

CICADA EMERGENCE IN SOUTHWESTERN RIPARIAN FOREST: INFLUENCES OF WILDFIRE AND VEGETATION COMPOSITION

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Abstract. Annually emerging cicadas are a numerically and ecologically dominant species in Southwestern riparian forests. Humans have altered disturbance regimes that structure these forests such that floods are less common and wildfires occur more frequently than was historically the case. Impacts of these changes on primary consumers such as riparian cicadas are unknown. Because cicadas are consumed by a variety of animal species, disturbances that alter timing of their emergence or abundance could have consequences for species at higher trophic levels. We trapped emerging cicadas (*Tibicen dealbatus*) in burned and unburned riparian forest plots along the Middle Rio Grande in central New Mexico (USA) to determine effects of wildfire and vegetation structure on their density and phenology. We measured vegetation variables and soil temperature at cicada traps and related these variables to variation in emergence density and phenology. We also experimentally heated soil under emergence traps to examine the relationship between soil temperature and emergence phenology. Emergence density was similar in wildfire and unburned plots, though emergence date averaged earlier in wildfire plots and experimentally heated traps. We identified models containing cottonwood proximity (distance from the nearest cottonwood tree) and cottonwood canopy coverage as the most parsimonious explanations of emergence density at each trap. Model selection results were consistent with the literature and field observations that showed that cottonwood trees are an essential resource for *T. dealbatus*. Cottonwood canopy was also correlated with low soil temperatures, which are associated with later emergence dates. Failure of cottonwoods to reestablish following wildfire could result in cicadas emerging at lower densities and at earlier dates. For cicadas to emerge at densities and times that provide the greatest benefits to birds and other riparian-obligate secondary consumers, riparian forests should be protected from fire, and native vegetation in wildfire sites should be restored.

Key words: Akaike's Information Criterion; annual cicada emergence; Middle Rio Grande; riparian vegetation; *Tibicen dealbatus*; vegetation structure; wildfire.

INTRODUCTION

Natural disturbances such as flood and wildfire are important aspects of many ecosystems (Hobbs and Huenneke 1992, Lytle and Poff 2004). In the Middle Rio Grande of central New Mexico, the effects of these disturbance regimes are pervasive (Molles et al. 1998). Accordingly, many plant and animal communities are adapted to cope with, or take advantage of regular disturbance events. Organisms adapted to a specific disturbance regime could suffer serious consequences if that regime is altered or replaced (Lytle and Poff 2004). The diverse riparian ecosystems of the western United States evolved with regular flooding disturbances that created germination sites for native vegetation such as cottonwoods (*Populus* spp.) and willows (*Salix* spp.). In recent decades, however, dams and levees have pre-

vented flooding within many riparian forests (Knopf et al. 1988). The consequent increase in aridity and fuel loads has increased wildfire frequency and intensity in these systems (Stuever et al. 1995, Bock and Block 2005). A shift in the primary disturbance process from flooding to wildfire may have profound consequences for native plants and animals occupying riparian forests (Busch 1995, Stromberg et al. 2002). If native species affected by such a shift have important functional roles, effects on these species will also affect ecosystem function and structure. These changes in structure and function may then produce effects in other species, leading to cascading effects in other trophic levels.

Each year, cicada nymphs (Homoptera: Cicadidae) emerge from the ground in Southwestern riparian forests, eclose into winged adults, reproduce, and die within a few weeks (see Plate 1). This annual emergence has a fundamental influence on riparian ecosystem dynamics, as cicadas transport subterranean resources, such as water and nitrogen, to the aboveground community (Andersen 1994). As a food item, cicadas

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represent an annual pulse of biomass that links the productivity of their host plant producers to a broad array of secondary consumers (Callaham et al. 2000). Despite this important ecosystem function, ecological factors that influence density and phenology of annually emerging cicadas remain poorly understood (Callaham et al. 2000).

Many cicada species are large-bodied and easy to capture, making them an important food source for birds and other animals (Steward et al. 1988). For example, in the southwestern United States, the Apache cicada (*Diceroprocta apache*) is consumed by a large variety of birds during the summer breeding season (Rosenberg et al. 1982). Andersen (1994) speculates that riparian cicadas are so important to avian nesting success that riparian birds select their breeding sites based on the habitat's potential for cicada emergence. In the southwestern United States, many cicada species emerge annually, including species associated with riparian forests (Roche 2000); however, studies of human-induced changes to riparian cicada emergence have been limited to the Apache cicada.

To evaluate effects of altered disturbance regimes on emergence of another potentially important cicada species, we trapped the cicada *Tibicen dealbatus* during its emergence in riparian forests of central New Mexico. *T. dealbatus* emerges annually in forests along the Middle Rio Grande dominated by Rio Grande cottonwood (*Populus deltoides* var. *wislienzii*). As in other Southwestern rivers, floods are controlled throughout much of the Rio Grande (Valett et al. 2005), and wildfires have increased in frequency within the riparian forest (Stuever et al. 1995). Coincident with the absence of natural flooding, exotic fire-tolerant vegetation such as saltcedar (*Tamarix ramosissima*) has spread through much of the forest understory and, aided by wildfire, has the potential to outcompete native vegetation and dominate much of the forest (Busch 1995). Effects of altered disturbance processes and vegetation structure on riparian cicada emergence are largely unknown (Andersen 1994). Long-term studies from tallgrass prairie have shown that cicada species associated with fire-intolerant plant species fail to emerge in experimentally burned plots, and cicadas associated with fire-dependent vegetation emerge only in burned plots (Callaham et al. 2002). To our knowledge, studies examining the relationships between fire, vegetation structure, and emergence have not been applied to riparian systems. An understanding of vegetative associations of riparian cicadas is necessary to determine how they respond to changes in vegetation structure brought on by natural and human-caused disturbance of their habitat, such as wildfire (Callaham et al. 2002). Here, we (1) identify vegetation and climate characteristics associated with variation in cicada emergence density and phenology, (2) evaluate and separate influences of vegetation composition and wildfire on *T. dealbatus* populations, and (3) describe likely effects of



PLATE 1. Cicada emergence following recent wildfires in the cottonwood bosque along the Middle Rio Grande of New Mexico, USA. Photo credit: D. M. Smith.

continued change in disturbance regime and vegetation composition on secondary consumers that rely on annual cicada emergence.

METHODS

Study area and species

Our field sites were located in riparian forests along the west bank of the Middle Rio Grande in Socorro County, New Mexico. The Middle Rio Grande is the portion of the Rio Grande and its floodplain located between Cochiti Lake and Elephant Butte Reservoir in central New Mexico (Crawford et al. 1993). The Middle Rio Grande riparian forest is one of the most extensive cottonwood gallery forests in the United States (Howe and Knopf 1991). Native canopy trees are Rio Grande cottonwood and Gooding's willow (*Salix gooddingii*). Native understory shrubs include coyote willow (*Salix exigua*), seepwillow (*Baccharis glutinosa*), New Mexico olive (*Forestiera neomexicana*), and false indigo (*Amorpha fruticosa*). Exotic saltcedar and Russian olive (*Elaeagnus angustifolia*) shrubs are abundant throughout the understory. Most riparian vegetation is confined between the levees and river channel and much of the natural floodplain has been converted to agricultural fields (Molles et al. 1998). Our trapping sites were located in the riparian zone between the levees and river channel. Soil types within the forest are Typic Usti-

TABLE 1. Descriptions of cicada emergence trapping sites.

Site and plot	Location	Year of wildfire	Wildfire area (ha)	Number of traps	
				2003	2004
San Francisco					
wildfire	MRGCD†	2003	20.0	9	14
unburned	MRGCD			0	14
Chavez					
wildfire	MRGCD	2002	9.4	10	14
unburned	MRGCD			9	15
San Pedro					
wildfire	BDNWR‡	1996	22.1	6	13
unburned	BDNWR			5	11

† Middle Rio Grande Conservancy District.

‡ Bosque Del Apache National Wildlife Refuge.

fluents (Valett et al. 2005) that vary from well-drained, sandy soils to poorly drained clays. Recent wildfire sites have a thin layer of ash above a layer of soil hardened by the fires. Wildfires typically top-kill native vegetation, including large cottonwood trees, as well as exotic vegetation (Stuever 1997). Both native and exotic trees and shrubs recover from wildfires by resprouting from root crowns (Stuever 1997). Postfire dominance of a wildfire site by native or exotic resprouts varies between sites (D. M. Smith, *unpublished data*). Our field sites were located on land managed by the Middle Rio Grande Conservancy District and the Bosque Del Apache National Wildlife Refuge (Table 1).

T. dealbatus is a large-bodied cicada found in riparian forests of the southwestern and south-central United States (Cranshaw and Kondratieff 2004). Like other Southwestern cicadas, *T. dealbatus* emergence occurs each year, but individuals live several years underground as nymphs, emerging during the final year of life to eclose and become flying adults. Newly emerged males congregate at chorus sites to sing and attract females. After mating, females fly into woody vegetation where they insert their eggs into small-diameter branches (Glinski and Ohmart 1984). Weeks later, small nymphs hatch and fall from the branches into the soil where they burrow to the roots of a host and feed for 3–5 years on its xylem (E. Toolson, *personal communication*). *T. dealbatus* nymphs are found near the roots of cottonwood trees in riparian forests and near exotic trees such as maples, elms, and sycamores that have been planted in urban areas (Cranshaw and Kondratieff 2004).

Cicada trapping

To estimate density and phenology of emergence, we constructed traps that captured cicadas as they emerged from the ground. We installed cicada traps at three sites along the Middle Rio Grande. Each site contained an unburned and wildfire plot, except in 2003 when one site contained only a wildfire plot (Table 1). To determine short- and long-term effects of wildfire on cicada emergence, we established wildfire plots within burns

that occurred in 1996, 2002, and 2003 (Table 1). These fires ranged from 9.4 to 22.1 ha in size. We selected unburned trapping plots that were similar in size and adjacent to wildfire plots. We assumed that vegetation structure in unburned plots resembled that of wildfire plots prior to burning. Emergence traps resembled small, round tents without floors and covered a 1-m² basal area. Traps were constructed of fiberglass window screening attached to a ring of 1.9 cm diameter PVC tubing. The tubing was secured to the ground with several stakes, and a 50-cm rebar stake was placed under the center of the trap to support the window screening. We installed similar numbers of traps within each pair of plots (Table 1). We placed traps at random distances from the levees that parallel the river channel. Traps were spaced at least 50 m apart. We collected all captured cicadas, identified them to sex, and stored each cicada in a separate envelope on which we recorded the date and location. To estimate biomass of emerging adults, we measured the dry mass of 20 cicadas captured in wildfire and unburned sites. These cicadas were dried in an oven at 100°C for 24 h and weighed to 0.01 g. We computed emergence biomass for each plot by multiplying the mean adult dry mass of the 20 cicadas by emergence density (cicadas/m²) at each plot.

To determine emergence phenology, we checked each trap every third day. We used the midpoint between trap checks as the emergence date for each captured cicada. We calculated mean emergence dates and standard errors only from plots where at least 10 cicadas were captured in 2004. We could not obtain detailed phenology data in 2003 because site access was restricted for several days in June and July due to fire danger.

Vegetation and temperature measurement

We measured the size and community composition of perennial woody vegetation near each emergence trap to relate vegetation variables with emergence density and phenology. We measured vegetation in unburned sites and in wildfire sites no earlier than four months post-wildfire. At each trap site, we recorded proximity to the nearest cottonwood tree and other tree or shrub species,

diameter at breast height (dbh, in centimeters) of the nearest trees or shrubs, and their condition. We classified condition of a tree or shrub as “good” if its crown was covered by $\geq 50\%$ of green leaves and it appeared likely that the individual would survive until the next year, “poor” if it contained $\leq 50\%$ green leaves and survival appeared unlikely, and “moderate” if it contained $\sim 50\%$ green leaves and survival was uncertain. We classified individuals as “dead” when no green leaves were visible. In wildfire sites, top-killed trees and shrubs were checked for resprouts and classified as “dead and resprouting,” or “dead and not resprouting.” To measure canopy coverage, which we assumed to be an indicator of the density of cicada oviposition sites, we used a spherical densitometer to record canopy species composition and percent branch coverage above each trap. In recently burned sites, the eggs of emerging cicadas were likely laid in the small branches of trees or shrubs prior to wildfire. We therefore estimated the prefire canopy coverage with a densitometer by recording coverage of the branches of standing dead trees or shrubs in a similar manner as in unburned sites.

Soil temperature has been shown to influence emergence phenology of some cicada species (Williams and Simon 1995). To determine if emergence of *T. dealbatus* is associated with temperature, we recorded soil temperature at four trapping plots in 2004 using HOBO dataloggers (Onset, Bourne, Massachusetts, USA). Dataloggers recorded soil temperature with a probe buried 5 cm in the ground, where cicadas can be found prior to emergence (D. M. Smith, *personal observation*). We moved dataloggers to different positions within each site every six to nine days. Dataloggers recorded soil temperatures every 30 min. To compare temperatures between plots and relate temperatures to emergence phenology, we calculated mean soil temperatures during June, when cicada emergence usually begins.

Experimental warming

In 2005, we experimentally heated the soil under cicada traps to test the prediction that increased soil temperatures result in early cicada emergence. We sought to replicate conditions in wildfire plots, which generally have higher temperatures than unburned plots (D. M. Smith, *personal observation*). Blackened soil from wildfire plots was spread over 2 m² of ground on top of which traps were installed. We made three folds in a 3 × 0.5 m sheet of aluminum flashing and stood it on its side to box-in each trap. We draped clear plastic sheeting over the flashing to create boxes covering the experimental traps. With this setup, sunlight was reflected to the soil surface, where it was absorbed by the blackened soil and the warmed air was trapped inside the flashing, increasing the temperature of the upper soil layers where cicada nymphs waited to emerge. These warming treatments were installed around four experimental traps located in two unburned plots. We installed 12 control traps where the soil was not warmed above

normal temperatures. Experimental and control traps were located 1 m from cottonwood trees of similar size and condition. We checked all traps every two to three days to determine emergence date of each captured cicada. We installed dataloggers with soil probes at two experimental traps and at two control traps to confirm that soil temperatures were higher at experimental traps. We calculated the mean soil temperatures for the months of June and July 2005 and compared the combined means of two experimental traps with the combined means from two control traps for which temperatures were recorded. We used a *t* test assuming unequal variance (Proc TTEST, SAS Institute 1999) to test for significant differences in numerical emergence dates of individual cicadas captured in experimental and control traps.

Emergence density modeling

We constructed linear regression models with Poisson distribution (Proc GENMOD, SAS Institute 1999) to determine the importance of vegetation, wildfire, and spatial variables to variation in emergence density between traps. In this analysis, the cicada trap was the experimental unit, and a Poisson distribution was used because the data fit the shape and we felt that assumptions that values of count data are proportional to size of area sampled and independent values per sampling unit were met. We used the log link function in Proc GENMOD to log-transform the mean cicada count (i.e., response variable; SAS Institute 1999). We constructed the a priori set of 19 linear regression models using experience in the field and previous cicada studies to choose environmental variables that were likely to explain cicada emergence density. Models had cicada density as the dependent variable and various combinations of the 12 explanatory variables (Table 2). Explanatory variables included measurements of vegetation structure and composition (described previously), trap location (distance from trap to the river), and wildfire history (burned or unburned, year since burned).

To evaluate linear models, we used information-theoretic model selection and parameter estimation (Burnham and Anderson 2002). An information-theoretic approach is useful in identifying environmental factors that limit the abundance of organisms (Welch and MacMahon 2005). We used Akaike's Information Criterion (AIC), corrected for small sample size and over-dispersed data (QAIC_c), to select the most parsimonious models supported by the data (Burnham and Anderson 2002). QAIC_c was used because the Pearson chi-square goodness of fit estimation was > 1.0 for the global model, indicating over-dispersion of data (Burnham and Anderson 2002). We calculated QAIC_c for each model using log-likelihood function reported in SAS and the numbers of variables (*K*) included in each model. We compared models using relative QAIC_c values, with the lowest values belonging to the best-fit

TABLE 2. Explanatory variables used to model cicada emergence density at each trap.

Variable	Description
Burned	whether the plot was recently burned (last 10 years) or not
Distance river	distance from trap to river channel (m)
Distance levee	distance from trap to levee (m)
Cottonwood canopy	cottonwood canopy cover (0–100%)
Exotic canopy	exotic vegetation canopy cover (0–100%)
Cottonwood proximity	proximity to nearest cottonwood (m)
Cottonwood size	diameter at breast height of nearest cottonwood (cm)
Cottonwood condition	condition of nearest cottonwood (good, moderate, poor, burned and resprouted, or burned and not resprouted)
Exotic proximity	proximity to exotic tree or shrub (m)
Year since burn	years since last wildfire (1, 2, 3, 4, 5, 6, 7, 8, 9, or >10)

models (Burnham and Anderson 2002). We calculated ΔQAIC_c for each model by subtracting its QAIC_c value from the lowest QAIC_c value in the model set. This subtraction gives the best-fit model a ΔQAIC_c value of 0 and each other model a greater value. We examined all models with ΔQAIC_c value ≤ 4.0 , which Burnham and Anderson (2002) identify as a cutoff for models that are likely to be supported by the data. We used ΔQAIC_c to calculate Akaike weights (w_i), which estimate the probability of each model in our set being the best to explain emergence density (Burnham and Anderson 2002). To reduce bias in parameter estimation and incorporate model selection uncertainty, we calculated model-averaged parameter estimates that reflect the effect of a variable on emergence density. These estimates incorporated Akaike weights across all the models in which the estimated parameters were used (Burnham and Anderson 2002). We used Akaike weights to calculate unconditional variances of the parameter estimates that were used to construct 95% confidence intervals (Burnham and Anderson 2002).

RESULTS

Emergence density and biomass

In 2003, 70 *T. dealbatus* adults were captured in 41 emergence traps. In 2004, 179 *T. dealbatus* adults were captured in 79 emergence traps. The only other cicada species captured was *Diceroprocta cinctifera*, which is a smaller, plant generalist species found along much of the Lower Rio Grande (Sanborn and Phillips 1996). Only two adults of this species were captured in the Chavez wildfire plot in 2004 and they were not included in our analyses. In 2003, we captured more cicadas in wildfire plots than in unburned plots (Table 3). In 2004, however, a greater number of cicadas were captured in unburned plots than in wildfire plots (Table 3). Standard errors of density estimates were large and overlapping, suggesting that densities were not different between unburned vs. wildfire plots during either year. Emergence densities were also similar between paired unburned and wildfire plots in 2003 and 2004 (Table 3).

The dry mass of *T. dealbatus* was 0.78 ± 0.032 g (mean $\pm$ SE, $n = 20$ cicadas) and ranged from 0.50 to 1.11 g. Consistent with other cicada species, females

were heavier (0.87 ± 0.04 g, $n = 10$) than males (0.61 ± 0.03 g, $n = 10$). Adult dry mass was similar between cicadas emerging in wildfire (0.77 g, $n = 5$) and unburned (0.76 g, $n = 15$) plots. Emergence biomass ranged from 0.28 to 2.71 g/m². Biomass was slightly greater in wildfire plots than in unburned plots in 2003 and the reverse was true in 2004 (Table 2).

Emergence phenology

In 2003 and 2004, the first captured cicadas emerged at the San Francisco wildfire site around 1 June. During both years, the last cicadas to emerge came from unburned sites around 10 August. In 2004, mean emergence date for all wildfire plots was considerably earlier than the mean emergence date for unburned plots (Fig. 1). At two recently burned plots, mean emergence date was earlier than in their paired unburned plots (Fig. 1). We did not compare emergence phenology between plots at the San Pedro site because fewer than 10 cicadas were captured at this site (emergence density: 0.4 cicadas/m²).

Trap plot temperatures and experimental warming

Mean soil temperatures for June were strongly associated with cicada emergence (Fig. 2). In 2004, mean emergence date was earliest in the plot with the highest mean June soil temperature (25.9°C), and plots with the lowest mean June temperatures (19.0–21.0°C) had the latest mean emergence dates.

We were able to raise soil temperatures under experimental emergence traps (heated mean = 26.9°C, unheated mean = 23.4°C, Fig. 3). In 2005, cicadas emerged during the months of June and July in heated and unheated traps; however, mean emergence date of cicadas captured in heated traps was significantly earlier than in unheated traps ($t = 2.6$, $df = 22.3$, $P = 0.02$, Fig. 3).

Emergence density model selection

Information-theoretic model selection identified four linear regression models that were well supported by the emergence density data, all of which contained cottonwood-related variables (Table 4). The model containing percent cottonwood canopy coverage and cottonwood proximity as explanatory variables was identified as the model that best explained variation in emergence

TABLE 3. Estimated cicada emergence density and emergence biomass at trapping sites in 2003 and 2004.

Study area	Emergence density†		Biomass density‡ (g)	
	2003	2004	2003	2004
Unburned plots				
All sites	1.36 (0.48)	2.60 (0.60)	1.06	2.03
San Francisco§	...	3.36 (0.58)	...	2.62
Chavez	1.89 (0.66)	3.47 (1.40)	1.47	2.71
San Pedro	0.40 (0.40)	0.36 (0.28)	0.31	0.28
Wildfire plots				
All sites	1.96 (0.42)	1.80 (0.49)	1.53	1.40
San Francisco	2.56 (0.73)	3.00 (1.20)	2.00	2.34
Chavez	1.60 (0.61)	1.57 (0.52)	1.25	1.22
San Pedro	1.83 (1.01)	0.92 (0.61)	1.43	0.72

† Cicadas/m² (mean with SE in parentheses).

‡ Biomass density was calculated by multiplying emergence density by mean dry cicada mass calculated in 2004.

§ Cicada traps were not installed at the San Francisco unburned site in 2003.

density. Akaike weights suggest that this model is at least three times more likely to be the best model than any other in the set (Table 4). Model-averaged parameter estimates showed that the distance to the nearest cottonwood ($\beta = -0.118$, CL: -0.119 , -0.117 , all values are mean and 95% CL) had a negative effect on emergence density; as did wildfire ($\beta = -0.51$, CL: -0.512 , -0.508). Cottonwood canopy coverage ($\beta = 0.009$, CL: 0.009 , 0.009), cottonwood dbh ($\beta = 0.004$, CL: 0.004 , 0.004), cottonwood condition ($\beta = 0.092$, CL: 0.092 , 0.092), and the interaction between cottonwood canopy and wildfire status ($\beta = 0.018$, CL: 0.018 , 0.018) had positive effects on emergence density.

DISCUSSION

Determinants of emergence and biomass density

Variation in emergence density was largely explained by cottonwood-related variables. From these results and observations in the field, we determined that cottonwood trees provide oviposition sites in their canopy, belowground feeding sites for nymphs, and aboveground feeding sites for adults. For these reasons, cottonwoods are the most important resource for sustaining the emergence of this cicada. Variation in emergence density among traps was best explained by proximity of traps to cottonwood trees and percentage of cottonwood canopy covering traps. Parameter estimates showed that emergence density increases with canopy coverage and decreases with distance from cottonwood trees. These results support the notion that *T. dealbatus* relies on mature cottonwood trees for all aspects of its life cycle. We expected that cottonwood canopy would be an important variable in explaining emergence density just as canopy characteristics have been correlated with Apache cicada emergence (Ellingson and Andersen 2002). We most likely underestimated cottonwood canopy coverage (oviposition sites) in wildfire sites, in relation to unburned sites, because many trees fall in the years after fires and many branches

were likely burned during wildfires. Despite this underestimation, cottonwood canopy coverage was included in three of the four models that best explained emergence density. Cottonwood proximity was also found in the best-supported models and likely explains much of the variation in emergence density because it is a measure of proximity of the trap site to oviposition sites and nymph feeding sites. Male cicadas also used large cottonwood trees as chorusing centers (D. M. Smith, *personal observation*) to attract females. These findings illustrate a link between Rio Grande cottonwood and the life cycle of *T. dealbatus*.

Model selection results and observations in the field suggest that cicadas only emerge in areas where live cottonwoods are in close proximity (≤ 10 m, Fig. 4). Because cicada nymphs live three to five years underground prior to emerging, emergence continues for several years in recently burned areas that lack a live

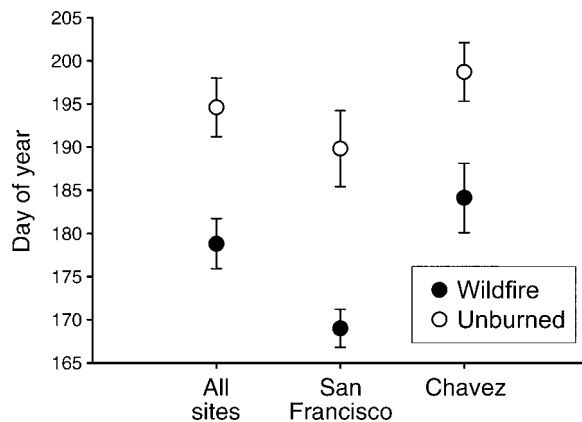


FIG. 1. Comparisons of mean emergence date (± 2 SE) in unburned and wildfire plots at all sites, the San Francisco 2003 wildfire and unburned site, and the Chavez 2002 wildfire and unburned site. Phenology data from the San Pedro site were not included because of low emergence density. In 2004, cicada emergence dates ranged from 1 June (day 153) to 11 August (day 221); day 1 is 1 January.

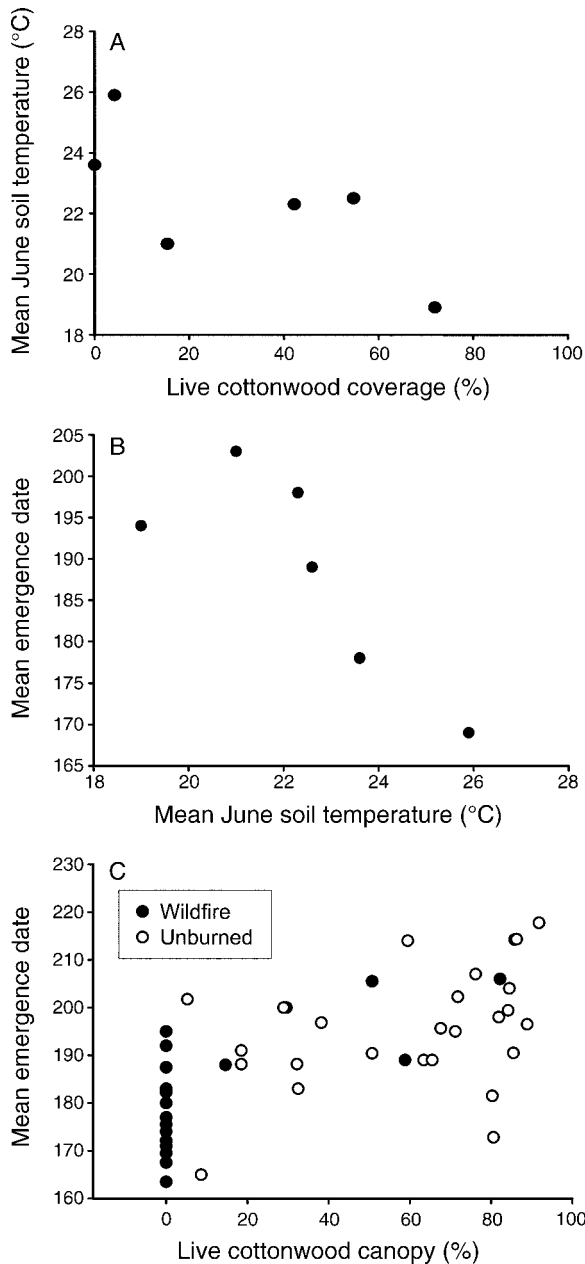


FIG. 2. Relationship between (A) mean soil temperatures during June 2004 and percent cover of live cottonwood at the six cicada trapping plots, (B) mean emergence date in 2004 and mean soil temperature during June 2004 at six cicada trapping plots, and (C) mean cicada emergence date at traps where cicadas were captured in 2004 and percent canopy cover of live cottonwood. Note that most cicadas that emerged after day 180 (28 June) were captured in traps with at least 15% cottonwood canopy cover.

cottonwood canopy. In these burned forests, cicada nymphs appear to survive by feeding off the roots of top-killed, but resprouting cottonwoods. At the San Pedro wildfire plot, which was burned in 1996, cicadas did not emerge in areas where the cottonwood canopy was burned and not replaced. Emergence did occur in

areas of this plot where some cottonwood trees survived the wildfire and maintained a live canopy. This observation suggests that, following a wildfire, cicada nymphs can survive underground on cottonwood roots, but when cottonwood canopy is completely consumed by wildfire, oviposition sites are lost and cicadas are unable to oviposit in a wildfire site until the canopy recovers or is restored. If cottonwoods do not fully recover from a wildfire, cicada emergence will eventually cease at that site or be confined to areas with cottonwoods that survived the wildfire or resprouted after the wildfire.

We were unable to detect any large or consistent differences in emergence density between wildfire and unburned plots. Emergence was patchily distributed at many sites, and field observations and data suggest that density was similar among plots (Table 3). Emergence densities in wildfire and unburned plots were similar despite stark vegetation differences because (1) in recently burned plots (Chavez and San Francisco), cicadas were oviposited in cottonwoods, hatched prior to wildfires, continued to feed on surviving cottonwood root crowns, and emerged after wildfires; and (2) in the older wildfire plot (San Pedro) some traps were located under large cottonwood trees that survived the wildfire, provided oviposition sites, and fed cicada nymphs. The apparent ability of nymphs to survive on roots of top-killed cottonwoods is an interesting phenomenon that warrants further study. Researchers have shown that stresses applied to host plants rarely negatively affect herbivorous insects (Koricheva et al. 1998). This lack of response appears consistent with the short-term interactions among wildfire, cottonwoods, and cicadas, but additional research is needed to fully understand these interactions.

Despite similarities in emergence density between wildfire and unburned sites along the Middle Rio Grande, long-term decline of cicada emergence follow-

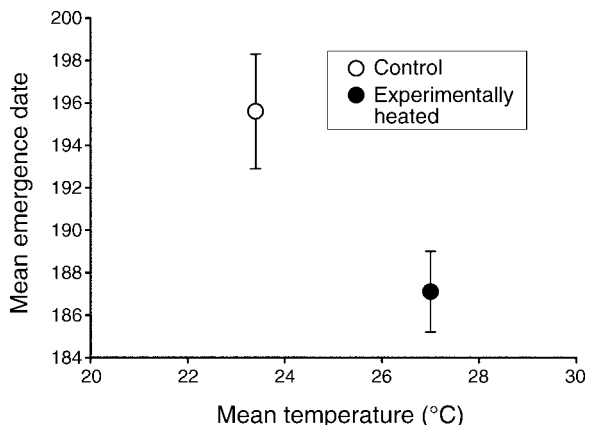


FIG. 3. Emergence dates (mean $\pm$ 1 SE) at control and experimentally heated traps in 2005. Experimental traps were warmer than control traps, and cicadas emerged earlier in experimental traps than in control traps ($P = 0.02$).

TABLE 4. Explanatory variables and QAIC components for the four linear regression models predicting cicada emergence density that were supported by the data ($\Delta\text{QAIC}_c \leq 4$).

Model variables	K	ΔQAIC_c	w_i
Cottonwood proximity, cottonwood canopy	5	0	0.52
Cottonwood proximity	4	2.3	0.16
Cottonwood proximity, cottonwood canopy, cottonwood condition, cottonwood size	7	2.6	0.14
Cottonwood canopy, burned, cottonwood canopy $\times$ burned†	6	3.1	0.11

Note: Abbreviations are: K , number of parameters; ΔQAIC_c , difference in Akaike's Information Criterion adjusted for small sample size and overdispersed data; w_i , Akaike weights.

† The interaction effect of percent cottonwood canopy cover and the burned status of the plot.

ing wildfire is probable because many cottonwoods fail to resprout following fires (Stuever 1997), and many cottonwood resprouts do not survive their first year following wildfire (D. M. Smith, *unpublished data*). Factors that could contribute to the death of resprouts include herbivory (particularly livestock grazing), exposure to pathogens, water table depth, and competition with exotic species (Busch 1995). Model selection, however, showed no effect of exotic vegetation on emergence density. This lack of effect is probably attributable to exotic saltcedar and Russian olive growing primarily in the understory of unburned sites where they do not affect the existing native canopy. In some wildfire sites, however, saltcedar and Russian olive appear to outcompete native vegetation during early seral stages and form an exotic canopy (Sher et al. 2000; D. M. Smith, *unpublished data*). In the absence of good growing conditions for cottonwood resprouts, continued occurrence of wildfire could trigger conversion of a forest dominated by flood-dependent, nonfire-adapted cottonwood to fire-adapted saltcedar (Hobbs and Huenneke 1992, Busch 1995). In this situation, there will be fewer oviposition sites for *T. dealbatus* because oviposition apparently occurs only in cottonwoods. Management action in the form of flood restoration may be necessary to maximize cottonwood resprout growth in the presence of exotic vegetation in recent wildfire sites (Nagler et al. 2005).

Effects of wildfire on emergence phenology

We found considerable differences in emergence phenology between unburned plots and recently burned wildfire plots. At both the Chavez and San Francisco sites, cicadas began and ended emergence earlier in the wildfire plot than in the unburned plot. Studies of periodical cicadas (*Magicalcadas* spp.) have shown that emergence phenology is associated with host plant seasonal cycles (Karban et al. 2000) and soil temperature (Williams and Simon 1995). Periodical cicada nymphs track seasonal cycles of their host trees. A specific number of annual cycles trigger nymphs to tunnel near the soil surface, where emergence is later initiated when the soil temperature reaches a threshold (Williams and Simon 1995, Karban et al. 2000). We found evidence that *T. dealbatus* emergence is triggered in a similar fashion. Prior to the start of emergence, we found cicada nymphs sitting several centimeters below the soil as periodical

cicadas have been observed to do prior to emergence. In addition, emergence timing was associated with soil temperatures at wildfire and unburned plots (Fig. 2). Wildfire plots were warmer than unburned plots, and unburned plots with low cottonwood canopy coverage were warmer than unburned plots with high canopy coverage (Fig. 2). By experimentally heating trapping sites, we found further evidence that increased soil temperatures result in earlier cicada emergence (Fig. 3). Based on these observations, we conclude that disturbances that reduce cottonwood canopy coverage elevate soil temperatures in turn altering cicada emergence phenology.

Ecosystem consequences of wildfire

Due to the construction of dams and other hydrological projects, major flooding has not occurred within much of the Middle Rio Grande riparian forest since 1942 (Howe and Knopf 1991). Wildfires have recently increased in frequency due to the accumulation of woody debris, spread of combustible exotic vegetation, and increased human activity within the forest (Busch 1995, Stuever et al. 1995). As in other western U.S. habitats, long-term drought has created xeric conditions that have also contributed to wildfire frequency (MacKenzie et al. 2004). These factors have created a situation in which the natural disturbance regime of flooding is being replaced by a very different disturbance regime involving wildfire. We found evidence that a shift from a

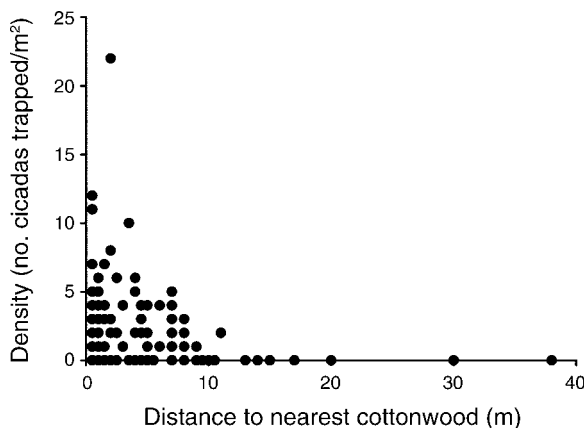


FIG. 4. Relationship between number of cicadas captured at each emergence trap in 2003 and 2004 and distance to the nearest cottonwood tree.

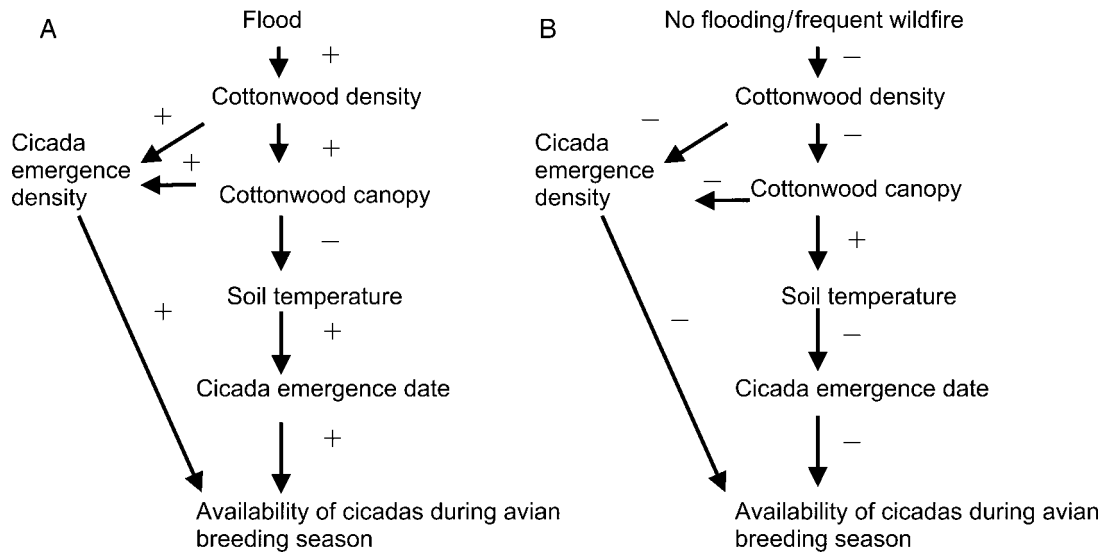


FIG. 5. Diagram of the possible effects of two disturbance regimes on populations of producers (cottonwoods), primary consumers (cicadas), and secondary consumers (nesting birds) in the Middle Rio Grande riparian forest. Pluses and minuses represent positive and negative effects, respectively. Under a natural flood regime (A), cottonwood density is maintained or increased, which results in an increase in cottonwood canopy cover and emergence density. Increased canopy cover lowers soil temperatures, resulting in late emergence phenology that benefits birds that reproduce late in the summer (i.e., Yellow-billed Cuckoos). When the natural flood regime is halted and wildfires occur frequently (B), cottonwood density and cicada emergence density are reduced, low canopy cover results in increased soil temperatures, and cicadas emerge early in the season and are not available for birds.

flood-driven disturbance regime to one driven by wildfire results in annual cicadas emerging earlier in the season than in unburned sites. Failure of cottonwoods to recover in wildfire sites will likely result in cicadas emerging at lower densities than in unburned sites due to their strong association with cottonwoods. These changes in cicada emergence could have considerable impacts on riparian animal communities. In Arizona riparian forests, Apache cicadas make up the bulk of many riparian birds' diets during their breeding seasons (Rosenberg et al. 1982). Anderson (1994) indicated that any decreases in the availability of this resource have the potential to reduce nesting success of riparian birds (Andersen 1994). *T. dealbatus* is larger than the Apache cicada and is consumed by many animals (birds, *Falco sparverius*, *Coccyzus americanus*, *Tyrannus verticalis*, *Myiarchus cinerascens*, *Poecile atricapilla*, *Passerina caerulea*, *Pheucticus melanocephalus*, *Pipilo maculatus*, *Icterus bullockii*, *Passer domesticus*; reptiles, *Aspoadocelis* spp.; arthropods, *Latrodectus* spp., *Sphecius speciosus*, Formicidae; J. Kelly and M. Smith, *personal observations*). The range of biomass density from *T. dealbatus* emergence (Table 3) at our plots is equal to or greater than estimates of biomass density of the Apache cicada along the Colorado River (0.02–1.9 g/m², Andersen 1994). We therefore suspect that reduced availability of *T. dealbatus*, in response to habitat changes caused by wildfire, will have a negative impact on the riparian bird community of the Middle Rio Grande, by limiting food

availability for adults and young during the critical period of reproduction.

For example, the Southwestern population of Yellow-billed Cuckoos (*Coccyzus americanus*) feeds heavily on annual cicadas (Rosenberg et al. 1982, Hughes 1999) and has been considered for listing as a threatened species (Hughes 1999). The relatively late nesting period of this population is thought to be an adaptation to the typical timing of cicada emergence (Rosenberg et al. 1982). In New Mexico, nesting of cuckoos and other bird species coincides with peak cicada emergence in unburned plots (Howe 1986). Emergence of cicadas prior to the cuckoo breeding season could therefore be detrimental to the cuckoo's nesting success (Andersen 1994). Recovery and sustainability of the Yellow-billed Cuckoo population in the Middle Rio Grande riparian forest may thus depend on ensuring timely emergence of *T. dealbatus* in cuckoo breeding territories.

The relationships among cottonwood canopy cover, soil temperatures, and emergence phenology (Fig. 2) suggest that when flood-adapted producers (cottonwoods) are negatively affected by wildfire disturbance, the density and phenology of primary consumers (cicadas) are altered due to increased soil temperatures and loss of feeding and oviposition sites. These changes in emergence could then negatively impact populations of secondary consumers such as birds if they are unable to adapt to low cicada densities and early cicada emergence (Fig. 5). Additional research examining the relationship between cicada abundance and breeding

bird productivity is needed to verify these predicted effects of wildfire disturbance on organisms in multiple trophic levels within this system.

Management recommendations

We found that cottonwood density is an important factor in cicada emergence density and phenology. Model selection results show that cottonwood dbh and condition had smaller effects on emergence density. Therefore, the age and health of a cottonwood stand is perhaps not as important to emergence density as the density of trees within the stand. In recently burned sites, prefire conditions appear to be important in determining emergence density, while current conditions, such as percentage of remaining live canopy cover, appear to be important in determining emergence phenology.

The spatial structure of the Middle Rio Grande riparian forest has been heavily altered in the last 60 years (Whitney 1996). Prior to construction of dams and levees, the riparian forests formed a mosaic of different-aged stands along dynamic river courses (Whitney 1996). From 1935 to 1989 alone, human development of the Middle Rio Grande floodplain reduced the amount of riparian forest cover by 1300 ha (Crawford et al. 1993). At the same time, agricultural land increased by 2850 ha, and urban development increased by 10 000 ha (Crawford et al. 1993). These changes have resulted in riparian vegetation being confined to narrow bands of forest with high densities of old and decadent cottonwoods undergoing little recruitment due to flood control (Howe and Knopf 1991, Molles et al. 1998). As the total number of hectares from which *T. dealbatus* emerges is reduced, each remaining hectare becomes more important to the ecology of this species and the consumers who depend on it. It is therefore important to maintain habitat that will support high emergence densities of *T. dealbatus*, wherever possible, in order to ensure the persistence of this cicada and to benefit the insectivorous animals in the Middle Rio Grande floodplain.

Frequent wildfires change vegetation structure and composition in areas such as riparian forests where wildfire was historically infrequent (see Busch 1995, Mackenzie et al. 2004). To preserve native riparian forest structure and ensure that cicadas continue to emerge at densities and times that benefit riparian animal communities, large wildfires should be prevented (Busch 1995, Nagler et al. 2005). In addition, cottonwood recruitment should be aided in unburned sites to ensure replacement of aging trees (Howe and Knopf 1991). Comparisons of soil temperature, emergence phenology, and cottonwood canopy cover at traps (Fig. 2) show that ~10–20% cottonwood canopy cover is necessary to maintain low soil temperatures and ensure that cicadas emerge later than early July, when cuckoos and other migratory birds nest in Southwestern riparian forests. At least 15% live cottonwood canopy

coverage should therefore be provided by moderate-to-high densities of medium or large cottonwood trees in order to maintain low soil temperatures and prevent premature cicada emergence. To maintain high emergence densities, cottonwood trees should be growing at distances no greater than 20 m apart. At this spacing, the distance between any spot on the forest floor and the nearest cottonwood tree will be <10 m, the distance at which emergence density begins to decline (Fig. 4). When wildfires do occur, it is essential to restore the cottonwood canopy lost during the fire by aiding the growth of resprouts. Failure to aid cottonwood recovery will result in reduction or loss of *T. dealbatus* emergence from a wildfire site.

For this study, we measured emergence of cicadas in areas where the natural flood disturbance regime has been halted (unburned sites) or replaced by wildfire. Experimental studies examining population dynamics under the natural flood regime and altered disturbance regimes should also be performed to further explore the effects of various disturbance processes on populations of cicadas and other riparian organisms.

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