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Spatial variability in oviposition damage by periodical cicadas in a fragmented landscape

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Abstract Effects of the periodical cicada (*Magicicada* spp.) on forest dynamics are poorly documented. A 1998 emergence of *M. cassini* in eastern Kansas led to colonization of a fragmented experimental landscape undergoing secondary succession. We hypothesized that per-tree rates of oviposition damage by cicadas would reflect: (1) distance from the source of the emergence, (2) patch size, and (3) local tree density. Ovipositing females displayed clear preferences for host species and damage incidence showed predictable spatial patterns. Two species (smooth sumac, *Rhus glabra*, and eastern red cedar, *Juniperus virginiana)* were rarely attacked, whereas others (rough-leaved dogwood, *Cornus drummondii*; slippery elm, *Ulmus rubra*; box elder, *Acer negundo*, and honey locust, *Gleditsia triacanthos)* were strongly attacked. The dominant early successional tree, dogwood, received on average the most attacks. As predicted, attacks per stem declined strongly with distance from the emergence source, and with local stem density (a "dilution" effect). Contrary to expectations, there were more attacks per stem on larger patches. Because ovipositing cicadas cut damaging slits in host tree branches, potentially affecting tree growth rate, competitive ability, and capacity to reproduce, cicada damage could potentially influence spatial variation in secondary succession.

Keywords Colonization · Ecological succession · Habitat fragmentation · Oviposition damage · Periodical cicadas

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Introduction

Herbivores are important drivers of plant community dynamics (Huntly 1991; Davidson 1993). Selective herbivory can significantly impact the abundance or performance of plant species, altering plant community dynamics by affecting competitive dominance. For example, small mammal herbivory is often intense in old fields and grasslands, retarding succession via attacks on woody seedlings (Weltzin et al. 1997; Ostfeld et al. 1997; Schweiger et al. 1999). In this paper, we document how the spatial attributes of a fragmented landscape – in particular, patch size and distance from continuous habitat – influence the magnitude of oviposition damage inflicted on the local tree community by an emerging cohort of periodical cicadas.

Because many insects vary dramatically in abundance, the severity of insect herbivory should show substantial temporal variability. Olff and Ritchie (1998) note that in "typical" years, insect herbivores may have weak effects on community dynamics, but that in years of peak abundance these species can defoliate dominant plant species and so play key roles in species replacements. Such temporal variability in herbivory should be particularly evident in species with "outbreak" population dynamics. For example, the introduced gypsy moth (*Lymantria dispar*) and the spruce budworm (*Choristoneura fumiferana*) exhibit population explosions in temperate forests of North America, defoliating large areas (Williams et al. 1991; Zoladeski and Maycock 1991). Even occasional episodes of severe insect herbivory could modify plant community dynamics over long temporal scales and so may be particularly important during succession (Brown 1984; Brown and Gange 1992; Olff and Ritchie 1998).

In principle, periodic emergences of insect herbivores at high abundance can also generate severe, transient pulses in herbivory. One insect taxon that could exert strong episodic effects on succession is the periodical cicada (*Magicicada* spp.). Periodical cicadas have extremely long (13- to 17-year) nymphal stages and percussive mass emergences over large areas (e.g., Karban 1997), often in staggering abundance. In this paper, we suggest that the impact of cicadas on tree successional dynamics during an emergence could be substantial, and that there should be strong, predictable spatial variation in such impact related to landscape attributes such as patch size and isolation.

Biology of periodical cicadas

During an emergence, periodical cicadas are usually enormously abundant for up to 6 weeks (Lloyd and Dybas 1966a, b). During an emergence cicadas are the most common animal by weight in deciduous woodlands of the eastern United States, with large potential effects on local food webs. Ecological studies of periodical cicadas have largely focused on their role as food source for vertebrate predators [e.g., birds (Strehl and White 1987; Williams et al. 1993), and small mammals (Hahus and Smith 1990)]. Other arthropods may benefit indirectly by predator satiation, though conclusive evidence is still lacking (Stephen et al. 1990). Less is known about the trophic impact of cicadas on their own food resources, except for studies of effects on commercial plantations and ornamentals (Karban 1983; Hogmire et al. 1990; Van der Zwet et al. 1997).

Periodical cicadas could affect tree communities via several modes of resource exploitation. After mating, females create linear series of conspicuous slits for oviposition on the underside of small tree branches (Miller and Crowley 1998). A given female can make multiple slits per stem and oviposit on multiple stems. The branch portion distal to the slits quickly loses its leaves and the end may droop; this phenomenon is called “flagging” (Williams and Simon 1995). Repair of this damage requires the plant to use resources otherwise available for growth and reproduction; slits placed in larger branches also allow entry to pathogens (Anderson et al. 1979). Newly hatched nymphs drop from nest branches in slits, and begin a long-lived nymphal stage feeding underground, extracting nutrients from tree root xylem. The tremendous density of cicadas could cumulatively impose a substantial below-ground herbivore load on host plants (White and Strehl 1978). This consumption could potentially reduce an individual tree’s capacity for growth and reproduction (although not always, see Karban 1985). Adult cicadas feed by sucking plant fluids, but the long-term impact of oviposition is likely to exceed greatly that of adult feeding (Williams and Simon 1995). Our study focuses on spatial variation in direct oviposition damage following emergence. Our design will also permit assessment of longer-term damage in the coming years.

Potential sources of spatial variation in cicada impact

Prior studies have identified three likely sources of spatial variability in cicada impact upon their host plants, which we argue could generate predictable, heterogeneous impact on plants in a fragmented landscape: (i) spatial variation in cicada emergence density, (ii) limited dispersal, and (iii) habitat preference.

1. The local density of emergence varies greatly (Williams and Simon 1995; W. Cook personal observations), potentially leading to substantial spatial variability in the location of cicada assembly and oviposition sites.
2. Adult periodical cicadas are weak, clumsy fliers. Besides predator avoidance, cicadas have two primary reasons to move: assembly by both sexes at congregational choruses of males (Williams and Smith 1991), and female selection of hosts for oviposition. After mating, females disperse to oviposit. In one study, most cicadas dispersed less than 50 m across an open field or along a forest edge (Karban 1981), although there is a record of heavy infestation in a 3-year-old orchard 0.8 km from the cicadas’ presumed site of origin (cited in Karban 1981). In another study, dispersal by females led to oviposition up to 150 m from emergence sites, with a gradient of declining oviposition with distance (Lloyd et al. 1982). Given spatially clumped mating aggregations, limited dispersal capability should tend to produce spatial patchiness in oviposition damage.
3. Periodical cicadas occupy a range of habitats (e.g., flood plains, woodland edges and mature forests, Williams and Simon 1995) but do show habitat preferences. In prior studies, the greatest density of egg-nests (and the most severe damage to woody tissues) was from saplings at woodland edges (White 1980; Rodenhouse et al. 1997). Rodenhouse et al. (1997) showed that the shape and composition of habitat fragments affected the density and spatial distribution of periodical cicadas. In their study, cicadas gathered primarily at forest edges, with oviposition mainly near chorus sites. Damage should thus be particularly pronounced at the edges of patches of woody vegetation.

Host species selection

Periodical cicadas oviposit in many woody plant species (trees, shrubs and vines) but avoid non-woody taxa. In one community study, 18 of 22 potential host species in a woody plant assemblage were used, though different cicada species preferred different tree species (White 1980). Identification of cicada host preferences matters for analyses of community effects, because differential attacks on species associated with different stages of ecological succession can change a system trajectory (Davidson 1993). Even if consumption does not directly kill plants, it can slow growth, modify branch architecture, and alter phenology, placing heavily attacked species at a competitive disadvantage with other species (Louda et al. 1990). Differential attack rates on different

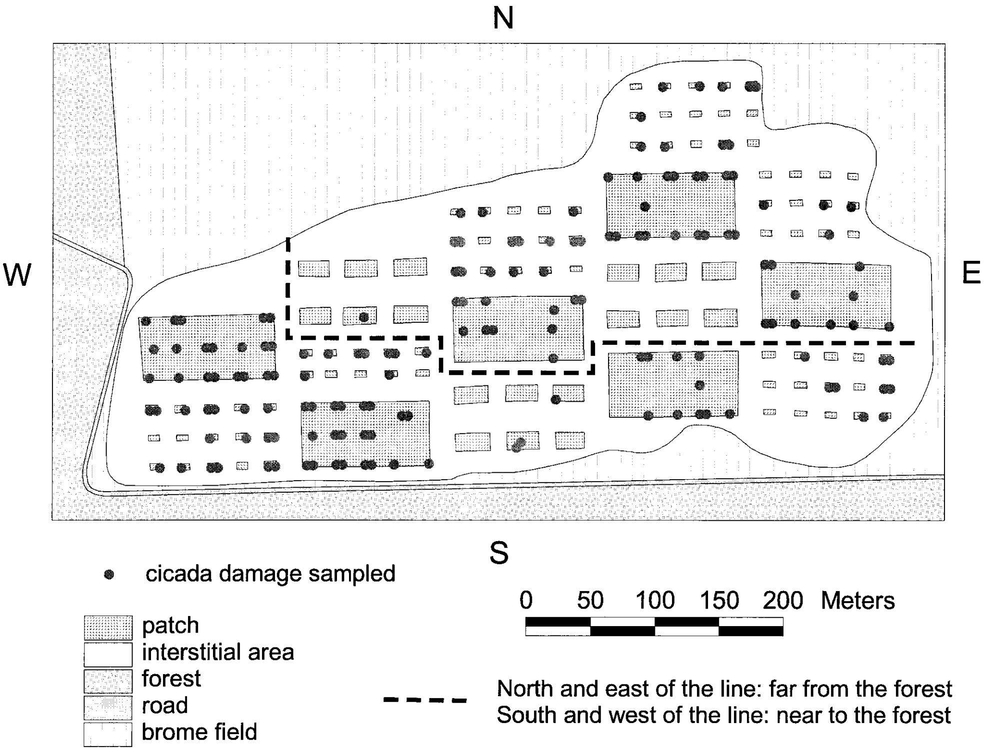

Fig. 1 Diagrammatic map of Kansas Fragmentation Study, Nelson Environmental Study Area, Kansas Ecological Reserves, Jefferson County, Kansas

taxa could influence the pattern of species replacement during succession.

Study site

In 1984, a long-term experiment examining impacts of patch size and landscape position on succession was initiated in northeast Kansas (Robinson et al. 1992; Holt et al. 1995; Schweiger et al. 2000). The project comprises a mosaic of habitat patches (arranged to represent different degrees of habitat fragmentation) arrayed in a closely mown interstitial matrix (Fig. 1). The adjacent landscape is heterogeneous, with extensive woods to the south and west, wooded hedgerows and fields to the east and a brome grass field to the north. Since site initiation, succession has proceeded unimpeded on the patches. A principal goal has been to analyze how patch size influences spatial patterns in plant succession. In recent years, species colonizing from the adjacent forest have become increasingly abundant, replacing initially dominant annual forbs and grasses (Robinson et al. 1992; Holt et al. 1995). Effects of patch size and distance to the forest have developed, as woody plants are now significantly more common on large than on small habitat fragments, and on patches near to rather than away from the forest (Yao et al. 1999). This spatial variability in succession has created a spatially heterogeneous landscape of large and small habitat patches with differing amounts of woody vegetation.

In the previous emergence (1981), large numbers of cicadas emerged in the woods just south and west of the study site (R.D. Holt, unpublished observations). The current research site was in agriculture through 1984, unsuitable for cicada occupancy or colonization. Thus, it is reasonable to surmise that nearly all periodical cicadas present on the site during the 1998 emergence invaded from the adjacent woods.

Hypotheses

Based on prior work (White 1980; Lloyd et al. 1982; Rodenhouse et al. 1997), we expected cicada oviposition damage in the emergence of 1998 to be strongly variable in space. Our a priori hypotheses were as follows:

1. Cicadas would be trophic generalists, utilizing most of the available woody tree species for oviposition, albeit at differing rates among species.
2. There should be a gradient in oviposition damage, declining with distance from the forest. (The distance from mature trees outside the site to the closest habitat patch is 5 m, whereas the farthest distance is more than 200 m. Given their relatively weak dispersal ability, cicadas should oviposit more frequently in fragments near the forest, the site of emergence.
3. Because cicadas appear to prefer forest edges, we predicted cicada damage should be greatest in small patches (which in essence are “all-edge”).
4. Cicadas should oviposit less in areas of high than in low stem density. (If a given patch is colonized at a fixed rate of individuals per unit area, there could be a “dilution” effect, with a given oviposition load spread

over more stems in a high-density area, leading to fewer attacks per stem.)

5. Given the great abundance of periodical cicadas, our long-term prediction is that damage inflicted on resident trees could be sufficient to modify successional trajectories on our site.

Materials and methods

This study was from May to November 1998. Figure 1 depicts the experimental landscape, and its relation to neighboring woodlands. The large patches are 50×100 m, medium patches 12×24 m, and small patches 4×8 m. Smaller patches are clustered into groups, with aggregate area similar to a large patch (see Fig. 1). In this study, we largely contrast large and small patches. To analyze distance effects, patches were divided into two groups: near to the forest (<110 m) and 'far' (>110 m, see Fig. 1).

Cicada emergence census

Large numbers of cicadas emerged in the forest in May 1998. To assess the spatial distribution of emerging adults, a census of shed exuviae was conducted on 27–29 May. A transect 1,180 m long and 1 m wide was set up along the west, south and east sides of the site, along the edge of the forest adjacent to the study site, with 1-m quadrats for censusing every 10 m. All exuviae were counted on each quadrat. Between quadrats, we used an index to estimate cicadas' abundance (classes 0, 1–25, 26–75, 76–150, >150). The patterns for the latter dataset parallel the direct counts, so we only report direct counts below. Because cicadas might emerge after the census, we removed casts from every fourth quadrat, and sampled at later times to search for uncounted, newly emerged exuviae. Because additional emerging cicadas were not detected in significant numbers 1 week later, the data of 27–29 May were assumed to be complete.

Cicada species identity

The 1998 cicadas belong to the 17-year periodical cicada Brood IV, found from southwestern Iowa to northeastern Texas. In many emergences, three morphologically and behaviorally distinct species emerge simultaneously (Williams and Simon 1995). However, all specimens observed in the study site in 1998 were *Magicicada cassini*. *M. septendecim* was heard calling at distant sites in the surrounding woods, but none were found on the site. The third potential species, *M. septendicula*, was neither seen nor heard near the site.

Potential host species

Prior studies on the site provide a detailed census of the resident plant community, which by 1998 included 3,743 individually tagged and measured trees greater than 2 m in height in permanent quadrats (Holt et al. 1995; Yao et al. 1999). The dominant tree in our mid-successional community is rough-leaved dogwood *(Cornus drummondii),* comprising 93% of all stems greater than 2 m. The next five most common species by rank abundance are slippery elm *(Ulmus rubra),* eastern red cedar *(Juniperus virginiana),* smooth sumac *(Rhus glabra),* honey locust *(Gleditsia triacanthos),* and box elder *(Acer negundo).*

Tree sample selection

To assess spatial variability in oviposition damage, we used a three-way factorial design, based on three variables; patch size, distance, and local stem density. We stratified our sampling to ensure, wherever possible, equal sample sizes for each (area)×(distance)×(density) class, as follows:

Prior to the 1998 emergence, trees of each species were randomly selected from the 1997 dataset of tagged trees based on distance to the forest (near or far, see Fig. 1), size of patch (large or small), and tree density within the quadrat (density classes of 1–2, 3–5, 6–10, 11–15, and >15 stems per 4×4 m^2, summed across species). Where enough trees were available, we randomly selected ten individuals for each combination of distance, patch size and density. Only dogwood was sufficiently abundant in the 1997 dataset to allow the full set of 200 stems required for a complete three-way factorial design. For the other species, we selected individuals based on distance to the forest and patch size, creating a two-way factorial design. To create larger sample sizes for those species, we also marked additional stems outside the permanent quadrats. Local stem density data was not a priori available for these individuals in our 1997 dataset, preventing analysis of density effects. Five additional species provided enough data to examine within-species spatial patterns of cicada attacks. (Due to the complete absence of sumacs from small patches, we included data from trees on medium patches for this species.) The sample sizes available for species (other than dogwood) are in Table 1.

Oviposition damage measures

In October and November 1998 we examined each selected tree to assess damage inflicted by cicada oviposition. Two damage indices were used: the number of branches with "flags," and the cumulative length of oviposition slits. For each tree, the number of flagged branches was counted. To standardize among trees differing in size, crown volumes were estimated by measuring maximal width in the N-S and E-W directions, and by measuring tree height. Because other authors have found flag counts to be potentially misleading because of variation in tree size and shape (White 1981), we measured a second index of slit abundance. For each selected tree we chose the farthest emergent branch in each of four cardinal directions, and assessed the proportion of the branch with observed slit damage within its outer 50 cm.

Dogwood damage was analyzed using multi-way balanced ANOVAs, to assess combined effects of distance from the forest, patch size, and stem density. As insufficient individuals of other species were available to permit full balanced designs, one-way ANOVAs were performed to determine effects of patch size or distance from the forest. To investigate the effects of local stem density on these species, we used post hoc randomization tests to analyze the statistical significance of visually apparent trends.

Table 1 Sample sizes and spatial arrangement of host tree species (except dogwood, see text)

	Ulmus rubra		*Juniperus virginiana*		*Acer negundo*		*Rhus glabra*		*Gleditsia triacanthos*	
	Near	Far	Near	Far	Near	Far	Near	Far	Near	Far
Large	10	2	10	10	7	0	8	0	4	5
Small	10	2	8	8	7	0	10[a]	0	0	0

[a] Medium patches used, no individuals available in small patches

Results

Cicada origination from the adjacent forest

As hypothesized, the forest on the west and south sides of the experimental site produced by far the most cicadas. Mean cast counts per square meter were 21.5 cicadas emerged on the west side, 7.1 on the south, and 5.9 and 0.7 on the two hedgerow transects on the east. Although the west figure is significantly larger than the others, the emergence numbers from the south edge were not significantly larger than those from the eastern transects. However, direct observations prior to the exuviae census make us confident that the primary source of invading cicadas was from the south and west. (The south census figure is artificially low, because a county road crew unfortunately trimmed vegetation along the south edge of the site the day immediately prior to our count, destroying many exuviae.) Within the site itself, we found just a few exuviae, at one location within one small patch. Of all the experimental patches, this patch is the closest to adult trees outside the study site (~5 m). We surmise that nymphs may have traveled along the tree roots of a large elm outside the site, penetrating the site below ground to emerge within the patch. Otherwise, all cicada damage at our site seems to have been inflicted by dispersers emanating from external sources, mainly to the west and south.

Variation in damage among host species

We assumed that slit damage would not vary significantly by cardinal direction. Averaged over the entire data set, this assumption proved correct (ANOVA, F=0.99, df=3, P=0.40). The average slit length per half meter of stem varied significantly by species (ANOVA, F=11.23, df=10, P<0.001). Species fell into two clear groups: dogwood, box elder, honey locust and elm formed one group, all damaged at fairly high rates. Red cedars were damaged occasionally, and sumacs not at all (Fig. 2).

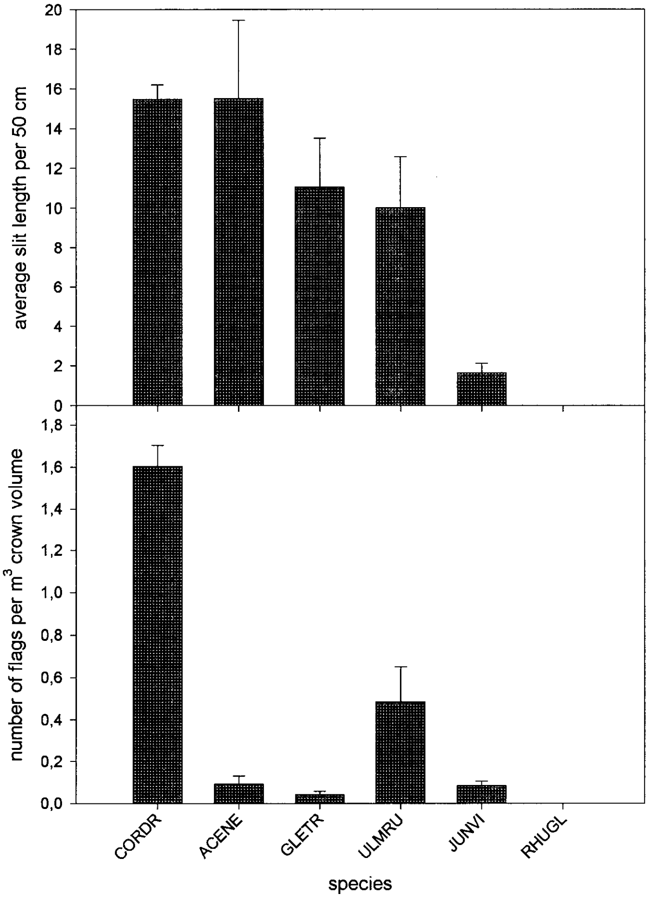

Fig. 2 Magnitude of cicada oviposition damage on six tree species, measured by average slit length on the outer 50 cm of branches, and by number of flagged twigs per tree crown volume. Means ±SE are shown. *CORDR*, *Cornus drummondii*; *ACENE*, *Acer negundo*; *GLETR*, *Gleditsia triacanthos*; *ULMRU*, *Ulmus rubra*; *JUNVI*, *Juniperus virginiana*; *RHUGL*, *Rhus glabra*

When flagging data were corrected for crown volume and analyzed, there was also a significant species effect (ANOVA, F=6.91, df=10, P<0.001). Dogwoods had a significantly higher number of flags than all other species, except for species with extremely small sample siz-

Table 2 Oviposition damage inflicted on all tree species, averaged across space

Species	*n*	Flags/Volume		Slit damage per 50 cm	
		Mean	SE	Mean	SE
Ash (*Fraxinus* spp.)[a]	15	0.05	0.02	18.50	2.71
Box elder (*Acer negundo*)	14	0.09	0.04	15.52	3.90
Cottonwood (*Populus deltoides*)[a]	1	0.01	–	1.25	–
Hackberry (*Celtis occidentalis*)[a]	1	0.30	–	13.75	–
Honey locust (*Gleditsia triacanthos*)	11	0.04	0.02	11.07	2.45
Kentucky coffee tree (*Gymnocladus dioica*)[a]	1	0	–	0	–
Mulberry (*Morus rubra*)[a]	5	0.01	0.01	3.05	1.19
Red cedar (*Juniperus virginana*)	35	0.08	0.02	1.68	0.48
Rough-leaved dogwood (*Cornus drummondii*)	200	1.60	0.01	15.48	0.73
Slippery elm (*Ulmus rubra*)	10	0.27	0.11	13.35	4.49
Smooth sumac (*Rhus glabra*)	20	0.00	0.00	0.00	0.00

[a] Species not discussed in text due to small sample size or lack of spatial distribution

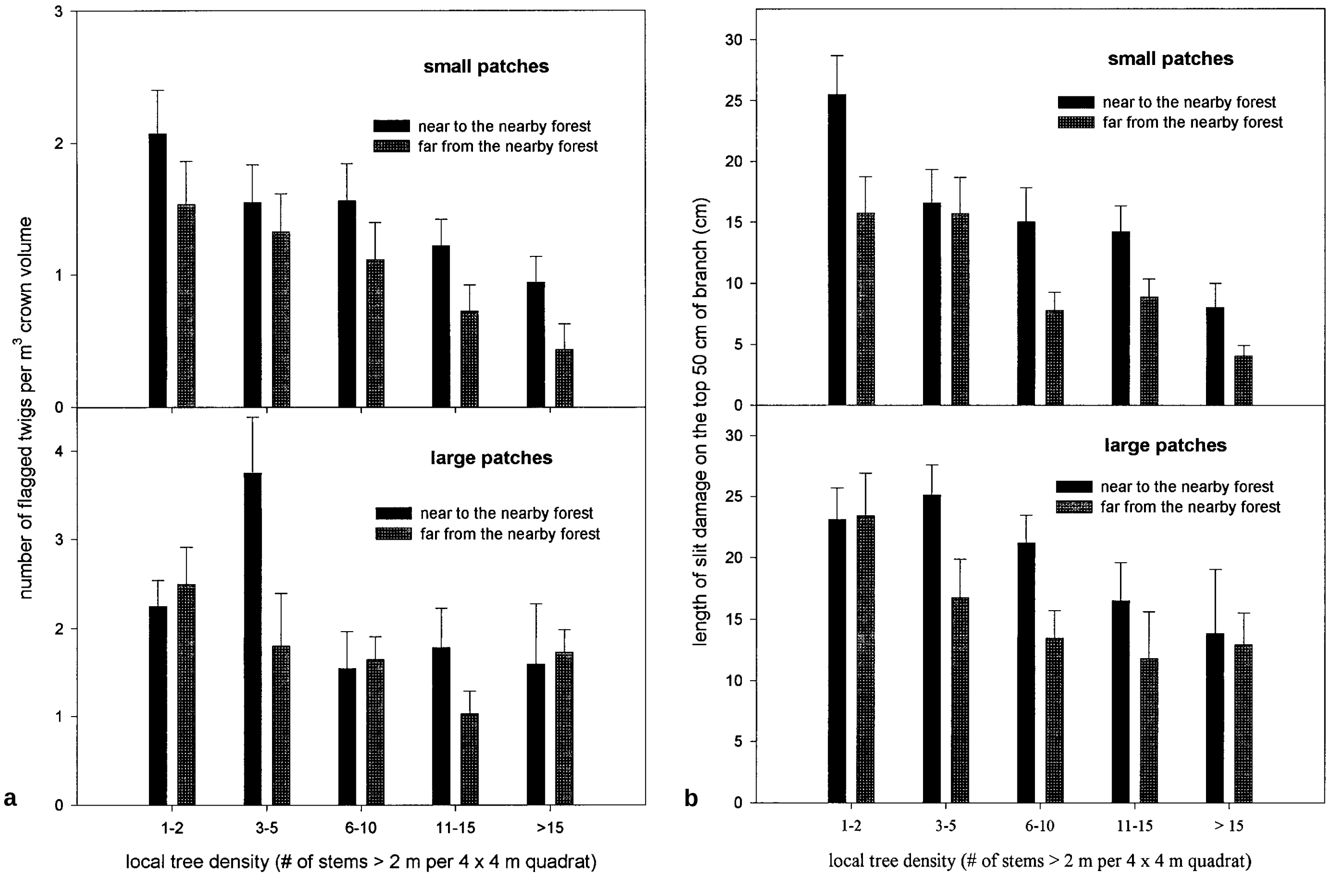

Fig. 3 **a** Effects of patch size, distance to the nearby forest, and local tree density on cicada flag damage on *Cornus drummondii*. Mean flags per cubic meter of crown volume ±1 SE are shown. Note that vertical scale differs for large vs small patches. **b** Effects of patch size, distance to the nearby forest, and local tree density on cicada slit damage on *Cornus drummondii*. Mean slit length per outer 50 cm of branches ±1 SE are shown

es (n<5). The other species sustained moderate flagging damage, except red cedar (little damage) and smooth sumac (none). Aggregated damage estimates by species are reported in Table 2. Overall, considering both damage measures dogwood was the most damaged species.

Spatial variation in damage within the rough-leaved dogwood, *Cornus drummondii*

Overall, cicadas inflicted considerable damage on dogwoods. Cicadas were more likely to oviposit on dogwoods (per stem) when the dogwood was near the forest, on large patches, and in low-density stands. All three primary variables had a strong, statistically significant effect for each damage measure, and none of the interaction terms were significant (Fig. 3, Table 3).

Spatial variation in damage within the slippery elm, *Ulmus rubra*

We found only four available elms in patches far from the forest, so we could not test a distance effect. Examining only elms in near patches, we found that there was no patch size effect on mean slit length (ANOVA, F=0.09, df=1, P=0.77). Adjusted flag count showed the same trend (ANOVA, F=0.07, df=1, P=0.79). We noticed, however, that the five elms with the highest slit damage were all in quadrats with stem density less than 5 per 16 m^2. To test the significance of this trend, we used a randomization test. Out of 23 elms where local stem density (summed over all species) was available, the 5 with the highest slit damage had a mean local density significantly lower than the mean of a random sample of 5 out of the 23 elms (P<0.01, two-tailed test). However, a similar randomization test on the five elms with the highest adjusted flag index showed a mean local density not statistically different from a random sample of 5 of the 23 elms (P=0.21). We tentatively conclude that attacked trees are not a random sample with regard to local density, and that elms suffer more oviposition per stem when located in a low-density stand (Table 4).

Spatial variation in damage within red cedar, *Juniperus virginiana*

Because there were at least eight cedars available in each distance-patch size class, we randomly omitted four trees from the data to carry out a balanced two-way ANOVA for mean slit damage and adjusted flag index. In the analysis, neither distance to the forest nor patch size had

Table 3 Results of spatial analyses of dogwoods (ANOVA)

Source	*df*	SS	MS	*F*	*P*
Mean slit damage					
Patch size	1	1,093.58	1,093.58	13.75	<0.001
Near/far	1	1,174.53	1,174.53	14.77	<0.001
Density	4	3,699.61	924.90	11.63	<0.001
Patch size×Near/far	1	16.92	16.92	0.21	0.65
Patch size×Density	4	172.97	43.24	0.54	0.70
Near/far×Density	4	127.12	31.78	0.40	0.81
Size×Near/far×Density	4	403.49	100.87	1.27	0.28
Error	180	1,4310.93	79.51		
Total	199	20,999.15			
Number of flags per crown volume					
Patch size	1	25.54	25.54	15.24	<0.001
Near/far	1	9.80	9.80	5.85	0.017
Density	3	34.40	8.60	5.13	0.001
Patch size×Near/far	1	0.00	0.00	0.00	0.99
Patch size×Density	3	7.62	1.91	1.14	0.34
Near/far×Density	3	6.73	1.68	1.00	0.41
Size×Near/far×Density	3	10.96	2.74	1.64	0.17
Error	180	301.55	1.65		
Total	199	396.60			

Table 4 Effects of direction, distance to the nearby forest, patch size and local tree density on cicada damage on different host tree species

	Damage index	*Cornus Drummondii*	*Ulmus rubra*	*Juniperus virginiana*	*Acer negundo*	*Gleditsia triacanthos*	*Rhus glabra*
Directional preference	Slit	No	No	No	No	Marginally prefer east	
Distance effect	Slit	High damage near forest	N/A	No	N/A	No	
	Flagging	High damage near forest	N/A	No	N/A	High damage near forest	
Patch size effect	Slit	High damage in large patches	No	No	High damage in small patches	N/A	No damage At all
	Flagging	High damage in large patches	No	No	No	N/A	
Density effect	Slit	High damage at low density	High damage at low density	High damage at low density	High damage at low density	N/A	
	Flagging	High damage at low density	No	High damage at low density	No	N/A	

a significant effect on slit damage or adjusted flag count, although trends were consistent with those in dogwoods (see Table 4).

Out of 32 cedars for which we had local tree density data, only 16 had slit damage, and 15 had flag damage. The 16 cedars with slit damage have a mean local density that is statistically less than a random sample of 16 of 32 ($P<0.01$, two-tailed test). Furthermore, the 15 flag-damaged cedars have a mean local density that is significantly lower than the mean density of a random sample of 15 out of 32 ($P<0.01$, two-tailed test). We conclude that red cedars in dense stands tend to be left alone by cicadas, whereas cedars standing alone are more vulnerable to oviposition. Overall, however, compared to other species cedars experienced a low rate of oviposition damage (Fig. 2).

Spatial variation in damage within the box elder, *Acer negundo*

Box elders only occurred in patches adjacent to the surrounding forest, so we could not test for a distance effect. Patch size had a highly significant effect on slit damage (ANOVA, $F=79.30$, $df=1$, $P<0.001$); trees in small patches were damaged at a much higher rate than those in large patches. Patch size had a similar effect on adjusted flag count, but not a significant one (ANOVA, $F=1.10$, $df=1$, $P=0.31$).

Of 14 sampled box elders, the 5 trees with the highest slit damage had a mean local density significantly lower than that of a random sample of 5 of the 14 ($P<0.03$, 2-tailed test). However, the five trees with the highest flag damage had a mean density that is not statistically different from the mean of a random sample of 5 out of the 14 (P=0.68, two-tailed test). These two measures suggest very different conclusions. One potential explanation could be that flagged branches had dropped before we did the census, leading to a systematic underestimation of the damage.

Spatial variation in damage within the honey locust, *Gleditsia triacanthos*

The sample size for honey locusts was small, and all individuals were in large patches, so we could only test for distance effects. There was a marginally significant directional effect in the slit data (ANOVA, F=2.65, df=3, P=0.07, greatest damage on eastern branches), but we analyzed the lumped data to be consistent with the above analyses. Distance did not have a significant effect on the slit index (ANOVA, F=0.58, df=1, P=0.47), but did have a significant effect on adjusted flag count (ANOVA, F=5.65. df=1, P<0.05), indicating that honey locusts were damaged at a slightly higher rate near the forest. Sufficient data were not available to test local density effects.

Spatial variation in damage within smooth sumac, *Rhus glabra*

No oviposition damage was found on smooth sumac at all; apparently this species is specifically avoided. Sumacs were common in patches near the forest where considerable damage was done to other tree species, so the cicadas had ample opportunity to attack them, but did not.

Discussion

Periodical cicadas colonized essentially the entire study site during the emergence of 1998. Nonetheless, their oviposition damage showed clear spatial patterns, varying as a function of host tree species identity, stem density, and patch characteristics. Because the long-term objective of this experimentally fragmented study site focuses on the role of patch size and position on secondary succession, we here reflect on the potential long-term implications of cicada damage for plant community dynamics.

Host species selection

Periodical cicadas are generalists in host tree selection (White 1981). Host tree species in our studies match these observed elsewhere, at either the specific or generic level (Skeels 1907; Hunter and Lund 1960; Smith and Linderman 1974; Forsythe 1976; White 1980; Rodenhouse et al. 1997). Little is known about the mechanisms underlying the observed preferences. In Kentucky, White (1981) reported that *Juniperus virginiana* and *Ulmus rubra* were attacked, and that resin from oviposition wounds in red cedars injured eggnests; this may explain avoidance by cicadas of cedar. Maier (1982) observed only a few oviposition slits on red cedars; other conifer species with more copious resin responses were completely avoided (see also White et al. 1982). The unusually smooth texture of smooth sumac (hence the name) may have discouraged ovipositing female cicadas. Sumacs and relatives (e.g. poison ivy) are also known for their unusual resins.

In our study, most species experienced *Magicicada cassini* oviposition. Based on mean slit damage, dogwoods, elms, box elders, and honey locusts were damaged at statistically comparable rates. However, dogwood, the most abundant species, had the highest damage rate per stem. As predicted, periodical cicadas were more likely to attack dogwoods on patches near the adjacent woods, leading to a gradient of diminishing damage rates, moving away from the adjacent forest across the fragmented landscape. Damage in the form of flagged twigs displayed a similar pattern when corrected for tree volume (i.e., dogwoods were affected the most). Red cedars were attacked less. Box elders and (particularly) smooth sumacs were attacked less than reported in other studies (Hunter and Lund 1960; Forsythe 1976; White 1980).

Overall, it seems fair to conclude that the dominant tree species at this stage of succession (rough-leaved dogwood) was differentially attacked by ovipositing cicadas.

Patch size effects for oviposition on dogwoods

Because prior literature (Rodenhouse et al. 1997) suggests that cicadas are often particularly abundant at edges, we hypothesized that oviposition damage should be concentrated on small patches. Instead, we found that in dogwoods, oviposition damage was substantially *greater* on larger patches. Several mechanisms could explain this pattern. For instance, more cicadas per unit area may have been attracted to larger patches. Observed from the woodland edge, patches varying in size are simultaneously available. If cicadas preferentially move towards larger expanses of woody vegetation, or are more reluctant to leave larger patches, one would the observed patch size effect. A complementary, more subtle explanation comes from considering the dynamics of short-term, within-patch movement following initial colonization (Holt 1992). On a small patch, ovipositing females will usually arrive from an external source. On a large patch, an additional source of immigration into a given quadrat could be individuals that first colonize elsewhere in the patch, then move within that patch to oviposit in the quadrat.

Tree density effects for oviposition on dogwoods

We hypothesized that the extent of damage per tree would decline with increasing tree density. This prediction was confirmed for dogwood, suggesting a “dilution” effect within patches. Since individual cicadas have a relatively fixed egg load, a female may distribute this load among stems locally, leading to areas of low stem density receiving disproportionate damage per stem.

If cicadas preferentially oviposited in areas with high stem densities, and large patches have higher stem densities (Yao et al. 1999), this could indirectly generate a correlated pattern of patch size differences in attacks. The fact that we observed an *inverse* correlation between oviposition damage and local tree stem density suggests that the spatial patterning in attacks by patch size and by distance arises from other behavioral mechanisms. The overall spatial pattern of attacks likely reflects the simultaneous operation of multiple behavioral mechanisms operating at different spatial scales (e.g., large-scale movements, local stem selection).

Landscape and density effects in other species

Given that dogwoods are preferentially attacked, it seems sensible that any patch size effects would be more evident in this preferred species. Moreover, the sample size for dogwood is much larger than that for the other species (see Table 2), so the following statements about spatial patterns and density effects are necessarily somewhat tentative. Red cedars were more likely to be damaged in large patches, and in patches far from the forest (a different pattern than dogwoods), but neither result was statistically significant. Overall, red cedars were affected much less than most other tree species, consistent with prior studies. However, local tree density did have a significant effect, in that isolated cedar trees suffered some damage, whereas trees surrounded by individuals (of other species) suffered none. We did not detect a patch size effect for damage on slippery elms, but did observe lower damage in denser stands. In contrast to dogwood, box elders were more often attacked on small patches; tests of a density effect were mixed. Honey locusts showed a distance effect. Smooth sumacs were the only species totally avoided by ovipositing cicadas. In general, though, the spatial patterns in cicada damage for other species broadly match the patterns found in dogwoods, particularly with respect to distance and local density. Small sample sizes prevent strong conclusions about the magnitude or possible causes of apparent differences among the rarer hosts.

Potential long-term consequences of the cicada emergence

Because the Kansas fragmentation experiment focuses on the impact of habitat fragmentation on succession, we now reflect on potential long-term effects of the 1998 emergence. Our institutional commitment ensures the indefinite persistence of this experimental landscape, so the following thoughts will help guide future studies. Prior studies suggest a diverse range of potential effects (e.g., contrast Miller (1997), who did not see important effects of cicadas, with Elmer (1964) and Karban (1980), who did). Cicada oviposition damage (and later, nymphal feeding) may have one of several effects on successional dynamics. On the one hand, the visibly apparent damage to trees seen in 1998 may have no long-term successional consequences. If trees can mobilize stored resources and compensate for the loss of leaves and terminal branches without markedly affecting growth rate, survival or fecundity, the cicada emergence will not have a long-term effect on tree population dynamics. On the other hand, the emergence event could differentially damage the most abundant species, rough-leaved dogwood (which received most damage per stem in 1998), thus releasing competitive pressures on later successional species. For example, oaks and maples are just now beginning to invade our successional community (B. Patrick, unpublished data). If faster-growing, early successional species (dogwoods and elms) are competitively suppressing these species as seedlings, foliage and biomass loss in early successional species could create gaps, allowing later successional trees to establish and grow. Finally, the presence of early-successional species could facilitate the growth of later-successional species (Connell and Slatyer 1977). For instance, oaks and maples may require a canopy or thick litter layer during their early growth stages. If so, cicada-induced mortality in dogwoods and other currently abundant species might slow colonization by late successional species, and so the cicada emergence could retard succession.

Finally, if this cicada damage has long-lasting effects on tree dynamics, spatial variation in oviposition damage could potentially alter existing current spatial patterns in the rate of succession (Yao et al. 1999). First, heavy damage in areas where dogwoods are abundant (large patches) could reduce the present spatial variation in tree abundance. Conversely, if trees with greater available resources can compensate rapidly with new growth, the greater density of attacks on less dense stands might exaggerate the current spatial patterns of variation in dogwood abundance. Our continuing long-term monitoring of individually tagged stems should permit us to discriminate among these hypotheses about potential cicada impact.

The next 17-year cicada emergence will occur in 2015. We tentatively predict that the spatial patterns of the next emergence then may be correlated with the current spatial pattern of oviposition. However, underground movement and mortality of nymphs, and shifting gradients in tree establishment and mortality may obscure spatial trends that we have identified in 1998. Moreover, there will be substantial shifts in the plant community, occurring for many reasons other than interactions with periodical cicadas. While the spatial attributes of our experimentally fragmented site seem to have led to clear trends in cicada colonization in 1998 (with potential long-term effects on plant succession), further monitoring of the plant and insect communities will be needed to provide detailed understanding of the relationship between fragmentation, ecological succession, and the episodic disturbance provided by periodical cicada emergences.

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