

POTENTIAL CONTRIBUTION OF RESPIRATION BY *ANABRUS SIMPLEX* (MORMON CRICKETS) TO NET CO₂ EXCHANGE IN THREE GREAT BASIN ECOSYSTEMS

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ABSTRACT.—Disturbance events can significantly influence net CO₂ exchange (NCE) in ecosystems. High densities of *Anabrus simplex* (Mormon crickets) periodically afflict large areas of the western USA; their sheer numbers could make them a significant source of CO₂. We modeled cricket respiration at the ecosystem level using air and body temperatures and insect gas exchange measurements. Cricket CO₂ efflux values were compared to ecosystem CO₂ flux from eddy covariance measurements in 3 Great Basin ecosystems: a juniper woodland, a sagebrush shrubland, and a crested wheatgrass pasture. Mean respiration from Mormon crickets was 0.96 g CO₂ · m⁻²d⁻¹. Since Mormon crickets are present when NCE is otherwise near 0, they can potentially alter NCE between 20% (juniper woodland) and 60% (crested wheatgrass pasture). Transient pests such as Mormon crickets can be an important component of NCE.

Key words: insect respiration, net ecosystem exchange, Mormon cricket, eddy covariance, big sagebrush, Utah juniper, crested wheatgrass.

Net CO₂ exchange (NCE) is the difference between CO₂ assimilation by autotrophs and respiration by autotrophs and heterotrophs (Chapin et al. 2002). Net CO₂ exchange is influenced by abiotic and biotic factors and ecosystems can be net sources or sinks of CO₂ depending on local conditions (Goulden et al. 1998). Disturbance events can significantly influence NCE over short and long timescales. For example, fire results in a large efflux of CO₂, potentially shifting an ecosystem from a net sink for CO₂ to a net source (Harden et al. 2000, Suyker and Verma 2001). Other disturbances such as grazing or drought can significantly alter NCE for varying lengths of time depending on duration of the disturbance (Milchunas and Lauenroth 1993, Hobbs 1996, Weltzin et al. 2003).

Many ecosystems experience periodic outbreaks of insect pests, which can influence ecosystem processes. Well-known examples are the gypsy moth in the hardwood forests of Europe and North America (Schowalter et al. 1986, Elkinton and Liebhold 1990), spruce budworm in boreal forests (Schowalter et al. 1986, Bonan and Shugart 1989), and locusts and grasshoppers

in grasslands and deserts (Lomer et al. 2001). These outbreaks can kill or severely damage individuals of susceptible species over large areas (Schowalter et al. 1986, Bonan and Shugart 1989). During outbreaks, insects can decrease CO₂ assimilation by drastically reducing photosynthetic tissue (Schowalter et al. 1986). Insect outbreaks can also cause nitrogen loss from ecosystems (Eshleman et al. 1998) or promote immobilization by microbes (Lovett and Ruesink 1995, Lovett et al. 2002), thereby reducing availability of nitrogen to plants. Finally, insects at high density may significantly increase ecosystem heterotrophic respiration simply through an increase in the biomass of heterotrophs and conversion of plant biomass and litter to CO₂ via their respiration.

In the western United States, *Anabrus simplex* Haldeman (Mormon cricket) numbers dramatically increase during outbreak years. Mormon crickets, classified as shieldbacked katydids (Family Tettigoniidae), are found from the western Great Plains to the Sierra Nevada and from southern Canada to northern Arizona (Wakeland 1959). Severe outbreaks have occurred several times in the past century

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including some in recent years. During outbreak years, density in infested areas can be above 12 crickets \cdot m⁻² (Swain 1944). Adult crickets aggregate into bands 1–2 km wide and 2–16 km long, which migrate 1–2 km \cdot day⁻¹ during the spring and summer (MacVean 1987, Lorch and Gwynne 2000). Thus, a single location can experience intense herbivore pressure, though generally only for several days (Swain 1944), while the ecosystems as a whole experience high cricket density as bands migrate throughout the growing season. Approximately 77,000 km² of the western U.S. were affected in 1939 (Wakeland 1951).

The actual damage caused by outbreaks of Mormon crickets is debatable (Redak et al. 1992). Severe damage to plants appears localized and infrequent, with crickets removing an average of ca. 15% of the forage available to livestock (Swain 1944). Mormon crickets are opportunistic feeders and will consume plant and animal residues as well as foliage in native ecosystems (MacVean 1987); crop species are readily consumed (Swain 1944, MacVean 1987). Damage by Mormon crickets is aggravated by weather conditions and intense grazing pressure by livestock (MacVean 1987). If Mormon crickets remove only minimal photosynthetic tissue in native ecosystems, then their primary influence on NCE would be through the high density of respiring individuals.

Arid and semiarid ecosystems are inherently driven by resource pulses (Noy-Meir 1973, Loik et al. 2004); high NCE occurs immediately following a pulse but NCE is low and tends toward net CO₂ efflux during interpulse periods (Huxman et al. 2004). Throughout much of the cold desert region of the semiarid Intermountain West, maximum rates of photosynthesis are achieved only during spring and early summer following snowmelt; the hot summer is characterized by minimal CO₂ assimilation (Caldwell 1985). Because many arid ecosystems are characterized by little NCE for much of the warm part of the year, disturbances such as insect outbreaks during the summer can potentially alter NCE substantially.

The objective of this study was to examine the potential contribution of respiration by Mormon crickets to the NCE of 3 ecosystems in the Great Basin of the western U.S. We developed a simple model to predict cricket respiration from ambient air temperature and quantify the influence of this respiration on

NCE in sagebrush shrubland, juniper woodland, and a managed crested wheatgrass pasture. We hypothesize that Mormon crickets will have the greatest influence on pasture land because livestock grazing removes photosynthetic tissue, thereby suppressing CO₂ uptake; also, Mormon crickets will have the least influence on juniper woodland because Utah juniper maintains carbon uptake throughout the growing season (Leffler et al. 2002).

METHODS

Our study was conducted in Tooele County, Utah, near the town of Rush Valley (112°28'W, 40°17'N, ca. 1600 m elevation). Climatically, the area is typical of the Great Basin, with cold winters during which soil moisture accumulates and hot summers with little precipitation (Caldwell 1985). During the summer of 2001, Mormon crickets were present at our study sites at high density from the middle of May until the middle of August. The crickets were adults by late May.

We examined the potential influence of cricket respiration on CO₂ flux (NCE, net CO₂ exchange, negative values indicate uptake of CO₂) in 3 ecosystems. First was a woodland of *Juniperus osteosperma* (Torr.) Little (Utah juniper) located in the foothills. This ecosystem is dominated by *J. osteosperma* with few sagebrush individuals and grasses in the understory. Second was an *Artemisia tridentata* var. *wyomingensis* (Beetle and A. Young) Welsh (big sagebrush) shrubland located in the valley. This ecosystem was dominated by *A. tridentata* with scattered individuals of *Sarcobatus vermiculatus* (greasewood), *Chrysothamnus nauseosus* (rubber rabbitbrush), and various grasses. Third was a managed monoculture of *Agropyron desertorum* (Link) Schultes (crested wheatgrass) planted for livestock forage. Approximately 50% of the ground area was covered by *A. desertorum*, which was grazed by livestock during the summer.

Respiration by Mormon Crickets

Respiration by Mormon crickets was modeled from ambient temperature. This model had 2 components: (1) the relationship between ambient temperature and cricket body temperature, and (2) the relationship between cricket body temperature and respiration. We

measured cricket body temperature by capturing crickets in the field and inserting a thermocouple under the pronotum without piercing the body. The measurement took less than 10 seconds. Measurements were made on 2 individuals (1 male and 1 female) every 30 minutes on 4 different days in June and July 2001. Two different individuals were measured each time and individuals were collected from all study sites. Temperature was measured in the field because Mormon crickets thermoregulate by basking during cool periods and seeking shade in vegetation when hot. Ambient temperature data were collected ca. 2 m above ground at a weather station (Campbell Scientific, Logan, UT) located ca. 500 m from the *A. desertorum* and *A. tridentata* sites, and ca. 3 km from the *J. osteosperma* site. Air temperature, rather than soil-surface temperature, was used to model body temperature, because Mormon crickets spend significant time in vegetation canopies during the summer. Air temperature ranged from 13°C to 40°C, and cricket body temperature ranged from 12°C to 33°C during the 4 days of field measurements. The best-fit function ($r^2 = 0.75$, $P < 0.001$) to these data was a negative 2nd-order quadratic (Fig. 1):

$$T_b = -17.7(\ln T_a)^2 + 131(\ln T_a) - 206 \quad \text{eq. 1}$$

where T_a is ambient temperature (°C) and T_b is body temperature (°C). The body temperatures of males and females were not significantly different ($t = 1.22$, $df = 74$, $P = 0.23$).

Cricket respiration was measured on individuals at different body temperatures on 14 June and 15 June, 1–2 days after crickets were captured in the field. Crickets were fed locally available grasses while in captivity. Crickets were held at the target temperatures of 10°, 20°, 30°, and 40°C in an environmentally controlled chamber for 2–3 hours prior to measurement of respiration. Body temperatures of crickets were similar to target temperatures at the time of measurement. All respiration measurements utilized a flow-through infrared gas analyzer (IRGA, model 6400, Li-Cor Inc., Lincoln, NE) with crickets in a 0.25-L cuvette. The cuvette was regulated at the target temperature with a peltier-type chiller, and relative humidity varied from 12%–60% depending on temperature; the CO₂ concentration of the airstream entering the cuvette was maintained at 400 $\mu\text{l} \cdot \text{L}^{-1}$; flow-through rates var-

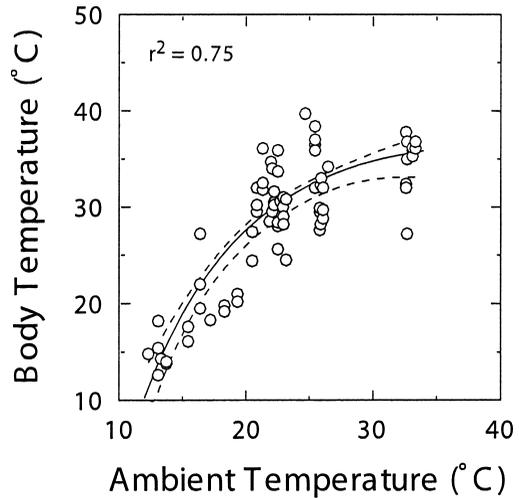


Fig. 1. The relationship between ambient temperature and body temperature of Mormon crickets determined from field measurements. Dashed lines indicate the 95% confidence interval around the fit line.

ied from 300 to 500 $\mu\text{mol} \cdot \text{s}^{-1}$. This commercially available system is capable of resolving CO₂ changes $< 1 \mu\text{L} \cdot \text{L}^{-1}$ and has a minimal lag time because the IRGAs are directly attached to the cuvette. Respiration was measured over a 5-minute period with data recorded every 5 seconds (averaged to obtain a mean respiration value for each individual); the cuvette was covered with a black cloth during measurements. Twenty crickets (mixed males and females) were measured at the 4 target temperatures (5 at each temperature). All crickets were weighed following measurements (mean fresh mass = 2.13 g). We fit an exponential function ($r^2 = 0.96$, $P < 0.01$) to these data (Fig. 2):

$$R_c = 5.32(10^{0.029T_b}) \quad \text{eq. 2}$$

where T_b is cricket body temperature and R_c is respiration in $\mu\text{mol} \cdot \text{g}^{-1}\text{h}^{-1}$.

Many insects, including some orthopterans, respire by discontinuous ventilation (Lighton 1996). In this method of gas exchange, spiracles remain closed ca. 90% of the time while CO₂ increases and O₂ decreases. Spiracles then open and rapid gas exchange occurs. We measured gas exchange for 60 minutes on 2 Mormon crickets and did not observe discontinuous ventilation, although we cannot conclude that discontinuous ventilation would not

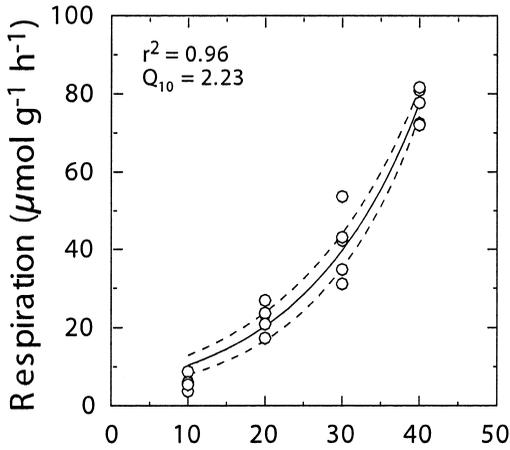


Fig. 2. Laboratory measurements of respiration by 5 Mormon crickets at each target body temperature. Dashed lines indicate the 95% confidence interval around the fit line.

have occurred after 60 minutes of rest in the cuvette. Crickets exhibited “escape behavior” and were highly active just after we placed them in the cuvette, perhaps inducing continuous ventilation (e.g., Hadley and Quinlan 1993). The cuvette, however, was covered during the measurement period, so we could not assess cricket activity; it is unknown if Mormon crickets can maintain high gas exchange rates for extended periods. Nevertheless, we did not observe a significant temporal trend in respiration during the two 60-minute measurements ($\bar{x} = 7.1 \pm 1.0$ and 10.1 ± 1.1 $\text{nmol} \cdot \text{g}^{-1}\text{s}^{-1}$, respectively); we concluded that our 5-minute measurements were adequate to describe mean gas exchange in this species.

Respiration by crickets was modeled using ambient temperature data and equations 1 and 2 (Fig. 3a). Confidence intervals (CI_{95}) for respiration were modeled by using the upper and lower predictions (CI_{95}) of body temperature as input values for the upper and lower (CI_{95}) predictions of fit for the relationship between body temperature and respiration. We used ambient temperature data from only 2002; we wished to compare cricket respiration to ecosystem CO_2 flux when Mormon cricket numbers were negligible at our site. Ecosystem CO_2 flux data were not available during the summer of 2001; hence, a direct comparison of NCE during and after cricket presence was not possible. Additionally, comparisons between

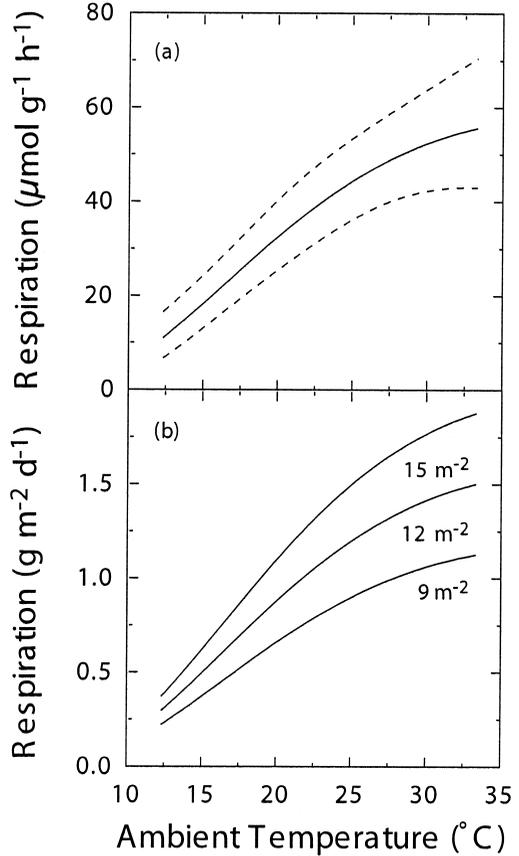


Fig. 3. (a) Modeled relationship between ambient temperature and respiration by Mormon crickets. The model was developed by combining equations 1 and 2. Dashed lines indicated the 95% confidence interval of the model constructed from upper and lower 95% estimates of equations 1 and 2. (b) Modeled relationship between ambient temperature and respiration by Mormon crickets at the ecosystem level. This model was constructed using 3 different densities of crickets (9, 12, and 15 crickets $\cdot \text{m}^{-2}$) as an estimate of error associated with scaling.

years with and without crickets were not made due to the large number of factors that can affect NCE among years; an active eradication program implemented by the Bureau of Land Management and local land owners also greatly reduced the density of Mormon crickets beginning in 2002. Our model had a 30-minute time step and predicted cricket respiration from 15 May 2002 until 15 August 2002. Input temperature data ranged from -6°C to 40°C but 88% of the values were between 10°C and 40°C , the range over which our model was constructed. Respiration by Mormon crickets was set to 0 at ambient temperatures lower

than 10°C because of poor body temperature prediction at these temperatures.

Ecosystem CO₂ Flux

Ecosystem CO₂ flux was measured using the eddy covariance technique (Baldocchi 2003). This technique allows calculation of NCE by measurement of the CO₂ density and the direction and velocity of eddies as they are exchanged between the land surface and atmosphere. The flux tower held a 3-D sonic anemometer (model CSAT3, Campbell Scientific, Logan, UT) and an open-path CO₂/H₂O IRGA (model 7500, Li-Cor Inc., Lincoln, NE). Data were collected at 10 Hz and 30-minute raw covariances were stored in a datalogger (model 23X, Campbell Scientific, Logan, UT). The planar fit coordinate rotation was employed to define a mean streamline coordinate system and to compute the tilt-corrected stresses (Wilczak et al. 2001). Flux data were corrected for density effects (Webb et al. 1980) and frequency response (Massman et al. 2000, 2001).

One flux tower was located in each of the 3 ecosystems. In the *J. osteosperma* ecosystem, the instruments were mounted 8 m above the 2- to 4-m-tall canopy and had a FETCH (up-wind area sampled by the sensors) of ca. 600 m. Instruments at the *A. desertorum* and *A. tridentata* sites were mounted ca. 2 m above the ground and each had a FETCH of ca. 500 m.

All eddy covariance data contain gaps due to aberrant instrument behavior and data rejection (Falge et al. 2001). For the time period examined here, we had 83% data coverage at the *A. desertorum* site, 80% at the *A. tridentata* site, and 99% at the *J. osteosperma* site. Short gaps (<2 hours) were ignored. Gaps within a day, those longer than 2 hours but shorter than 12 hours, were filled with the average of the 3 previous and 3 subsequent days during the same time period. Gaps of 1 or 2 days were filled with the mean daily value of the 3 previous and 3 subsequent days. Gaps of 3 or more days were filled by linear interpolation between the mean of the 3 days before and after the gap. A gap of 2 days at the end of the time period of interest for the *A. tridentata* site was filled with the mean of the 3 days prior to the gap, because data from subsequent days were also missing. Large gaps at the *A. tridentata* (5 June–20 June) and *A. desertorum* (22 July–7 August) sites are evident (Fig. 4). Energy

balance closure during summer days was ca. 0.8 in each ecosystem.

Data Analysis

Data were summed from 30-minute-average net CO₂ flux and cricket respiration to daily totals. Respiration by Mormon crickets was converted from a cricket-mass basis to a land-area basis using an average cricket mass of 2.13 g (measured in the laboratory) and a density of 12 crickets · m⁻² (Swain 1944) to facilitate comparison with CO₂ flux data. We used the same value of 12 crickets · m⁻² for all ecosystems because crickets were present at high density in all ecosystems; this density is commonly cited in literature and considered the “outbreak” density by the USDA. We did not directly measure cricket density at our study sites because the crickets had left the area before the measurement protocol could be implemented. Additional estimates of CO₂ flux at various densities are included as an estimate of error associated with scaling (Fig. 3b).

We calculated the potential change in NCE for each of the 3 study sites by addition of cricket respiration to CO₂ exchange. We also report the percent change due to crickets. Because the addition of cricket respiration can change NCE from uptake to efflux, we calculated percent from the absolute value and have indicated the sign change in the data presentation. The potential influence of crickets on NCE from 15 May to 15 August included 4 distinct climatic periods: cool and wet, warm and wet, cool and dry, and warm and dry. The wet periods occurred in mid- to late May when soil water potential was generally above -1.0 MPa. The dry periods were in July and August with low soil water potentials (Table 2). We measured temperatures using the weather station described above.

RESULTS

Respiration by Mormon crickets and NCE of each ecosystem varied through time while crickets were present (Fig. 4). Cricket respiration ranged from near 0 to ca. 1.5 g CO₂ · m⁻²d⁻¹ (Table 1). Measured net CO₂ flux from each of the ecosystems was significantly more variable (Table 1) than was modeled cricket respiration, ranging from net CO₂ uptake (negative values) to net CO₂ loss (positive values). Throughout the period from 15 May to

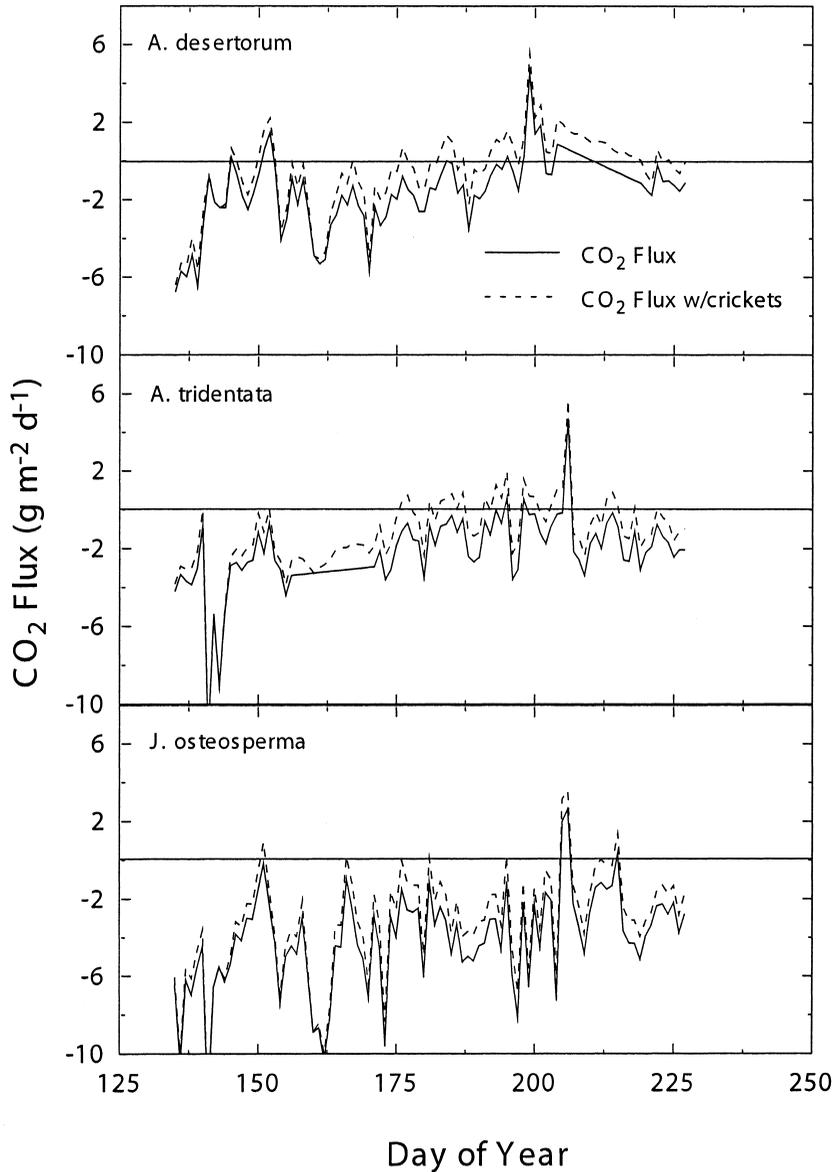


Fig. 4. CO_2 flux from *Agropyron desertorum*, *A. tridentata*, and *Juniperus osteosperma* ecosystems during 2002; and estimated flux from each ecosystem if Mormon crickets were present from 15 May until 15 August at a density of 12 crickets $\cdot \text{m}^{-2}$. Horizontal lines indicate zero CO_2 flux.

15 August, each ecosystem was a net sink for CO_2 . *Juniperus osteosperma* had the largest CO_2 uptake, *A. desertorum* the smallest.

Respiration by Mormon crickets has the potential to reduce mean NCE between 15 May and 15 August by 20%–60% depending on the ecosystem. As expected, *A. desertorum*, the ecosystem with NCE closest to 0, would be most influenced by cricket respiration (63%

mean change toward efflux), whereas *J. osteosperma*, the ecosystem with the strongest sink for CO_2 , would be least affected (23%). Taken over the period 15 May to 15 August, all ecosystems would remain net sinks for CO_2 even if crickets were present. However, if cricket respiration were factored in, NCE would have switched from sink to source in all 3 species for a limited time: 39 days in the *A. desertorum*

TABLE 1. Mean, minimum, and maximum cricket respiration and NCE for each ecosystem in the absence of crickets for the period 15 May–15 August. Minimum NCE for crickets is not presented because values of respiration were not modeled below 10°C ambient temperature.

	Cricket flux (g · m ⁻² d ⁻¹)	<i>A. desertorum</i> (g · m ⁻² d ⁻¹)	<i>A. tridentata</i> (g · m ⁻² d ⁻¹)	<i>J. osteosperma</i> (g · m ⁻² d ⁻¹)
Mean (s)	0.96 (0.36)	-1.5 (1.9)	-2.2 (1.9)	-4.1 (2.6)
Minimum	N/A	-6.8	-11.8	-12.7
Maximum	1.5	4.6	4.7	2.6

TABLE 2. The influence of cricket respiration on NCE during days of cool-wet (23–25 May), warm-wet (18–20 May), cool-dry (9–10 August), and warm-dry weather (13–14 July). Means are for the entire cricket season (15 May–15 August). NCE in the absence of crickets is presented for each ecosystem with the potential percent change in flux due to crickets given in parentheses. Percent change cannot be presented in cases for which NCE changed from uptake to efflux for 1 day during the period of comparison and those cases are indicated with an asterisk.

Date	Mean temperature (°C)	Cricket flux (g · m ⁻² d ⁻¹)	<i>A. desertorum</i> (g · m ⁻² d ⁻¹)	<i>A. tridentata</i> (g · m ⁻² d ⁻¹)	<i>J. osteosperma</i> (g · m ⁻² d ⁻¹)
23–24 May	6.6	0.10	-2.4 (4.1%)	-7.1 (1.9%)	-5.9 (1.6%)
18–20 May	19.6	0.85	-4.8 (19%)	-2.6 (50%)	-5.7 (15%)
9–10 August	17.9	0.72	-0.98 (*)	-1.3 (68%)	-2.9 (26%)
13–14 July	27.9	1.30	-2.4 (*)	-1.4 (*)	-5.1 (25%)
Mean	21.6	0.96	-1.5 (61%)	-2.2 (42%)	-4.1 (23%)

ecosystem, 25 days for *A. tridentata*, but only 8 days for *J. osteosperma*. Without crickets, these ecosystems would be sources for 13, 3, and 3 days, respectively. The switch from sink to source typically occurred in the later growing season, and net CO₂ efflux averaged ca. 1.1 g · m⁻²d⁻¹ in *A. desertorum*, 0.85 g · m⁻²d⁻¹ in *A. tridentata*, and ca. 1.2 g · m⁻²d⁻¹ in *J. osteosperma* on those days. Without crickets, net CO₂ uptake would have been -0.6 g · m⁻²d⁻¹ in *A. desertorum* and *A. tridentata*, and -0.9 g · m⁻²d⁻¹ in *J. osteosperma*.

The possible influence of respiration by Mormon crickets on NCE increased as the growing season progressed (Fig. 4). Respiration effects were negligible, ca. 5% or less, during a cool period in May (Table 2). The greatest influence occurred under high temperatures in July (Table 2). During this period, NCE changed substantially; these large changes were associated with a switch from net CO₂ uptake to net CO₂ efflux in *A. desertorum* and *A. tridentata*.

DISCUSSION

Respiration by Mormon crickets has the potential to substantially decrease net CO₂

uptake (increase NCE) in many ecosystems of the western U.S. On average, projected cricket respiration was 0.96 g CO₂ · m⁻²d⁻¹; carbon fixation by deserts worldwide is estimated at approximately 2 g CO₂ · m⁻²d⁻¹ (derived from Saugier et al. 2001). Since cricket bands typically range in size from 2 to 32 km² (MacVean 1987), a single band of crickets can respire between 180 t and 2900 t of CO₂ in a single growing season, and multiple bands may exist in the same locality (Lorch and Gwynne 2000). Large-scale estimates of CO₂ flux from Mormon crickets (i.e., estimates for the western U.S.) would require detailed information on size, number, and movement of individual bands.

The pasture of *A. desertorum* was the ecosystem most influenced by cricket respiration. Grasslands can be sinks for CO₂ (Suyker and Verma 2001, Flanagan et al. 2002, Xu and Baldocchi 2004) but the pasture examined here was not irrigated and was grazed; little photosynthetic tissue remained after mid-July. The *J. osteosperma* woodland was least influenced by cricket respiration because CO₂ uptake remained high in this ecosystem during mid-summer compared to the other species (Fig. 4). Although *J. osteosperma* individuals have low rates of photosynthesis in individual

leaves, these ecosystems have a high leaf area index throughout the year (Leffler et al. 2002). Conversely, the *A. tridentata* ecosystem was highly influenced by crickets because *A. tridentata* substantially reduces its leaf area, and consequently whole-plant carbon uptake, during the summer (DePuit and Caldwell 1973).

The potential influence of Mormon crickets on net CO₂ exchange was greatest on warm, dry days in July and August and least on cool, wet days in May (Table 2). We expected this result because carbon acquisition is tightly coupled with soil moisture in these ecosystems (Noy-Meir 1973, Caldwell 1985, Huxman et al. 2004), whereas respiration by animals is dependent on body temperature. Climate change models generally predict more extreme weather events in the future (IPCC 2001, Karl and Trenberth 2003). If these predictions hold, we may expect future outbreaks of Mormon crickets to have a greater influence on net CO₂ exchange in these ecosystems.

We have not incorporated the potential influence of Mormon crickets on NCE via decreased leaf tissue available for carbon assimilation. The potential influence of crickets on photosynthesis in native ecosystems may be minimal. Although we observed crickets at our study sites from mid-May until mid-August, we did not observe great reductions in photosynthetic tissue, an observation consistent with previous studies (Swain 1944, Redak et al. 1992). This conclusion, however, is only applicable to natural systems; crops are readily consumed by crickets (Swain 1944, MacVean 1987). The possibility of compensatory growth (Paige and Whitham 1987) in response to herbivory by crickets also exists; many species may actually increase growth and photosynthesis in response to moderate herbivory (Stowe et al. 2000), and increased plant productivity may mask the influence of herbivory on NCE. If compensatory growth is occurring, availability of other resources required for the compensatory response (i.e., water and nitrogen) may be influenced by Mormon crickets.

Although we know of no other studies on respiration among tettigoniids, respiration measurements from orthopterans are quite variable. Metabolic Q₁₀ for *A. simplex* was 2.29 and can range from 1.8 to 2.6 in other species (Quinlan and Hadley 1993, Rourke 2000), but can be as high as ~3 in scorpions (Lighton et al. 2001). On a biomass basis, we report a respiration rate

of 0.98 mL CO₂ · g⁻¹h⁻¹ (34.8 μmol · g⁻¹h⁻¹) at 30°C. Our values are somewhat higher than those presented for 2 acridid grasshoppers (*Romalea guttata*, ca. 0.25 mL O₂ · g⁻¹h⁻¹; *Taeniopoda eques*, ca. 0.35 mL O₂ · g⁻¹h⁻¹; Quinlan and Hadley 1993) but similar to those reported for the acridid grasshopper *Aeropedellus clavatus* (ca. 1.2 mL O₂ · g⁻¹h⁻¹; Hadley and Massion 1985). A recent respiration equation for multiple insect taxa suggests ca. 0.25 mL O₂ · g⁻¹h⁻¹ at 30°C for a resting insect (Lighton et al. 2001). Our values are considerably higher than this estimate (assuming a respiratory exchange ratio of 1), possibly due to the high activity of insects in the cuvette. Although we would not expect insects in the field to exhibit highly active behavior, they would not be sedentary. The true respiration value for Mormon crickets at 30°C likely falls between 0.25 and 1.0 mL · g⁻¹h⁻¹. Even if our estimates of CO₂ flux by Mormon crickets at the ecosystem scale are double the true flux, CO₂ emission by Mormon crickets would still be ca. 25% of the daily CO₂ uptake by deserts (Saugier et al. 2001).

An additional source of potential error in estimating CO₂ flux from Mormon crickets at the ecosystem scale is cricket density. In our model we have used a density of 12 crickets · m⁻², which is cited by the USDA as the “outbreak” density. Varying densities of individuals will alter model results (Fig. 3b), and this error is not related to temperature in a linear fashion. For example, at 15°C, daily CO₂ flux from crickets at densities from 9 to 15 crickets · m⁻² is between 0.22 and 0.37 g · m⁻²d⁻¹, a range of 0.15 g · m⁻²d⁻¹; and at 35°C, the value is between 1.1 and 1.9 g · m⁻²d⁻¹, a range of 0.8 g · m⁻²d⁻¹.

Our respiration model makes several assumptions: (1) density of Mormon crickets is constant from 15 May until 15 August; (2) density of crickets is the same in each ecosystem; (3) the relationship between ambient temperature and body temperature does not change during the summer; and (4) respiration response by crickets to temperature is constant from 15 May until 15 August. We observed cricket density to be relatively constant during the summer followed by a rapid decline in mid-August, although we made no quantitative measurements. Mormon crickets typically aggregate into bands and begin migration when they are adults (MacVean 1987, Lorch and Gwynne

2000). We observed adults by mid-May, but no apparent migration. We may have observed the unique situation of a large band, which emerged at our sites, but which took nearly 3 months to move off our study area. Migration may have been occurring, but we could not observe it. We observed high cricket density in each ecosystem, but it is likely that crickets congregate for an extended period in ecosystems with lush vegetation, possibly increasing their influence in crops and pastures while decreasing their influence in woodlands and shrublands. The relationship of body temperature versus ambient temperature may change during the summer as cricket behavior changes (e.g., aggregative versus nonaggregative thermal behaviors; Blanford and Thomas 2000). Finally, respiration may change with cricket age. In the desert locust *Schistocerca gregaria*, low respiration was observed in the first 2 days of adulthood, high respiration in several subsequent days, but little variation between 10 and 70 days of adult age (Hamilton 1964). Alternatively, increases in body mass during the adult instar can cause increases in whole-animal CO₂ emission as individuals age (Greenlee and Harrison 2004); but our body mass data were collected nearly 2 months after the emergence of adults.

Mormon crickets are a conspicuous pest and they garner much media attention, partly due to their cultural significance (Gwynne 2001). However, other insect outbreaks may potentially affect net CO₂ exchange to a greater extent. In the western U.S., grasshoppers, even though they are much smaller than Mormon crickets and contribute only a fraction of the CO₂ on a per-unit-area basis, affect a much larger area (Kauffman 2002). The gypsy moth (*Lymantria dispar*) affects much of northeastern North America (Elkinton and Liebhold 1990) and forests can be completely defoliated during outbreaks (Lovett and Ruesink 1995). Studies have examined the influence of the gypsy moth on ecosystem processes such as nutrient cycling (Lovett and Ruesink 1995, Lovett et al. 2002), but we know of no estimates of their contribution to NCE. Likely, gypsy moths have the largest influence on NCE by defoliation rather than respiration, because potential carbon acquisition would be so much greater in this ecosystem.

Periodic disturbance is a characteristic of most ecosystems of the western U.S. Distur-

bances such as fires release large amounts of CO₂ to the atmosphere each year (Obrist et al. 2003) but are typically beneficial, promoting nutrient cycling and reducing woody-plant encroachment (Van Auken 2000, Wan and Lou 2001). Although the disturbance caused by significant herbivore presence is not nearly as intense as fire, it can be much more widespread. Researchers in the future should quantify the influence of Mormon crickets at high density using measures beyond NCE with an emphasis on determining if these insects play a significant role in ecosystem functioning.

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