used, PAS spectra were measured to 400 cm^{-1} with this spectrometer. It is much more difficult to measure spectra in the far infrared (< 400 cm^{-1}), however, because of the lack of radiant intensity of the sources used in this region.

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References and Notes

1. M. G. Rockley, *Chem. Phys. Lett.* **68**, 455 (1979).
2. ———, *Appl. Spectrosc.* in press.
3. ——— and J. P. Devlin, *ibid.*, in press.
4. M. G. Rockley, *FTS/IR Notes No. 32* (Digilab, Cambridge, Mass., 1980).
5. W. Vidrine, *Appl. Spectrosc.*, in press.
6. J. Tyndall, *Proc. R. Soc. London* **31**, 307 (1881).
7. W. C. Röntgen, *Philos. Mag.* **11**, 308 (1881).
8. A. G. Bell, *ibid.*, p. 510.
9. A. Rosencwaig, *Science* **181**, 657 (1973).
10. ——— and S. S. Hall, *Anal. Chem.* **47**, 548 (1975).
11. W. R. Harshbarger and M. R. Robin, *Acc. Chem. Res.* **6**, 329 (1973).
12. A. Rosencwaig and A. Gersho, *J. Appl. Phys.* **47**, 64 (1976).
13. L. B. Kreuzer, *ibid.* **42**, 2934 (1971).
14. M. J. D. Low and G. A. Parodi, *Appl. Spectrosc.* **34**, 76 (1980).
15. G. Busse and B. Bullemer, *Infrared Phys.* **18**, 255 (1978); *ibid.*, p. 631.
16. L. J. Boucher and J. J. Katz, *J. Am. Chem. Soc.* **89**, 1340 (1967).
17. J. P. Devlin, M. G. Rockley, R. Frech, in preparation.
18. *Sadtler Handbook of Infrared Spectra* (Sadtler Research Laboratories, Inc., Philadelphia, 1967), spectrum 8725k.
19. We gratefully acknowledge support of this work by the National Institutes of Health under grant 5R01GM25353-02 and support by the National Science Foundation for purchase of the FTIR spectrometer (grant CHE78-01764). We thank E. C. Nelson for supplying the samples used in these experiments.

24 April 1980; revised 14 July 1980

Resource Concentration and Herbivory in Oak Forests

Abstract. *Larvae of the fall cankerworm (*Alsophila pometaria*), a polyphagous defoliator of canopy trees, hatch at the time of budbreak of scarlet oak (*Quercus coccinea*), about 10 days before budbreak of white oak (*Quercus alba*). Thus the* Alsophila *population was dense in a site dominated by scarlet oaks and defoliated the scattered white oaks when they came into leaf. In a site dominated by white oaks, the* Alsophila *population was sparse and chiefly attacked scattered scarlet oak. Thus in each stand, the rarer species of tree suffered greater herbivory, in contrast to the more commonly reported observation that herbivore attack on a plant species increases with density.*

The principle that numerically uncommon species may suffer less intense predation than abundant species plays a large role in ecological and evolutionary theory. Predator-prey theory makes frequent recourse to "predator switching," in which predators prey to a disproportionately great degree on the more abundant species of prey (*1*); and in current studies on the interactions between plants and herbivorous insects, the increased herbivory suffered by majority plant species figures largely. Janzen (*2*) and Connell (*3*) proposed that frequency-dependent attack on seeds and seedlings may promote high species diversity in tropical forests; Feeny (*4*) and Futuyma (*5*) suggested that the evolution of chemical diversity among plants may be influenced by the advantages that minority species have in species-rich communities. Several authors (*6*) have documented cases in which herbivory is lower when a plant is grown in polyculture than in monoculture, leading Root (*7*) to postulate that insects will build up where their hosts are most concentrated. We report a counterinstance in which the plant species in the minority suffered greater herbivory.

Fig. 1. (Left) A white oak in a stand dominated by white oaks, where the population of fall cankerworm is sparse. (Right) A defoliated white oak in a stand dominated by scarlet oaks, where fall cankerworm is abundant. Branches of scarlet oak are visible in the background.

The study site was about 2 km south of the campus of the State University of New York at Stony Brook, in Suffolk County, where an extensive (≈ 1.3 km^2) woodlot dominated by scarlet oak (*Quercus coccinea*) gives way abruptly (at an ecotone about 300 m wide) to one made up almost exclusively of white oak (*Q. alba*); beyond the ecotone, each of the oaks that is dominant in one area is represented by scattered individuals in the other area. Foliage-feeding lepidopteran larvae are most abundant from late April to early June; of these, larvae of the fall cankerworm *Alsophila pometaria* (Geometridae) are by far the most abundant in most years; they were exceptionally abundant in the spring of 1979. This species hatches at the time of budbreak and completes larval development by the second week of June; as is the case with many other lepidopteran species (*8*), it is incapable of completing development on mature foliage (*9*). The larvae hatch from eggs laid in late fall by wingless females and are dispersed widely by wind, especially in the first instar.

In the course of our studies of *Alsophila* over the last 6 years, we have noted that it consistently hatches at about the time that scarlet oak comes into leaf. White oak does not break bud until about 10 days later. Because *Alsophila* larvae cannot survive for more than 2 to 3 days without food (*9, 10*), we predicted that the *Alsophila* population should be far more dense in the stand dominated by scarlet oaks than in the white oak stand. Within the white oak stand, *Alsophila* larvae were expected to have a greater impact on the few scarlet oaks than on the white oaks because only scarlet oak is in leaf during the early instars. In the site dominated by scarlet oaks, defoliation of the few white oaks should be heavier than that of scarlet oaks because the abundant *Alsophila* larvae disperse onto the white oaks when these break bud, offering highly palatable young foliage when the foliage of scarlet oak is becoming unpalatable. Thus in each area, the minority species should suffer greater defoliation in the early spring.

Table 1. Levels of herbivory and abundance of insect larvae in scarlet oak and white oak in areas dominated by scarlet oaks (S) and white oaks (W). Leaves were taken from two trees at each site except from the scarlet oak at the first site in W, in which case three trees were sampled.

Area	Site	Species	Leaves sampled	Mean damage level	*Alsophila* per leaf	Larvae per leaf
S	1	Scarlet	55	2.98	.632	.686
		White	77	3.58	.217	.236
	2	Scarlet	57	3.72	.493	.514
		White		5.00		
	3	Scarlet	70	3.77	.579	.644
		White		5.00		
	4	Scarlet	71	3.92	.614	.643
		White		5.00		
W	1	Scarlet	141	2.94	.100	.119
		White	95	2.61	.161	.256
	2	Scarlet	50	1.72	.193	.219
		White	87	1.81	.052	.075
	3	Scarlet	58	2.66	.198	.220
		White	104	1.48	.037	.050
	4	Scarlet	54	2.67	.097	.166
		White	69	1.29	.023	.123

On 1 June 1979, when most *Alsophila* larvae had entered the last instar, we clipped branches with a 5-m pruner from two scarlet oaks (three, in one instance) and two white oaks at each of four stations in both the site dominated by scarlet oaks (S) and the site dominated by white oaks (W). For each clipped branch we counted the number of leaves and of larvae, which we identified as *Alsophila* and "others." For each leaf on two randomly chosen branchlets on each branch, herbivory was visually estimated and assigned to classes ranked 1 to 5 ($1 = 0$ to 20 percent eaten, $2 = 20$ to 40 percent, and on up to $5 = 80$ to 100 percent). Insect abundance was greater in area S than area W. On scarlet oaks, the mean number of larvae (of all species) per leaf was 0.62 ± 0.057 and 0.16 ± 0.127 in areas S and W, respectively (mean ± standard error; $N =$ eight and nine trees, respectively; $t = 16.43$, $P < .0005$; one-tailed Mann-Whitney U test). The density of *Alsophila* larvae was 0.58 ± 0.054 and 0.142 ± 0.038 ($t = 13.97$, $P < .0005$) on scarlet oaks in areas S and W, respectively. The density of larvae on white oaks was not calculated in area S because white oaks in this site dominated by scarlet oak were completely defoliated and carried few larvae (Fig. 1). *Alsophila* constituted a greater proportion of the larvae in area S than area W ($U = 63$, $P < .005$; one-tailed test). The mean level of herbivory per tree was correlated with the total number of larvae per leaf for both white (Spearman's $r_s = .59$, $P < .01$) and scarlet ($r_s = .59$, $P < .01$) oaks, and was highly correlated with the number of *Alsophila* per leaf ($r_s = .55$, $P < .025$ for scarlet; $r_s = .95$, $P < .0005$ for white).

Figure 2 illustrates mean levels (based on the visually estimated scale described above) of defoliation for each tree, summarizing the data shown in Table 1. For both scarlet and white oaks, the extent of defoliation was greater in area S than in area W [for scarlet oak, $U = 60$, $N = 8$, 9, $P < .025$; for white oak, $U = 64$, $N = 8$, 8, $P < .005$ (one-tailed Mann-Whitney U test)]. Within area W, scarlet oak was more heavily defoliated than white oak ($U = 57$, $N = 9$, 8, $P < .025$; one-tailed test); within area S, white oak was more heavily defoliated than scarlet oak ($U = 54$, $N = 8$, 8, $P < .025$; one-tailed test). At three of the four stations in the scarlet-dominated area S, the white oaks were completely defoliated (Fig. 1).

Alsophila emerged in somewhat lesser numbers in 1980 than in 1979, but a visual examination of these woodlots on 16 June 1980 revealed the same qualitative pattern as in 1979; the white oaks were far more heavily defoliated than the scarlet oaks in area S, and the reverse was the case in area W.

Several authors have reported that physiological stress may lower the resistance of trees to insects (*11*). Thus we explored the possibility that each oak species is under greater physiological stress, and so is more heavily defoliated, in the area where it is uncommon. For ten trees of each species in each site, with similar diameters, we determined the mean width and coefficient of variation of the width of the 15 most recent annual growth rings, measured in cores taken from the trunk at breast height. Neither measure of the effect of the environment on growth differed significantly between areas for either oak species (*12*). Thus we believe that the simpler explanation for the variation in herbivory is the one postulated a priori: that the correspondence in phenology between hatching time of *Alsophila* and budbreak of scarlet oak maintains a high population of *Alsophila* ready to feed on scattered white oaks when they come into leaf, but that *Alsophila* cannot maintain a high population in a site dominated by white oak.

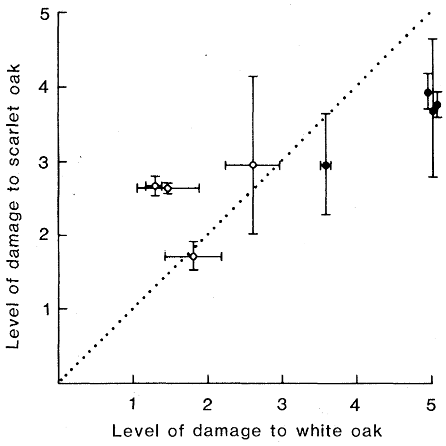

Fig. 2. Mean and range of variation in levels of defoliation of white oak and scarlet oak at each of four sites in a white oak-dominated stand W (open circles) and at each of four sites in a scarlet oak-dominated stand S (closed circles). The dotted line represents equal levels of defoliation of both species. The means lie above the dotted line for stand W and below the line for stand S, reflecting the higher level of damage to the minority species in each stand.

The disadvantage suffered by the minority plant species is a consequence of the broad diet of the major herbivore in this system and of the phenological relationships of these species. Our observation does not interfere with theories based on the responses of host-specific herbivores to variation in the density of the species on which they feed. It must frequently be the case, however, that uncommon species are prevented from increasing if they are fed on by a generalized predator that is maintained at high density by a common species of prey.

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References and Notes

1. W. W. Murdoch and A. Oaten, *Adv. Ecol. Res.* **9**, 2 (1975); M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems* (Princeton Univ. Press, Princeton, N.J., 1978).
2. D. H. Janzen, *Am. Nat.* **104**, 501 (1970).
3. J. H. Connell, in *Dynamics of Populations*, P. J. den Boer and G. R. Gradwell, Eds. (Proceedings, Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeck, 1970) (Unipub, New York, 1971), p. 298.
4. P. P. Feeny, *Recent Adv. Phytochem.* **10**, 1 (1976).
5. D. J. Futuyma, *Am. Nat.* **100**, 285 (1976).
6. D. Pimentel, *Ann. Entomol. Soc. Am.* **58**, 1 (1961); J. O. Tahvanainen and R. B. Root, *Oecologia (Berlin)* **10**, 321 (1972).
7. R. B. Root, *Ecol. Monogr.* **43**, 95 (1973).
8. P. P. Feeny, *Ecology* **51**, 656 (1970).
9. C. Mitter, D. J. Futuyma, J. C. Schneider, J. D. Hare, *Evolution* **33**, 777 (1979).
10. J. C. Schneider, thesis, Princeton University (1978).
11. R. W. Stark, *Ann. Rev. Entomol.* **10**, 303 (1965); T. C. R. White, *Oecologia (Berlin)* **16**, 279 (1974).
12. If either species of oak suffered greater physiological stress where it is rare, it might be expected to show a lower mean, or a greater coefficient of variation, or both, in the site where it is less abundant. Defoliation could also cause differences in growth rings [P. A. Morrow and V. C. LaMarche, Jr., *Science* **201**, 1244 (1978)], but it might be expected to cause a higher coefficient of variation for both species in the site dominated by scarlet oaks than in the site dominated by white oaks because exceptionally high populations of *Alsophila* occur only in the former site. Because no site-related differences in growth were found for either species, the growth ring data shed no light on either hypothesis.
13. We are grateful to R. Weiss for assistance in the field and to members of the informal plant-herbivore study group at Stony Brook for helpful comments. Supported by NSF grant DEB 76-20232. This is contribution 209 of the Program in Ecology and Evolution of the State University of New York at Stony Brook.

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28 November 1979; revised 7 July 1980

Reference: The Linguistic Essential

Abstract. *Three chimpanzees learned to label three edibles as "foods" and three inedibles as "tools." Two chimpanzees could then similarly categorize numerous objects during blind trial 1 tests when shown only objects' names. The language-like skills of the chimpanzee who failed (Lana) illustrates that apes can use symbols in ways that emulate human usage without comprehending their representational function.*

When chimpanzees use signs or lexigrams which they have been taught by human trainers, the question arises as to whether they know what these symbols represent or whether they simply learn contextually appropriate usages, as we have already suggested (*1*). We report on our effort to determine whether or not the abstract symbols used by our chimpanzee subjects were functioning at a representational level. We trained the subjects to label the names of three inedibles (stick, key, and money) as tools, and the names of three edibles (beancake, orange, and bread) as foods. We then presented these chimpanzees with the names of 17 other foods and tools and asked them to categorize these additional names as foods or tools. In order for the chimpanzees to make a categorical judgment of this sort on the first trial, it was necessary for them to recall some representation of the actual object, since the specific names of these foods and tools had never been paired with categorical labels.

Before this study was begun, each of the three chimpanzee subjects—Lana (8 years), Sherman (5 years), and Austin (4 years)—had extensive experience with the Yerkes computer-based language training system (*2*). The original training of these items was similar for Sherman and Austin, but differed for Lana (Table 1). Lana's initial training emphasized symbol sequencing and object naming, while Sherman's and Austin's training emphasized the pragmatic and semantic functions of symbols, and communication between chimpanzees (*2, 3*). In order to provide Lana with a vocabulary and experience more comparable to that of Sherman and Austin, we introduced to her the eight tools used by Sherman and Austin.

It was necessary for Sherman and Austin to learn to ask for tools which they needed to use before they were able to label these tools divorced from the context of usage (*2*). Lana, by contrast, readily learned to label all the tools long before she could accurately request them as needed. Such disjoint abilities suggest that the chimpanzee's capacity to produce a symbol when an object is desired (for example, to say "key" when a key is needed to open a padlock) may not necessarily be related to the ability to produce the same symbol when asked to name a visible object (for example, to say "key" when the experimenter holds up a key). In the case of Sherman and Austin, the demonstration of an object's function helped them to recall its name. If, for example, they could not recall the name for "key" when it was held up, using a key to unlock a padlock would enable them to recall its name. This was not true of Lana. It seemed that Sherman's and Austin's training led them to link the use of an object and the label of an object together. For Lana, the two skills appeared to remain separate. Before instituting training the categorical classifications of "food" and tool," we conducted blind tests of the abilities of all three animals to use the 11 specific food and tool names which would be the focus of our study. All three chimpanzees scored 100 percent during blind tests of request skills, labeling skills, and receptive skills.

Sorting objects. Categorical sorting of foods and tools was begun by requiring the animals to sort three foods (orange, bread, and beancake) into one bin, and three tools (key, money, and stick) into another. None of the foods or tools resembled each other physically, thereby precluding a match-to-sample response. The dimension for sorting was functional; the foods could be eaten and the tools could not. Training was facilitated in all three cases by emphasis on the functional distinction, which suggested that the animals might be classifying these items along the edible-inedible dimension (Fig. 1).

Labeling objects. When the animals reached a sorting criterion of 90 percent or better across 60 trials, we introduced the lexigrams for food and tool. The chimpanzees' task was to sort a food or a tool into the proper bin and then to select the lexigram representing either food or tool. Once the chimpanzees reliably selected a lexigram after sorting each object, the bins were removed and the task then was to label each of the six training objects as they were held up by the experimenter.

Training in this phase continued until the animals met all of the following criteria: (i) ability to label all training items correctly without eating the food or using the tool; (ii) ability to label all training items correctly on trial 1, after food and tool lexigrams were relocated on the keyboard; and (iii) ability to label all training items correctly under the conditions listed above for two consecutive sessions of more than 25 trials at 90 percent (or greater) correct.

It would be possible for the animals to learn the above tasks in either of two ways: (i) by forming a specific association between each item and the appropriate bin or lexigram for that item; or (ii) by formulating a classification rule, "This bin is for items that I eat and the other bin is for items that I do not eat." If such a concept or rule had emerged, then we would expect that the chimpanzees could use these generic symbols to categorize other items with no additional training. We tested the generalizability of this skill by presenting five additional foods and five additional tools. (The chimpanzees knew the specific lexigrams of each of these ten