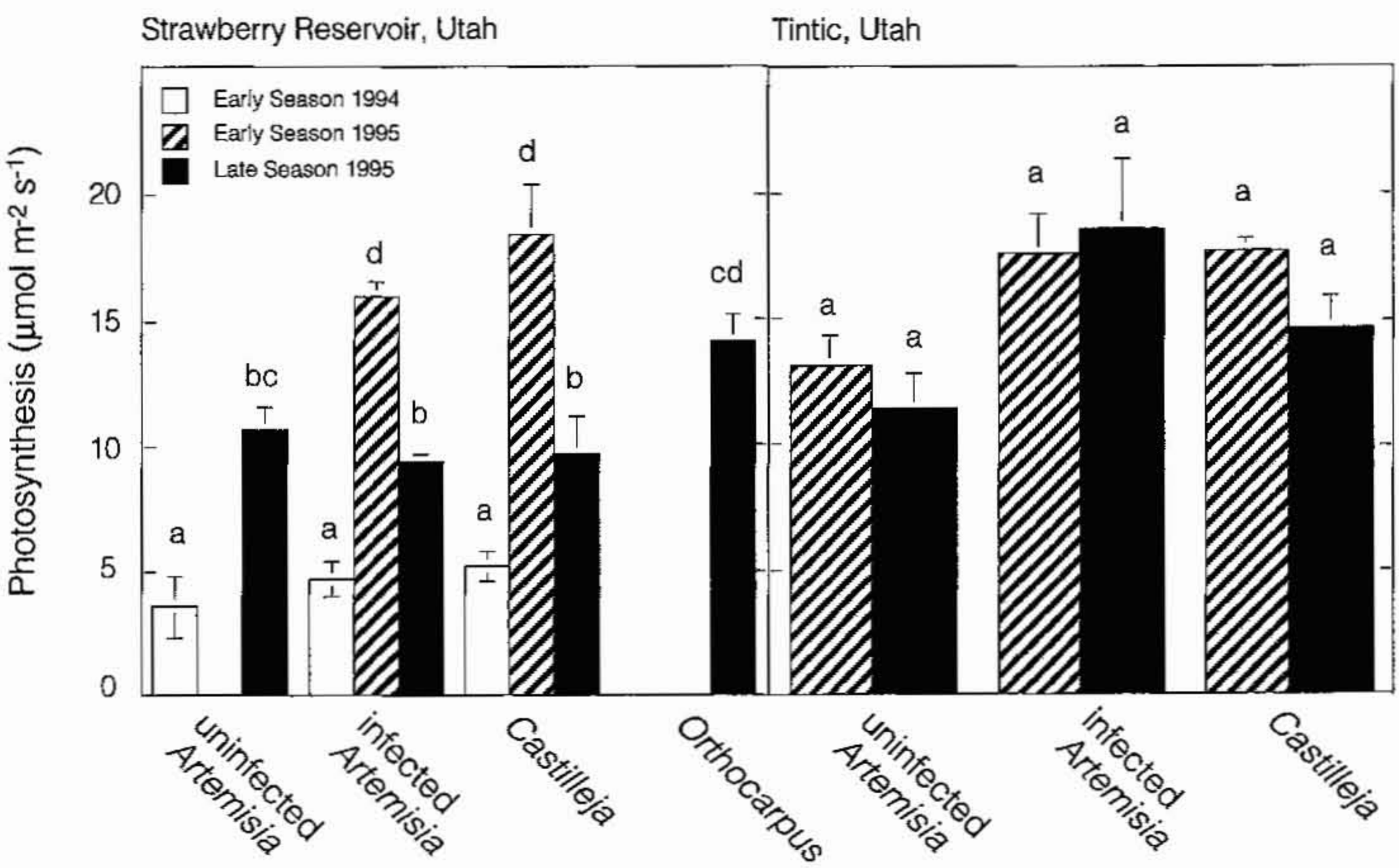

Fig. 1. Mean photosynthetic rates for hosts and parasites. Sites and sample sizes are as follows: Uninfected *A. tridentata* (Tintic: $n = 3$ for early season, $n = 4$ for late season; Strawberry Reservoir: $n = 3$ for late season), infected *A. tridentata* (Tintic: $n = 12$ for early season, $n = 7$ for late season; Strawberry Reservoir: $n = 7$ for early season, $n = 19$ for late season), *C. linariifolia* (Tintic: $n = 4$ for early season, $n = 6$ for late season; Strawberry Reservoir: $n = 3$ for early season, $n = 5$ for late season), *O. tolmiei* (Strawberry Reservoir: $n = 5$ for late season). Data are shown for Strawberry Reservoir (left panel) and Tintic (right panel) during the 1994 early season (open bars), 1995 early season (hatched bars), and 1995 late season (solid bars). Letters denote significant differences within each site. Error bars represent $\pm 1\ s_{\bar{x}}$.

photosynthetic rates at Tintic showed no seasonal differences (ANOVA, $F = 1.88$, $P = 0.134$; Fig. 1). In spite of annual and seasonal differences in photosynthesis for parasite and host plants, we found no difference in photosynthetic rates between *C. linariifolia* and infected *A. tridentata*. In contrast, *O. tolmiei* rates ($14.0 \pm 1.1\ \mu mol\ m^{-2}\ s^{-1}$) exceeded those for infected *A. tridentata* ($9.3 \pm 0.4\ \mu mol\ m^{-2}\ s^{-1}$; Tukey-Kramer, $\alpha = 0.05$; Fig.1).

At both sites we found no significant difference in predawn water potentials (Ψ_{pd}) between infected and uninfected *A. tridentata* ($P > 0.05$ for all dates, t test), although there was a general decline throughout the season (Fig. 2). The range in Ψ_{pd} was similar between sites; however, the values were slightly more negative at Tintic.

Carbon isotope ratios differed between years for infected and uninfected *A. tridentata*, with more negative values in 1995. However, $\delta^{13}C$ values for *C. linariifolia* did not differ between years (Tukey-Kramer, $\alpha = 0.05$; Table 1). Our results showed a slight seasonal decline in $\delta^{13}C$ values for parasites and hosts at Strawberry Reservoir, although only *O. tolmiei* and infected *A. tridentata* were significantly different (Tukey-Kramer, $\alpha = 0.05$; Table 1). This trend in seasonal reduction was not evident for plants at the Tintic site. Furthermore, we found that hemiparasite $\delta^{13}C$ ratios were significantly more negative than those of the hosts (*C. linariifolia*, $t = 12.57$, $P < 0.001$; *O. tolmiei*, $t = 11.94$, $P < 0.001$). In 1994 *C. linariifolia* $\delta^{13}C$ values (–28.9 ± 0.34‰) were nearly 3‰ more negative than those of the hosts (–26.2 ± 0.13‰), while this difference narrowed in 1995 to ~2‰ at Tintic and ~1.5‰ at Strawberry Reservoir.

Results from experiments in 1994 showed a significant mean difference of 1.34‰ between predicted and measured $\delta^{13}C$ ratios for *C. linariifolia* (paired t test, $t = 2.745$, $P < 0.05$; Table 2). Using this difference we calculated that, on average, 40% of *C. linariifolia* leaf carbon was host derived; individual plants ranged from 16 to 60% (Table 3). *C. linariifolia* heterotrophy is well within the range of values calculated for obligate hemiparasites. There was no statistical difference between measured and predicted $\delta^{13}C$ values for either infected or

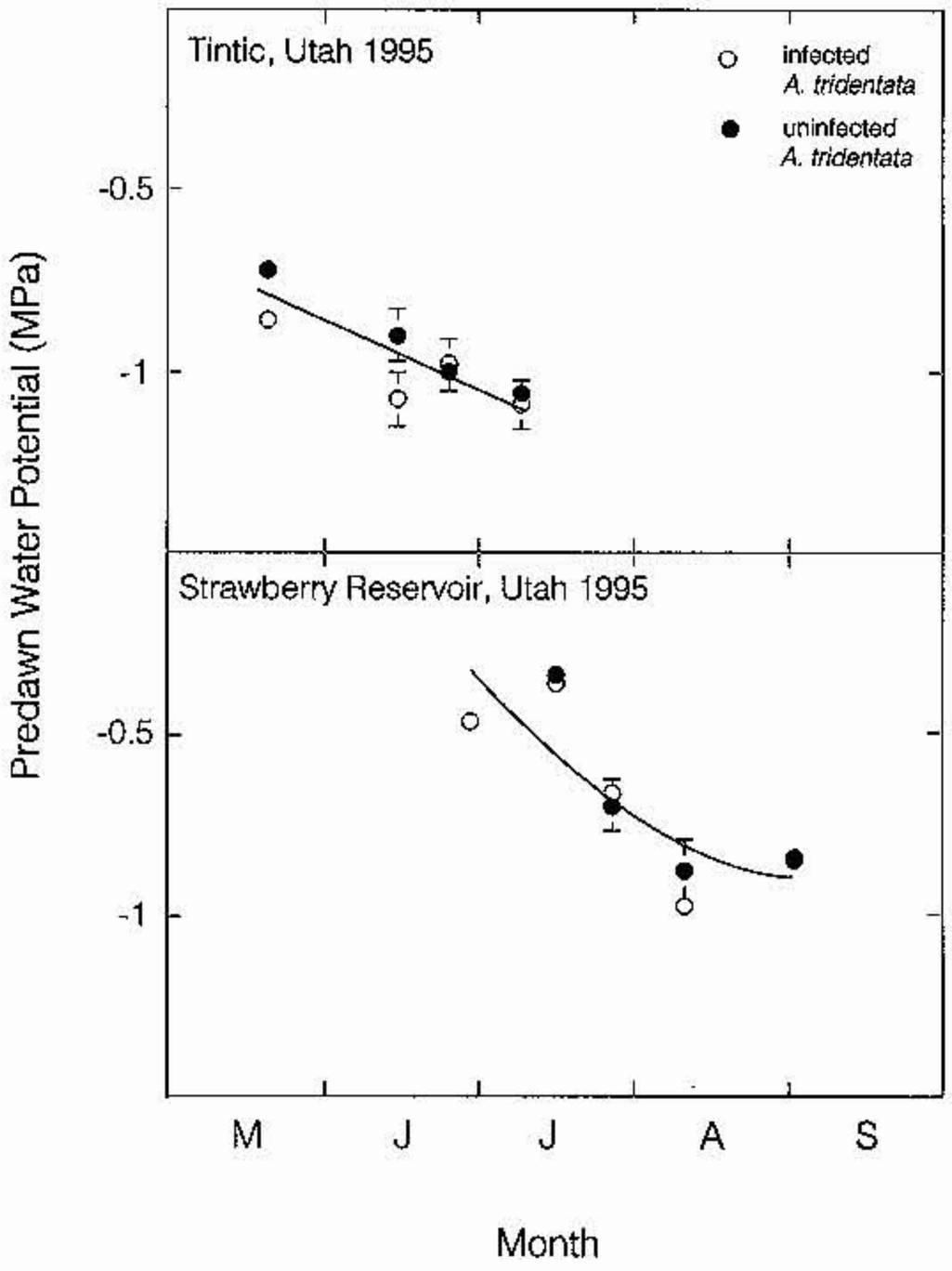

Fig. 2. Seasonal course of predawn water potentials for infected *A. tridentata* (open circles; $n = 11$) and uninfected *A. tridentata* (solid circles; $n = 5$). Data are provided for Tintic (upper panel) and Strawberry Reservoir (lower panel) from May to late August of 1995. Error bars represent $\pm 1\ s_{\bar{x}}$.

uninfected *A. tridentata,* indicating no heterotrophic carbon gain as expected.

DISCUSSION

Our results suggest that, with the exception of photosynthesis, the hemiparasites in this study behaved similarly to other hemiparasites. Photosynthetic rates for hemiparasites in this study were higher than rates for most other hemiparasites and similar to those of their autotrophic host plants. We also found large differences between years, which likely reflected differences in precipitation. In agreement with other studies, hemiparasite $\delta^{13}C$ ratios were more negative than those of the host (Press et al. 1987a, Marshall and Ehleringer 1990, Schulze et al. 1991, Richter et al. 1995). Furthermore, large differences in $\delta^{13}C$ ratios between the parasite and host suggested that the hemiparasite utilized a substantial amount of host-derived carbon. Despite relatively high photosynthetic rates, heterotrophy estimates for *C. linariifolia* range from 16% to 69%.

We found large interannual differences in photosynthetic rates and carbon isotope ratios for *C. linariifolia* and *A. tridentata,* which most likely indicated a response to precipitation differences. Climate records showed that the growing season at Strawberry Reservoir in 1994 was considerably drier than in 1995; the spring (March–May) of 1994 received only 96.3 mm of precipitation, whereas precipitation in the spring of 1995 totaled 216.4 mm (Utah Climate Center, Heber station). Differences in precipitation during the spring influence the amount of soil water available to the plants. This water supply can be indirectly assessed by measuring the plant's water potential before the sun rises and photosynthesis commences. Our Ψ_{pd} measurements corroborated that 1994 was a drier growing season; during 1994 the Ψ_{pd} range for *A. tridentata* (–1.7 to –3.2 MPa) was much more negative than the Ψ_{pd} range for *A. tridentata* in 1995 at either Tintic (–0.7 to –1.1 MPa) or Strawberry Reservoir (–0.3 to –0.9 MPa). Photosynthetic rates doubled during 1995, presumably in response to this increased precipitation. Interannual differences were most pronounced for *C. linariifolia,* which showed photosynthetic rates 3-fold higher in 1995 relative to rates in 1994. Carbon isotope ratios for autotrophic C_3 plants represent an estimate of long-term water-use efficiency (mmol C/mol H_2O; WUE), with more negative $\delta^{13}C$ ratios reflecting a lower WUE (Ehleringer and Osmond 1989). $\delta^{13}C$ ratios for infected and uninfected *A. tridentata* were significantly more negative during the wetter year, thus suggesting they were less conservative in their water use. Using $\delta^{13}C$ ratios as a measure of water-use efficiency is inappropriate for hemiparasites because of the potentially confounding effects of assimilating heterotrophic carbon. Therefore, it follows that the $\delta^{13}C$ ratio for *C. linariifolia* should also reflect influences from the import of host-derived carbon rather than simply the influences of increased precipitation. This prediction was supported by *C. linariifolia* data, where, despite the large increase in precipitation, we saw no difference in $\delta^{13}C$ ratios between years.

Photosynthetic rates also responded to seasonal influences, although rates were not different between parasites and hosts. Photosynthetic rates declined during the growing season, which, in part, may be attributed to the drier conditions late in the season as indicated

TABLE 1. Carbon isotope ratios ($\delta^{13}C$) for hosts and parasites. Sites and sample sizes are as follows: Uninfected *A. tridentata* (Strawberry Reservoir 1994: $n = 5$; Strawberry Reservoir 1995: $n = 3$ for early season; Tintic 1995: $n = 4$ for early season, $n = 5$ for late season), infected *A. tridentata* (Strawberry Reservoir 1994: $n = 5$; Strawberry Reservoir 1995: $n = 20$ for early season, $n = 30$ for late season; Tintic 1995: $n = 10$ for early season, $n = 11$ for late season), *C. linariifolia* (Strawberry Reservoir 1994: $n = 9$; Strawberry Reservoir 1995: $n = 7$ for early season, $n = 8$ for late season; Tintic 1995: $n = 11$ for early season, $n = 8$ for late season), and *O. tolmiei* (Strawberry Reservoir 1995: $n = 9$ for early season, $n = 19$ for late season). Letters denote significant seasonal differences within a site and species (Tukey-Kramer HSD, $\alpha = 0.05$). Values shown are means $\pm$ 1 $s_{\bar{x}}$. NA denotes data not available.

		A. tridentata			
Site	Year	Uninfected	Infected	*C. linariifolia*	*O. tolmiei*
Strawberry Reservoir	1994	-25.56 ± 0.32^{a}	-26.24 ± 0.13^{a}	-28.93 ± 0.34^{a}	NA
	1995				
	Early	-27.86 ± 0.1^{b}	-27.30 ± 0.11^{b}	-28.91 ± 0.15^{a}	-28.66 ± 0.09^{a}
	Late	NA	-27.80 ± 0.09^{c}	-29.33 ± 0.25^{a}	-29.50 ± 0.10^{b}
Tintic	1995				
	Early	-27.57 ± 0.19^{b}	-27.32 ± 0.21^{bc}	-29.19 ± 0.22^{a}	NA
	Late	-27.33 ± 0.19^{b}	-27.17 ± 0.16^{b}	-29.23 ± 0.15^{a}	NA

by predawn water potentials. Perhaps, the decline in *C. linariifolia* photosynthesis was also related to the phenology of the hemiparasite. It is possible that late in the season when these hemiparasites set fruit, they rely less on current photosynthesis and more on heterotrophic carbon gain. Most studies of hemiparasite-host gas-exchange dynamics found that hemiparasite photosynthesis was much lower than that of the host (Hollinger 1983, Press et al. 1987b, Pate et al. 1990, Marshall, Dawson, and Ehleringer 1994). *S. hermonthica* and *S. asiatica* have photosynthetic rates that are half of those for *Sorghum* hosts (Press et al. 1987b). In contrast, the photosynthetic activities of *C. linariifolia* in this study were similar to rates of *A. tridentata* hosts. This pattern remained stable from year to year, despite large differences in precipitation.

Hemiparasite gas-exchange rates have been used to make inferences about potential heterotrophic carbon use. After calculating that 8.8–18.9 h of light-saturated photosynthesis was necessary for 8 different species of facultative hemiparasites to reach zero net foliar carbon gain, Press et al. (1988) hypothesized that they must have had access to a heterotrophic carbon supply. Conversely, in *Bartsia trixago* and *Parentucellia viscosa* (Scrophulariaceae), where photosynthetic rates were very similar to autotrophic plants, it was predicted that these facultative root hemiparasites were less reliant on host-derived carbon (Press et al. 1993). Since *C. linariifolia* also has photosynthetic rates similar to those of its host, it follows that *C. linariifolia* might not contain significant amounts of heterotrophically derived carbon.

However, in our study this was not the case. We found a relatively large difference in $\delta^{13}C$ ratios between *C. linariifolia* and *A. tridentata* hosts, which likely indicates hemiparasite heterotrophy. Indeed, we calculated that *C. linariifolia* in this study utilized an average of 40% host-derived carbon. As with other parasitic plants, unusually high transpiration rates relative to the hosts represent the most likely driving force for this assimilation of host-derived carbon. While the estimates of heterotrophy found in this study are well within the range of those reported for other parasites, one must consider the inherent obstacles in using an instantaneous measure of photosynthesis as a basis for the predicted $\delta^{13}C$ ratios with an integrated measure of actual leaf $\delta^{13}C$ ratio. For instance, differences in gas-exchange characteristics at the time leaf carbon was incorporated may contribute to differences between predicted and measured $\delta^{13}C$ ratios. Although, we found no significant difference between predicted and measured $\delta^{13}C$ ratios for infected and uninfected *Artemisia*, a better control would have been autotrophic *C. linariifolia* plants if they had been available. As mentioned earlier, parasites may also access different pools of carbon at different times throughout the growing season; in turn, this may influence the $\delta^{13}C$ ratios measured in the leaf carbon. While these factors may appear troublesome at first, they represent a few of the many areas open to investigation in parasitic plant ecophysiology.

TABLE 2. Measured and predicted $\delta^{13}C$ values for uninfected and infected *A. tridentata* ($n = 5$) and *C. linariifolia* ($n = 9$) at Strawberry Reservoir in 1994. Means ± 1 $s_{\bar{x}}$ are presented. Also shown is the difference between the predicted and measured values. * denotes significant difference at $P < 0.05$ (paired t test).

	A. tridentata		
	Uninfected	Infected	*C. linariifolia*
$\delta^{13}C_{measured}$	–25.56 ± 0.32	–26.24 ± 0.13	–28.93 ± 0.34
$\delta^{13}C_{predicted}$	–26.54 ± 0.93	–25.11 ± 0.86	–30.26 ± 0.24
Difference	–0.98 ± 1.19	1.13 ± 0.94	–1.34 ± 0.48*

TABLE 3. Calculated heterotrophy of *C. linariifolia* in this study compared to heterotrophy calculated for other hemiparasites.

Species	Calculated heterotrophy in % (range)	Source
Castilleja linariifolia	40 (16–69)	This study
Striga hermonthica, *Striga asiatica*	28–35	Press et al. 1987, Graves et al. 1989
Phoredendron juniperinum	61	Marshall and Ehleringer 1990
Mistletoe species	60 (49–67)	Schulze et al. 1991
Australian mistletoe	15 (5–21)	Marshall et al. 1994b

Though no other study quantifies heterotrophic carbon gain by a facultative hemiparasite, a study by Hansen (1979) implied potential heterotrophy in *Castilleja chromosa*. Experiments measuring the difference of ^{14}C labeled sugar content in uninfected and infected *Artemisia tridentata* individuals showed less ^{14}C in the infected host tissues. Hansen (1979) hypothesized that this difference represented sugar lost to the *C. chromosa* parasite. With this indirect method, *C. chromosa* utilized, on average, 10% host-derived carbon. Using a more precise method, we would suggest from our study that 10% heterotrophy may be an underestimate.

Significant heterotrophic carbon gain by the hemiparasite can be associated with a decrease in host production. Graves et al. (1989) found that dry weight of *Sorghum* infected with *S. hermonthica* was 40% less than that of uninfected *Sorghum*, and hypothesized that the effects of *S. hermonthica* were due to (1) the direct reduction in host carbon by parasite heterotrophy and (2) the indirect reduction of host photosynthetic potential. Press and Stewart (1987) showed that photosynthetic rates for *Sorghum* infected by *S. hermonthica* were reduced by nearly half relative to those for uninfected *Sorghum*; stomatal conductance rates were also significantly decreased. In contrast, we saw no decrease in photosynthetic rates nor stomatal conductance rates for infected *A. tridentata*. Interestingly, there was an increase in host photosynthesis relative to uninfected *A. tridentata* late in the season at Tintic. Our study also showed no difference in Ψ_{pd} between infected and uninfected *A. tridentata*, suggesting that hosts in this study were not experiencing detectable water stress. Taken together these data seem to suggest that *C. linariifolia* do not negatively impact *A. tridentata* hosts. However, this conclusion may be relevant only during unusually wet years; *A. tridentata* may respond differently to hemiparasite infection when drought conditions prevail.

One well-supported aspect of the host-parasite relationship is the unusually high transpiration rates of the parasite, often 10 times greater than those of the host. It is generally believed that this high water flux results in a water potential gradient from the host to the parasite. Therefore, through this mechanism higher transpiration rates are thought to represent the driving force for the transfer of solutes from the host to parasite. Schulze et al. (1984) suggested that high transpiration rates may be necessary for mistletoe to acquire adequate nitrogen for growth. The nitrogen-gathering hypothesis has been the focus of several studies (Schulze et al. 1984, Ehleringer et al. 1985, Marshall, Dawson, and Ehleringer 1994). However, as Raven (1983) points out, these plants are also inextricably acquiring significant amounts of host carbon. Recent studies indicated that heterotrophy may be a widespread phenomenon occurring in a variety of obligate hemiparasites (Press et al. 1987a, Graves et al. 1989, Marshall and Ehleringer 1990, Marshall et al. 1994, Richter et al. 1995). Evidence from this study indicates that the facultative root parasite *C. linariifolia* obtains a substantial contribution of host-derived carbon, thus extending further emphasis to the importance of this carbon supply for hemiparasites.

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