INDIRECT HERBIVORE MEDIATION OF AVIAN SEED DISPERSAL IN PINYON PINE[1]

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Abstract. During a 4-yr study, we examined how an insect herbivore indirectly influenced pinyon pine by affecting its avian seed dispersal agents. Colorado pinyon pine, *Pinus edulis,* suffered reduced cone initiation and increased cone mortality primarily from infestation by the stem- and cone-boring moth *Dioryctria albovitella.* Because avian dispersal agents selectively foraged where cone crops were highest, individual trees and stands of trees with greater insect abundances were avoided. Even herbivore-resistant trees with substantial cone crops did not receive dispersal services if they were surrounded by susceptible trees because the birds often ignored entire stands of trees. A cone removal experiment showed that avian seed dispersers also ignored trees with artificially reduced crops even though many cones remained. We argue that masting, the production of large cone crops at irregular intervals, may have evolved to insure dispersal success. The decline in attractiveness of entire stands of trees to dispersal agents due to infestation may functionally alter the sex expression of uninfested individuals.

Key words: Clark's Nutcracker; crop size; Dioryctria albovitella; Gymnorhinus cyanocephalus; *indirect effects; insect herbivory;* Nucifraga columbiana; Pinus edulis; *Pinyon Jay; pinyon pine.*

INTRODUCTION

Herbivores have been shown to negatively influence plant growth, survival, sex expression, fecundity, and fitness (Dixon 1971, Morrow and LaMarche 1978, Raffa and Berryman 1982, Marquis 1984, Crawley 1985, Whitham and Mopper 1985, Sacchi et al. 1988). Few studies, however, have focused on herbivore impacts on seed dispersal (Thompson and Willson 1978, Benkman et al. 1984, Manzur and Courtney 1984) which, in addition to seed production (Herrera 1988), can be the most important factor influencing a plant's reproductive success (Janzen 1970, Clark and Clark 1981, Howe et al. 1985). Here we attempt to integrate two typically dissociated areas of plant–animal interactions, herbivore impact on seed crop size, and the influence of crop size on seed dispersal, by addressing the hypothesis that a herbivore's direct effect on pinyon pine cone crop size may also have an indirect effect on seed dispersal success.

Cone crops can vary greatly both within and among pinyon populations as a function of herbivore loads. Whitham and Mopper (1985) found that *Dioryctria albovitella* significantly reduced cone production in pinyon pine. The destruction of terminal cone-bearing shoots was so acute that some trees assumed a shrublike growth form and completely lost the ability to produce female cones. Infestation was, however, patchily distributed; within a stand some trees were chronically attacked, while other, often adjacent trees suffered little damage. The present study examines similar

differences in herbivory among populations; some stands suffer chronic insect attack while others do not.

Pinyon pine depends on several bird species for transport of seeds away from the parent plant to microsites that enhance germination (Vander Wall and Balda 1977, Ligon 1978; K. M. Christensen, *personal observation*). Clark's Nutcrackers (*Nucifraga columbiana*), Pinyon Jays (*Gymnorhinus cyanocephalus*), Scrub Jays (*Aphelocoma coerulescens*) and Steller's Jays (*Cyanocitta stelleri*) are the primary dispersers of pinyon pine (Vander Wall and Balda 1981). Nutcrackers and Pinyon Jays are the most important long-distance dispersers. They are also the only dispersers that can open green, closed cones of pinyon pine. Although these birds may act as seed predators when foraging early in the day or season, and when harvesting small seed crops (Ligon 1978, Vander Wall 1988; R. P. Balda, *personal communication*), they do provide dispersal services (up to 22 km from the parent plant) when harvesting larger crops. Vander Wall and Balda (1977) found that in years of abundant seed availability, individual birds dispersed and cached between 2.2 and 3.3 times the number of seeds needed for survival during the winter, and a flock of 150 nutcrackers cached between 3.3 and 5.0 × 10⁶ seeds in a good crop year. These unrecovered seeds have a greater probability of germination than undispersed seeds (Vander Wall and Balda 1977, Ligon 1978; K. M. Christensen, *personal observation*), and the birds are therefore important to the reproductive success of the plants.

Christensen et al. (*in press*) found that Clark's Nutcrackers in the field selectively harvested pinyon pine seeds from trees with larger cone crops. In the laboratory, when presented with a choice of two trees for

harvest, the birds harvested three times as many cones from a tree with 20 cones compared to a tree with 10 cones.

Because insect herbivores can partially or completely eliminate cone crops of individual trees (Whitham and Mopper 1985) and because avian dispersal agents are sensitive to cone crop size (Christensen et al., *in press*), avian seed dispersal may be affected by herbivory. Here we address the following questions: (1) Do herbivores create a mosaic of cone availability across the landscape? (2) Do dispersal agents choose between pinyon populations based on crop size just as they do between individual trees? (3) Do the birds respond to experimentally reduced crops in addition to herbivore-reduced crops?

METHODS

To examine the relationship between cone number and avian seed harvest within and among pinyon pine stands, we measured conelet (immature cones) initiation and survival and seed harvest by birds for 9–34 trees in eight haphazardly chosen pinyon stands from 1985 through 1988. The study sites were all within 25 km of the San Francisco Peaks in northern Arizona, at similar elevations (range 1759–1887 m). Each stand was separated from other stands by non-pinyon pine habitat. All trees were mature with a circumference between 79 and 108 cm. There were no significant differences among populations in mean tree circumference (ANOVA, $F = 1.87$, $P > .05$, df = 7, 126), nor was there a significant correlation between circumference and crop size for trees within this circumference range ($r = 0.256$, $n = 127$; $P = .273$). Because each of these stands was isolated from other stands, we hereafter refer to the trees at each site as an individual population.

Conelet initiation and survival

Conelets are initiated 2 yr prior to their maturation on terminal shoots (Little 1941). To determine crop size, 1st-yr cones were counted, branch by branch each fall, using the naked eye and/or binoculars. We initially repeated counts on the same trees and found that the counts were within 5% of each other, indicating a high degree of consistency. We feel that if any error was introduced by this method, it would be the underestimation of crop size for trees with very large crops. This error would lead to conservative conclusions, and should therefore not confound our results.

We determined conelet survival by marking 20 young conelets on each of the 127 trees in the fall with numbered laundry tags and followed their maturation and survival until harvest began the following summer. We haphazardly chose conelets from all portions of the tree. To determine crop size at the time of harvest, we again counted cones on each tree the following July (just prior to the onset of harvest by avian dispersal agents).

Insects other than *Dioryctria* have been found to infest and destroy pinyon pine cones (Keen 1958, Forcella 1980). Other cone-boring insects (*Conophthorus* sp. and *Eucosma* sp.) have been found in cones collected from our study sites, but the relative abundance of each species is unknown. In the remainder of this paper, we will not attempt to discern among cone mortality attributable to *Dioryctria, Conophthorus,* or *Eucosma.*

Herbivore impact on cone production

Because conelets are initiated on terminal shoots, terminal shoot mortality affects conelet initiation rates. Because Whitham and Mopper (1985) found a strong negative relationship between shoot mortality and initiation within a heavily infested site, we chose not to replicate those data. Instead, we measured shoot mortality and conelet initiation for trees at each site and averaged them to determine insect impacts on cone initiation at the population level. We regressed cone production on shoot mortality for these averages.

To determine shoot mortality in 1985, 1986, and 1988, we sampled ≈100 shoots per tree and determined the proportion destroyed by insects. The top, middle, and bottom of the tree were sampled in proportion to the natural distribution of shoots.

To determine whether or not the patterns of herbivore attack are maintained each year, we regressed shoot mortalities in 1986 with those in 1988 for the averages of each site. 1985 data were not used in this analysis because only two sites were sampled that year.

Seed harvest

We monitored cone harvest by seed-dispersing birds of 127 trees distributed among eight sites from the beginning of harvest in the fall until completion at 10–14 d intervals. At each visit, we recounted the number of cones on the tree, and counted the number of bird-opened cones in and under each tree. Birds typically open green cones in a branch fork on the same tree from which the cone is removed (Vander Wall and Balda 1977), and leave unique markings on the cone as a result of seed removal. We cross-checked the number found in and under each tree with the number missing from the tree at each visit. If there was a discrepancy in the numbers of 5% or more, then that tree was not used in the analysis (47 trees were not used).

If pinyon pine cones are not harvested early in the fall, they open on the tree and expose the seeds, which facilitates seed harvest by birds (Vander Wall 1988). After the cones open, it is not possible to determine the fate of the seeds. During this study, however, only 7.6% of the 71 320 monitored cones opened on the tree. Because relatively few cones opened, and because of the difficulty in determining the fate of seeds from open cones, we considered that avian harvest levels remained the same following cone opening as prior to opening. We feel that this assumption leads to conser-
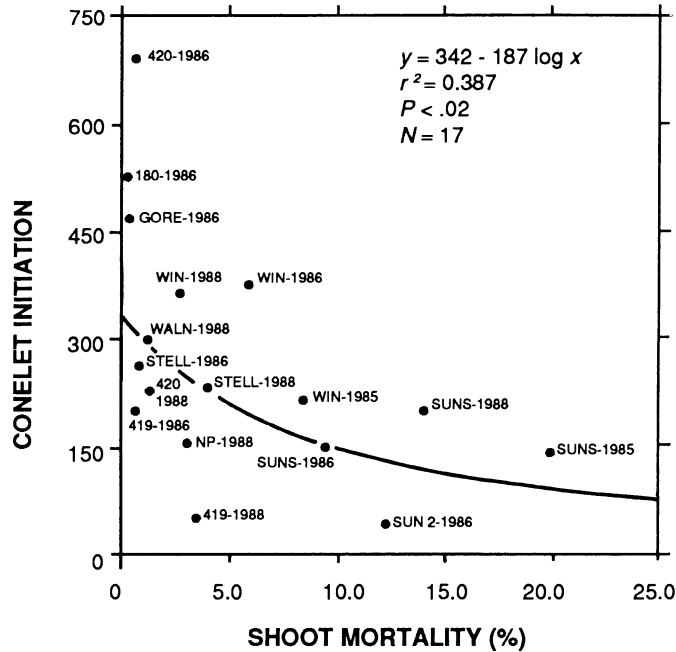
FIG. 1. Insect infestation and conelet initiation varied among sites. Here, each point represents the mean for each site, and data from 1985, 1986, and 1988 are given.

vative conclusions, in that the birds increase their seed extraction rates when harvesting from open cones, and it is typically only the trees with very large crops that have cones that open. Thus, avian harvest is probably greater on trees with large crops than we have considered.

To examine the influence of cone number on bird harvest both within and between sites, we used regression analysis (Dixon and Jennrich 1983) to predict seed harvest levels (absolute number and the percentage of the crop) of individual trees using cone number as the independent variable. In addition, we regressed the mean number and percentage of cones harvested on mean cone number for each site each year. In all analyses, percentages were arcsine square-root transformed prior to analysis.

To examine whether unharvested seeds might fall from cones to the ground and potentially germinate, we placed 100 seeds in an inconspicuous pattern beneath the canopy of 10 trees in the evening of three consecutive nights. We counted the number of seeds remaining the following morning. Different trees were used each night. Only 1 seed of the 3000 was found the next day, indicating that nocturnal rodents are very quick to gather unharvested seeds. The remaining seed was found to be inviable. These rodents have never been shown to act as dispersal agents of pinyon pine (Ligon 1978).

Cone removal experiment

To examine experimentally the response of avian seed harvesters to insect herbivory, we simulated her-

bivory by reducing the crops of individual trees in the fall of 1988 and monitored their harvest levels. At a site where nutcrackers were foraging, we chose eight pairs of mature trees with approximately equal cone numbers. Half of the cone crop from one tree of each pair was then removed. We monitored cone harvest by birds, as previously described, and compared the mean number and percentage of cones harvested for treatment and control trees using the Wilcoxon signed-ranks test (Conover 1980).

RESULTS

Conelet initiation across populations decreased significantly with increasing insect infestation (Fig. 1). This relationship is curvilinear; a slight increase in shoot mortality results in a rapid decrease in conelet initiation. For example, a 3% increase in shoot mortality can result in a 25% decrease in conelet initiation. Thus, insect infestation had a substantial impact on the number of seeds available to avian dispersal agents.

The impacts of herbivory varied greatly among pinyon populations (Table 1) resulting in a mosaic of cone production. Trees at the two Sunset Crater sites exhibited the greatest shoot mortality ($\bar{X}$ = 14.8 and 14.5%), suffering from 2.5 to 15 times as much shoot damage as other sites. These two sites also exhibited the lowest cone production of all sites.

In addition to reducing conelet initiation, herbivores also infested and killed maturing (2nd-yr) cones and further decreased crop size by an average of 57.2%. More than 51% of the trees suffered ≥50% reduction in crop size, while 13.9% lost their entire crop (sites

$\bar{X} = 57.2\%$
SE = 1.96
N = 237 trees
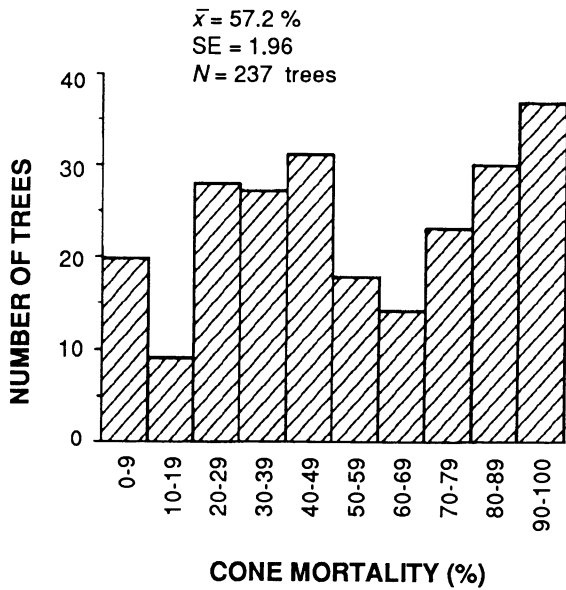
CONE MORTALITY (%)

FIG. 2. Cone mortality frequencies for all pinyon pines examined among all sites.

and years combined; Fig. 2). As cone mortality varied greatly among individuals (i.e., some trees lost their entire crop while others lost no cones), cone insects contributed to the variability in crop size within pinyon pine populations.

Cone mortality also varied significantly from one pinyon population to another (ANOVA $F = 16.4$, $P < .001$, df = 15, 217). Cone mortality ranged from 30.1 to 100% of a populations' crop ($\bar{X} = 57.2\%$; Table 1), demonstrating that insects directly eliminate a large portion of a population's cones that might otherwise be available to seed dispersal agents.

For pinyon populations, insect-caused shoot mortality is a good predictor of cone mortality (Fig. 3). This demonstrates that stands that are more heavily attacked by the shoot-destroying moth *D. albovitella* also, on average, lose more cones to the species of insects that infest cones.

If susceptibility to herbivory was transitory (i.e., occurred in some years but not others) then insect attack over the lifetime of the plant might not have much effect on its reproductive success. There is, however, a significant positive correlation between shoot mortality levels in consecutive years between sites ($r_s = 0.704$, $n = 10$, $P = .013$; Spearman rank correlation). Similarly, within sites, susceptible trees suffer heavy infestation every year (Whitham and Mopper 1985), and some have produced <50 mature cones in the past 5 yr (T. G. Whitham, *personal observation*).

The direct impact of herbivory is to reduce cone production dramatically, and to destroy an average of 57.2% of those cones that are produced. This herbivory, however, is not uniform; susceptible individuals

within stands and certain stands are chronically attacked year after year. Therefore herbivory produces a mosaic of cone availability within and among stands that could indirectly affect the foraging behavior of pinyon pine's avian mutualists.

Indirect effects of herbivores on avian seed harvest

We now examine how a reduction in cone crop size by insect herbivores might influence the harvest and dispersal of seeds by birds. If the birds are insensitive to crop size, then the impact of herbivory is simply the direct and indirect loss of cones described in the previous section. If the birds, however, are sensitive to reduced cone crops brought about by insect infestation and ignore trees or stands even though some good cones are available, then the impacts of herbivory on these trees may be far greater.

The following paragraphs examine avian seed harvesting at two levels: we compare bird harvest of individual trees within stands and we make comparisons of harvest levels across stands. Knowing how birds forage from individual trees and stands of trees reveals the relevant scale upon which birds discriminate among the seed resource. Furthermore, for each of these levels, we compare avian harvesting in terms of absolute number of seeds harvested and the percentage of the seed crop harvested. Differentiating between absolute number and percentage is important because while absolute number yields information regarding the reproductive success of the plant, the percentage of the crop har-

$y = 33.2 + 3.02x$
$r^2 = 0.632$
$P < .01$
$N = 11$

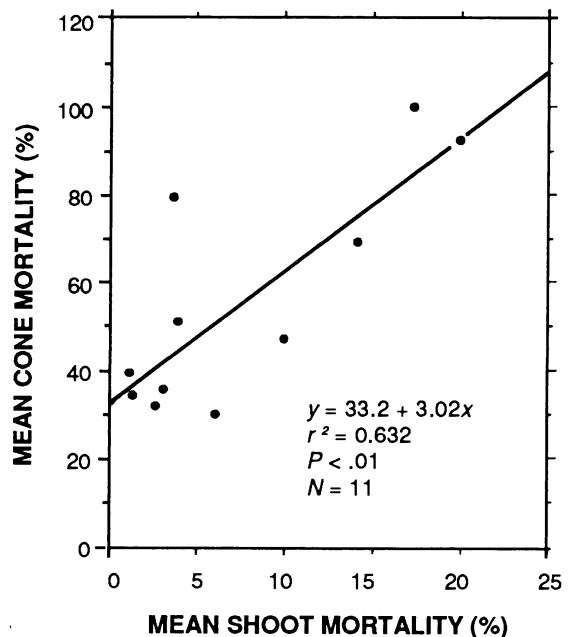**MEAN SHOOT MORTALITY (%)**

FIG. 3. At the population level, shoot damage is significantly correlated with cone mortality. Those sites suffering greater shoot mortality also suffered greater cone mortality.

TABLE 1. Shoot and cone mortality (percent) for the study sites when available from 1985 through 1988 (mean ± SE where applicable). Ellipses (···) indicate that no data were collected for that site and year.

Site	Type	N	Year				Mean
			1985	1986	1987	1988	
Sunset I	shoot	34	19.8	9.6	···	14.1	14.5 ± 2.9
	cone	10	93.2	46.7	81.1	69.4	72.6 ± 9.9
Sunset II	shoot	30	···	12.3	···	17.3	14.8 ± 2.5
	cone	30	···	···	98.3	100.0	99.2 ± 1.3
Winona	shoot	23	8.5	6.0	···	2.7	5.7 ± 1.7
	cone	23	···	30.1	···	32.4	31.3 ± 1.2
FS420	shoot	10	···	0.66	···	1.3	0.98 ± 0.3
	cone	10	···	···	54.6	34.6	44.6 ± 9.9
FS419	shoot	9	···	0.73	···	3.5	2.2 ± 1.4
	cone	9	···	···	30.3	79.5	54.9 ± 24.6
New Peaks	shoot	10	···	···	···	2.9	2.9
	cone	10	···	···	89.3	36.2	62.8 ± 26.5
Walnut	shoot	12	···	···	···	1.1	1.1
	cone	12	···	···	44.5	39.8	42.2 ± 2.3
Stellers	shoot	11	···	0.74	···	3.8	2.3 ± 1.5
	cone	11	···	···	89.2	51.2	70.2 ± 19.0

vested reflects the amount of return (reproductive success) a tree is receiving on its investment (cone production). Assuming equal fecundity and equal seedling vigor over the lifetime of the plants, those that have the greatest percentage of their crop dispersed will have the greatest relative fitness.

The absolute number of cones harvested by avian dispersal agents was significantly affected by crop size in five of seven populations examined (a representative relationship is given in Fig. 4). Trees with larger crops have more cones harvested and the seeds presumably dispersed. This result is intuitive; trees with more seeds

have more to be dispersed, and a demand for pinyon seeds by seed dispersal agents is indicated.

The percentage of a tree's crop harvested was significantly positively correlated with the number of cones in three of seven cases ($r = 0.69$, 0.73, 0.82; $P < .05$; the other four cases exhibited a positive trend but the correlation was not statistically significant: $r = 0.34$, 0.12, 0.41, 0.30; $P > .05$). For one site (Fig. 5), a curvilinear relationship between avian harvest and crop size indicated a threshold effect of cone number on harvest. Below ≈100 cones per tree, trees received low but variable harvest. Trees with crops >100 cones re-

1988 FS420

$y = 0.571x + 19.8$
$r^2 = 0.675$
$P < .01$
$N = 11$

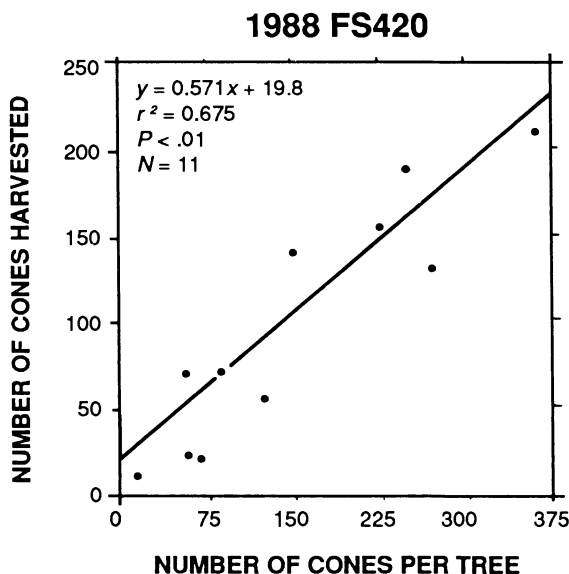NUMBER OF CONES HARVESTED

NUMBER OF CONES PER TREE

FIG. 4. A representative site where there was a significant positive correlation between the number of cones on a tree and the number of cones harvested by birds.

1984 WINONA

$y = -32.0 + 24.0 \ln x$
$r^2 = 0.665$
$P < .0005$
$N = 20$

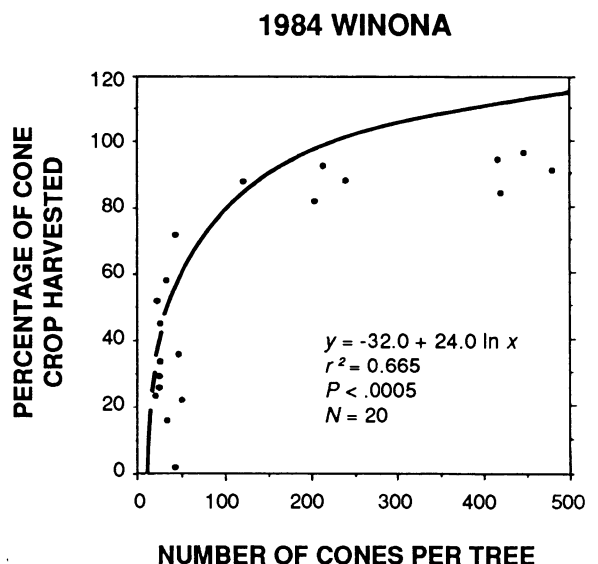PERCENTAGE OF CONE CROP HARVESTED

NUMBER OF CONES PER TREE

FIG. 5. A representative site where there was a significant correlation between the number of cones on a tree and the percentage of the crop harvested by birds.

1986, 1987, 1988

$$y = -22.6 + 0.225x$$
$$r^2 = 0.390$$
$$P < .01$$
$$N = 21$$
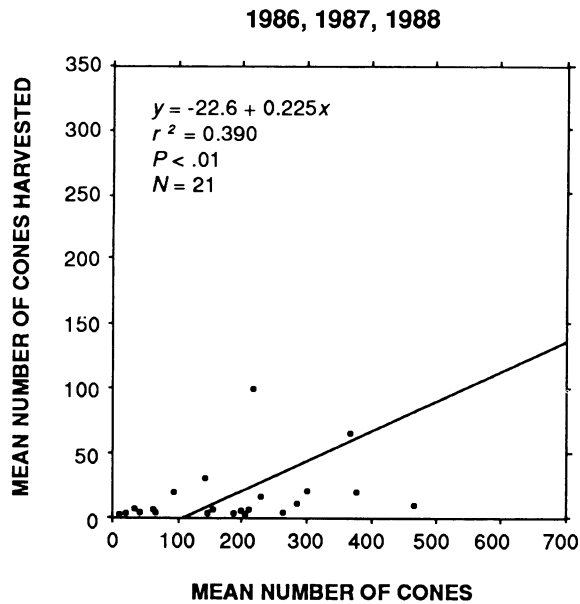
MEAN NUMBER OF CONES

FIG. 6. The influence of mean cone number on mean number of cones harvested. This figure combines all sites from 1986 to 1988. Each point represents a site.

ceived greater and more reliable harvest. Reduced crop size due to herbivory could then cause a precipitous decrease in seed harvest as cone number declined below this threshold.

Just as avian seed dispersers harvested from a greater number of cones of trees with larger crops, they also harvested more from pinyon populations with larger crops (Fig. 6). Again, this confirms that these birds are very discriminatory in their harvest behavior, as they chose between stands of trees based on relative cone availability. Because the mean number of cones harvested at each site was not correlated between years ($r = 0.19$, $P > .05$, $n = 10$; Spearman rank correlation), data from 1986, 1987, and 1988 were pooled.

There was also a significant positive correlation between population crop size and the percentage of the crop harvested in all three years examined (Fig. 7). In 1986 and 1987 there was a continuously increasing relationship. In 1988, the lowest production year examined, many stands showed little or no harvest by birds. The population with the largest crop did, however, have a large percentage of its crop harvested. Seed dispersers apparently discriminate among stands of pinyons as much as or more than they do among trees within stands.

To this point we have shown that herbivory has a negative impact on cone crop size, and that crop size is important to avian seed harvest. Given these two findings, there should also be a direct relationship between cone survival and dispersal, and we should be able to demonstrate this relationship experimentally. Consistent with expectation, cone survival was signif-

icantly correlated with cone harvest for individuals within a stand and across stands (Fig. 8a, b). Because herbivores have such a large impact on cone availability (a 57.2% reduction in cone number on average) they can apparently influence the foraging behavior of the birds. Because this correlation does not prove that the insects are the causal agents in affecting the birds' foraging behavior, we experimentally reduced cone crops to simulate insect attack and monitored the response of bird harvest.

Trees with 50% of their crop experimentally removed had on average 4.9 times fewer cones harvested than did controls (Fig. 9). There was also a decline in the percentage of the crop harvested (18.5 vs. 7.8%), although this difference was not statistically significant (Wilcoxon signed ranks test; $P = .294$). Thus, when cone quality remained the same, but cone number was reduced, the birds responded in the same way they did
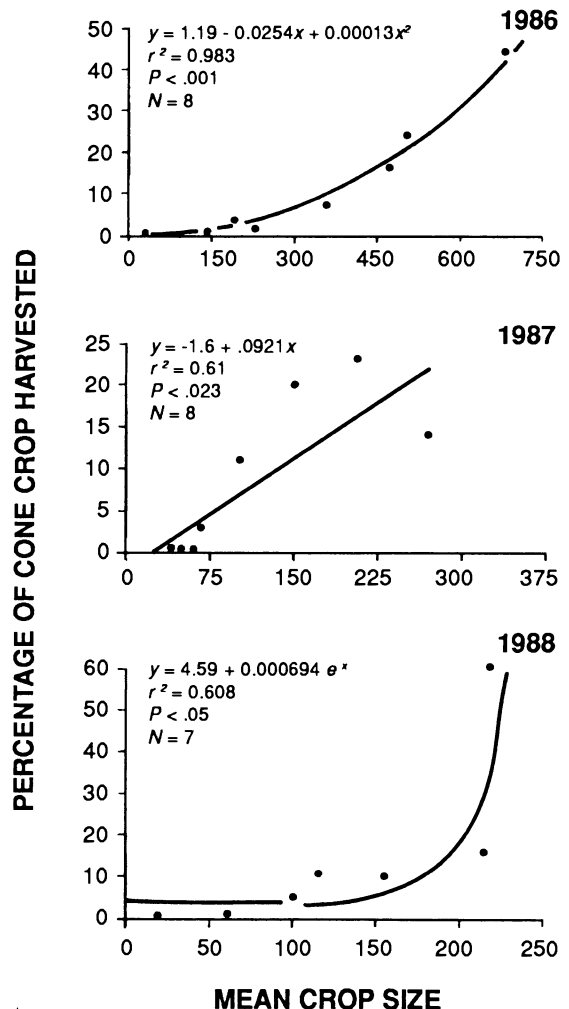

FIG. 7. The influence of cone number on the percentage of a population's crop harvested. Data from 1986, 1987, and 1988 are presented separately.
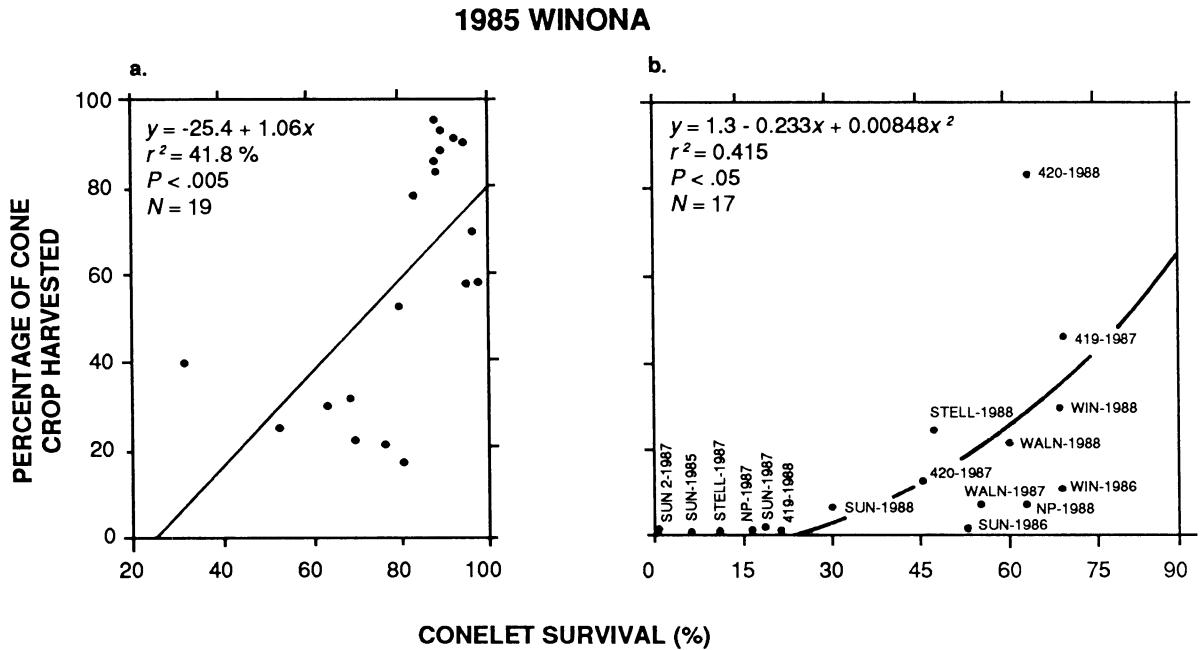
1985 WINONA

a.

$y = -25.4 + 1.06x$
$r^2 = 41.8\%$
$P < .005$
$N = 19$

PERCENTAGE OF CONE CROP HARVESTED

b.

$y = 1.3 - 0.233x + 0.00848x^2$
$r^2 = 0.415$
$P < .05$
$N = 17$

● 420-1988

● 419-1987

STELL-1988 ● ● WIN-1988

● WALN-1988

420-1987 ●

SUN 2-1987 SUN-1985 STELL-1987 NP-1987 SUN-1987 419-1988

WALN-1987 ● WIN-1986
● ● NP-1988

● SUN-1988

● SUN-1986

CONELET SURVIVAL (%)

FIG. 8. (a) The relationship between cone survival and the percentage of a tree's crop harvested for the Winona site in 1985. This result was typical of most sites. (b) Among sites there was also a significant correlation between cone survival and percent crop harvest. These data are for all sites from 1986 to 1988.

to trees with herbivore-reduced crops, lending further support to the assertion that insects do affect avian seed harvest.

DISCUSSION

The indirect effect of herbivory on seed disperser behavior is rarely considered as a factor affecting plant reproductive success. We found that herbivory reduced seed crop size, thereby affecting the success of pinyon pines in attracting avian seed dispersal agents for seed harvest. Differential dispersal success within and among pinyon stands may also affect local adaptation and the evolution of reproductive allocation patterns of pinyon pine populations, and realized sex expression of pinyon individuals.

The direct influence of herbivory on crop size indirectly affects the reproductive potential of pinyons by reducing seed harvest and presumably dispersal. Several studies have documented direct effects of herbivores on seed production (Rockwood 1973, Kinsman and Platt 1984, Louda 1984, Marquis 1984, Crawley 1985, Whitham and Mopper 1985, Sacchi et al. 1988), but to our knowledge, only Manzur and Courtney (1984) have examined the indirect effects of herbivory on subsequent seed dispersal by birds. They found that blackbirds harvesting fruits of hawthorn (*Crataegus monogyna*) had reduced foraging efficiency on bushes infested by *Blastodacna hellerella* larvae, which slowed down the removal of undamaged fruits. The delayed harvest of these individuals allowed great-

er seed predation by mice and other seed predators, so that 15% of the good fruits on infested bushes were not harvested by the dispersal agents. With pinyon pine, the mechanism involved in reduced seed dispersal of
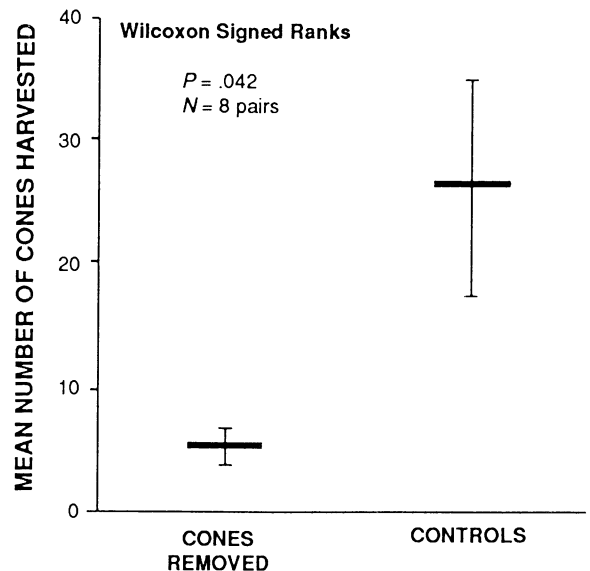
MEAN NUMBER OF CONES HARVESTED

Wilcoxon Signed Ranks

$P = .042$
$N = 8$ pairs

CONES REMOVED   CONTROLS

FIG. 9. Results of the cone removal experiment indicate that trees suffering simulated insect attack (crop size reduced by ≈half) received significantly lower harvest levels compared to controls (mean ± standard error is shown). The percentage of the crop harvested was greater for the controls, but not significantly.

infested trees includes not only a total lack of visitation by dispersal agents, but in many cases delayed visitation, allowing greater rodent seed predation (K. M. Christensen and T. G. Whitham, *unpublished manuscript*). Lack, or delay, of visitation results from reduced cone number and not from the visual display of damaged fruit or increased handling times associated with consuming damaged fruit, as in Manzur and Courtney (1984).

Indirect effects of herbivory on long-distance seed dispersal could have at least two major implications for pinyon pine individuals and populations: temporal patterns of reproduction, and realized sex expression of individuals.

The masting habit of pinyons may not solely function to satiate seed predators (Forcella 1980), but may also have evolved to ensure successful dispersal (Vander Wall and Balda 1977, Ligon 1978). We found that greater investment in seed production (assuming equal survival) increased the probability of successful harvest by dispersal agents. If dispersal is imperative for successful seed germination and survival as stated by Vander Wall and Balda (1977), Ligon (1978), Lanner and Vander Wall (1980), Hutchins and Lanner (1982), and Tomback (1982), then selection should favor those trees maturing the largest crops, resulting in an evolutionary trend toward increased energy investment in fecundity. During several nonproduction years, pinyons may be able to conserve the energy necessary to produce a large seed crop (Floyd 1987), which may then surpass the threshold necessary to attract dispersers.

The decline in attractiveness of entire stands of trees to dispersal agents due to infestation may functionally alter sex expression of uninfested individuals. Whitham and Mopper (1985) found that infestation of pinyons by *D. albovitella* altered sex expression, as some individuals lost the ability to produce female cones altogether. We found that herbivore-resistant pinyons (which do initiate and mature cones), may still be functionally male, because without dispersal there is a reduced chance of seed survival, as noted above. For example, one exceptionally fecund tree located in a stand that suffers relatively high herbivore loads has had seeds harvested from only 147 cones out of the 9654 it has produced in the last 5 yr compared to the 2345 cones out of 6455 that have been harvested from a tree growing 13 km away in a herbivore-resistant stand.

That herbivory can alter dispersal success of nearby uninfested individuals has not been previously described. Atsatt and O'Dowd (1976) elucidated the importance of a plant's neighbors to that plant's defense against herbivores. The idea of associational resistance opened a new dimension to plant defense theory. Here, we documented how the fecundity and susceptibility to herbivory of a pinyon tree's neighboring conspecifics can affect its own dispersal success. This lack of dispersal could effectively slow or prevent superior pinyon pines (e.g., trees that are herbivore resistant with high fecundity) from successfully expanding in a susceptible population.

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