Eq. 1 averages the force over space only, not time, and the droplet spends more time in the lower half of the crater, where both the hydrostatic pressure and the surface tension force are greater (thereby suggesting that $0.5 \leq K < 1.0$), and (ii) the submerged portion of each droplet (depicted in Fig. 2) is not completely surrounded by water. These successful mechanical analyses have made no use of the air layer hypothesis of Jayaratne and Mason (*3*).

As the normal incident momentum of a rebounding droplet stream is increased, eventually a point is reached above which no rebounds are observed. The threshold conditions for transition from rebounding to absorption were measured for various droplet sizes, and the results show that the incident normal components of momentum and energy increase with increasing droplet mass. In addition, the interdrop time interval increases monotonically with the incident normal component of momentum (Fig. 3). The explanation of these data remains unclear; however, they are reproducible and consistent and indicate the interface conditions between the two regimes of behavior.

Within the range of incident velocities and droplet diameters examined, single droplets were never observed to rebound. In each single droplet test the droplet control shutter allowed typically four droplets to pass through, and the leading droplet (taken as a single droplet) and all succeeding droplets were always absorbed. Droplet impaction photographs indicate large deceleration of the leading droplet in forming a crater so that this energy loss is sufficient to prevent the droplet from rebounding. Succeeding droplets, however, encounter a partially formed crater and thus must perform less work in the process of crater formation. The shaping of the crater continues, with each droplet losing all of its kinetic energy upon absorption. Finally, an impacting droplet retains enough kinetic energy to escape from the surface, after which all impacting droplets with the same characteristics rebound.

BRUCE CHING
MICHAEL W. GOLAY
THOMAS J. JOHNSON
Department of Nuclear Engineering, Massachusetts Institute of Technology, Cambridge 02139

References and Notes

1. A. M. Worthington, *A Study of Splashes* (Longmans, Green, London, 1908).
2. O. G. Engel, *J. Appl. Phys.* **37**, 1798 (1966).
3. O. W. Jayaratne and B. J. Mason, *Proc. R. Soc. London Ser. A* **280**, 545 (1964).
4. F. H. Harlow and J. P. Shannon, *J. Appl. Phys.* **38**, 3855 (1967).
5. P. V. Hobbs and A. J. Kezweeny, *Science* **155**, 1112 (1967).
6. P. V. Hobbs and T. Osheroff, *ibid.* **158**, 1184 (1967).
7. W. C. Macklin and P. V. Hobbs, *ibid.* **166**, 107 (1969).
8. P. R. Brazier-Smith, S. G. Jennings, J. Lantham, *Proc. R. Soc. London Ser. A* **326**, 393 (1972).
9. W. C. Macklin and G. J. Metaxas, *J. Appl. Phys.* **47**, 3963 (1976).
10. S. G. Jennings, *Phys. Educ.* **12**, 381 (September 1977).
11. R. M. Schotland, *Discuss. Faraday Soc.* **30**, 72 (1960).
12. C. A. Coulson, *Waves* (Oliver and Boyd, New York, 1955).
13. L. G. Parrat, *Probability and Experimental Errors in Science: An Elementary Survey* (Dover, New York, 1971).
14. We recognize the essential technical aid provided by the Stroboscopic Light Laboratory staff of H. E. Edgerton. This work was supported, in part, by the U.S. Department of Energy.

23 January 1984; accepted 24 August 1984

Leaf Herbivores Decrease Fitness of a Tropical Plant

Abstract. *Damage by insect herbivores to neighboring individuals of the shrub* Piper arieianum *in a neotropical wet forest varies greatly. This differential damage has a genetic basis and results in a 2-year decrease in growth, seed production, and seed viability, with larger plants recovering before smaller plants. The results provide evidence that leaf herbivores represent a potentially strong selective force for the evolution of plant defenses.*

Theoretical considerations of herbivore-plant interactions assume that the numerous mechanical and chemical characteristics of plants that decrease herbivore feeding, growth, and survival have evolved as a direct result of selection imposed by herbivores (*1, 2*). However, our understanding of the effects of leaf herbivores in plant evolution is either derived from agricultural systems or correlational evidence of herbivore-caused reductions in plant growth or survival in nature (*3, 4*). Realistic experiments are scarce (*5*). Studies of natural populations of the neotropical understory shrub *Piper arieianum* C.DC. (Piperaceae) show a link between intraspecific variation in leaf damage and differential reduction of plant fitness. Naturally high variation in herbivore damage between individual plants and clones appears to be related to substantial long-term effects of simulated herbivore damage on growth, seed output, and associated characters.

Piper arieianum is a common understory shrub at the La Selva Biological Station which is located in lowland tropical wet forest in northeastern Costa Rica (*6*). Loss of leaf area to herbivores in this species varies greatly between neighboring plants. For individual plants over short time periods (2 to 3 months), leaf area loss attributable to herbivores other than leaf-cutting ants is low, but variance is very high: for nine census periods, the mean percentage of damage and standard deviation ranged from 1.04 ± 1.14 to 6.63 ± 15.31 percent ($n = 25$ plants; extremes in individual plant damage, 0.00 to 25.95 percent) (*7*). Because leaves live for 1.5 to 2.5 years these relatively small losses over short time periods can sum to large amounts of damage observable at any one time. Single measurements of herbivore damage to entire plants range from 3.93 to 49.65 percent (mean ± standard deviation, 16.74 ± 8.84 percent; $n = 25$ individuals) (*8*). Statistically significant differences in herbivory between clones of *P. arieianum* strongly suggest that plant genotype differences influence this intraspecific variation in herbivory (*9*).

To relate intraspecific variation in herbivory to possible differences in plant fitness in *P. arieianum*, I defoliated plants in late November 1980, 2 months before the main flowering peak of the species (*10*). I used a paper punch to damage leaves for 18 days (*11*). Within a plant, most leaves receive little natural damage, and a few sustain heavy damage. I simulated these naturally uneven patterns of herbivory by removing small amounts of leaf area from most leaves and heavily damaging the remaining few leaves. The total area removed was 0, 10, 30, or 50 percent of the plant's total leaf area (*12*). To control for influences of plant size on the effects of defoliation, I classified plants into three size categories (small, medium, or large) at the beginning of the experiment (*13*) and randomly assigned individuals within each size category to a defoliation level (*14*). In addition, I completely defoliated 30 medium-sized plants over 1 day by clipping the blade from the midrib of the leaf and removing the cut material from the vicinity of the plant; this simulated damage by leaf-cutting ants.

Growth during the first year after defoliation showed a statistically significant reduction ($P < 0.05$) in small- and medium-sized plants from which 30 percent or more of the leaf area was removed (Fig. 1A) (*15*). For the full 2 years after defoliation, small- and medium-sized plants with ≥ 30 percent defoliation showed at least a 50 percent decrease in total growth compared to control plants (Fig. 1B). Large plants showed no significant differences in growth at any treatment level for the first year or for the full 2 years (Fig. 1, A and B). The plants that were completely defoliated showed a reduction in growth over the 2 years that was similar to plants of the 30 and 50 percent defoliation treatments (Fig. 1B). None died. After 2 years these fully defoliated plants had regained on average two-thirds of their original leaf area.

Seed production decreased with increasing defoliation for all plants during the first year (*16*) (Fig. 1C). The decrease for plants of all sizes with ≥30 percent defoliation was statistically significant ($P < 0.05$); plants with 100 percent defoliation produced no seeds the next year. Reduced fitness due to lowered seed production was compounded by changes in seed viability and flowering time. With 50 percent defoliation, seed viability was reduced by 25 percent compared to plants with ≤30 percent defoliation ($P < 0.05$) (*17*). The flowering peak of the fully defoliated plants was delayed by up to 2 months after the main flowering of the species, resulting in reduced likelihood of pollination and a total absence of fruit set in these plants (*18*).

The direct effect of the leaf area loss was long lasting; removal of 30 percent or more of the original leaf area in the small and medium plants caused a significant reduction in seed production in the second year after defoliation (Fig. 1D). For large plants, the effect of leaf removal on seed production did not persist through the second year.

The depression in growth in small plants after herbivore attack will prolong the time during which the damaged plant remains in a smaller size class. In this way, a single attack not only reduces immediate growth and seed output for a minimum of 2 years but increases the time during which subsequent attacks will have comparable effects. As such, single herbivore attacks may be extremely detrimental to the lifetime seed output of a particular genotype.

A probable explanation for the faster recovery of large plants after defoliation is that they have greater absolute amounts of leaf tissue and stem and root biomass than small and medium plants. This increased capacity to compensate for leaf area loss with increasing plant size suggests that there may be selection for decreases in defense as plants age. Seedlings, which are the most vulnerable stage of the plant life cycle, are known in some species to allocate proportionately more resources to defense than larger, more mature stages (*19*).

Through their detrimental effect on growth and seed output, phytophagous insects of *P. arieianum* decrease the probability that an individual genotype will be represented in ensuing generations. However, herbivore-mediated reduction in plant reproductive output by itself is not sufficient evidence that herbivorous insects shape the evolution of a plant's defense system. In addition, herbivores must exhibit selectivity with regard to genetically based, intraspecific variation in these defenses. In *P. arieianum*, intraspecific variation in

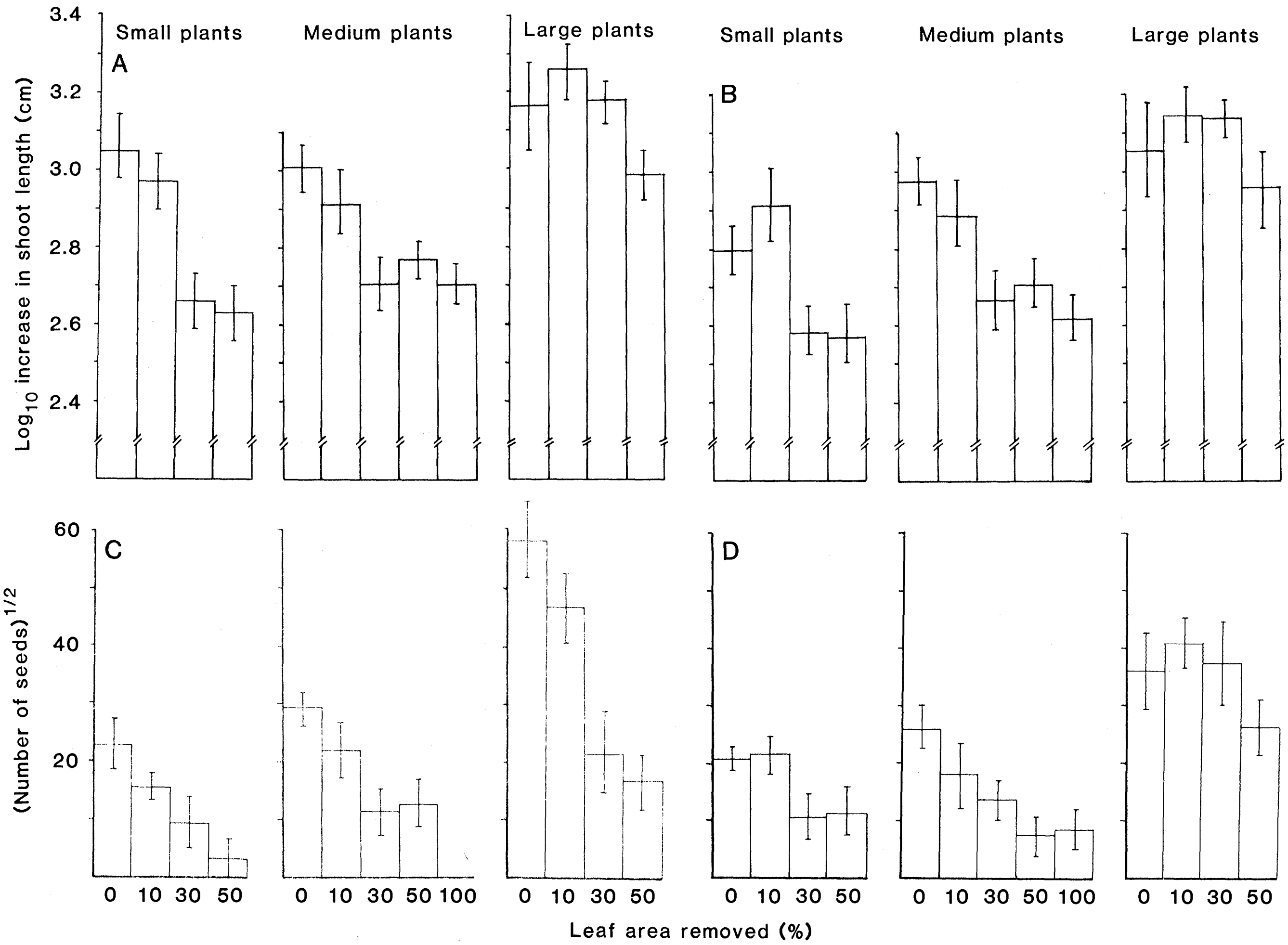

Fig. 1. The effects of varying levels of leaf area removal on growth and reproduction for three size classes of plants of *Piper arieianum*. (A) Total growth (*15*) during the first year after a single defoliation. (B) Growth during the full 2-year period after defoliation. (C) Seed production (*16*) during the first year after defoliation. (D) Seed production during the second year after defoliation. Standard errors of the means are shown.

damage levels has a genetic basis (*9*). There is apparently continuous selection for defenses in this plant species to reduce leaf area losses.

ROBERT J. MARQUIS*
Department of Botany and *Program in Ecology and Evolutionary Biology, University of Iowa, Iowa City, 52242*

References and Notes

1. G. S. Fraenkel, *Science* **129**, 1466 (1959); P. R. Ehrlich and P. H. Raven, *Evolution* **18**, 586 (1964); P. P. Feeny, *Recent Adv. Phytochem.* **10**, 1 (1976); D. F. Rhoades and R. G. Cates, *ibid.*, p. 168.
2. For example, see O. L. Chambliss and C. M. Jones, *Hortic. Sci.* **89**, 394 (1966); K. L. S. Harley and A. J. Thorsteinson, *Can. J. Zool.* **45**, 305 (1967); J. C. Parr and R. Thurston, *Ann. Entomol. Soc. Am.* **65**, 1185 (1972); T. Ikeda *et al.*, *Science* **197**, 497 (1977); M. Berenbaum, *ibid.* **201**, 532 (1978); P. A. Blau *et al.*, *ibid.* **200**, 1296 (1978); K. V. Raman *et al.*, *J. Econ. Entomol.* **72**, 337 (1979).
3. D. A. Jameson, *Bot. Rev.* **29**, 532 (1963); R. Bardner and K. E. Fletcher, *Bull. Entomol. Res.* **64**, 141 (1974).
4. H. Kulman, *Annu. Rev. Entomol.* **16**, 289 (1971).
5. N. Waloff and O. W. Richards, *J. Appl. Ecol.* **14**, 787 (1977); P. A. Morrow and V. C. LaMarche, Jr., *Science* **201**, 1244 (1978); A. G. Stephenson, *Ecology* **61**, 57 (1980); M. D. Rausher and P. Feeny, *ibid.*, p. 905; J. H. Myers, *J. Anim. Ecol.* **50**, 11 (1981); M. A. Parker and R. B. Root, *Ecology* **62**, 1390 (1981); M. J. Crawley, *Herbivory* (Univ. of California Press, Berkeley, 1983).
6. The study site is owned by the Organization for Tropical Studies [G. S. Hartshorn, in *Costa Rican Natural History*, D. H. Janzen, Ed. (Univ. of Chicago Press, Chicago, 1983), pp. 136–141].
7. Leaf-cutting ants (*Atta cephalotes*) at La Selva can completely defoliate individuals of *P. arieianum*. Twenty-five randomly selected leaves of each of 25 plants were traced. The tracings were then used to determine occurrence of new damage between five consecutive census periods. Areas of tracings were measured with an electronic area meter (model L1-3050A, LAMBDA).
8. All of the leaves from 25 plants were collected. A paper tracing was made of the potential area of each leaf, and the area of the real leaf and the paper leaf were measured with an area meter (*7*). Individual plants differed significantly in the amount of herbivore damage (analysis of variance, $P < 0.05$, $F = 3.30$).
9. Four individuals, selected from four different sites, at least 1 km apart, were cloned. Sixteen clones from each plant were planted at the same understory site in a randomized block design (14 by 14 m). After 14 months, clones differed significantly by genotype in the amount of accumulated herbivore damage (analysis of variance, $F = 3.14$, $P < 0.05$). The mean damage level by genotype for the surviving clones was 9.11, 11.78, 15.34, and 18.01 percent.
10. P. Opler *et al.*, *J. Ecol.* **68**, 167 (1980).
11. The method of removal was designed to reduce possible differences in plant response to mechanical versus insect damage [J. L. Capinera and W. J. Roltsch, *J. Econ. Entomol.* **73**, 258 (1980)]. Curculionid weevils [*Peridinetus laetus* Champion, *Peridinetus* sp., and *Ambetes* sp. (D. Whitehead, personal communication)] are major herbivores of *P. arieianum* and produce round to oblong holes, similar in size to those made with a paper punch. I randomly assigned leaves to a damage class (either 0, 10, 20, 40, or 80 percent) and randomly chose the day on which I damaged them. The proportion of an experimental plant's total leaves assigned to each damage class matched the average pattern for naturally damaged plants at a given defoliation level.
12. Defoliation pattern within a leaf for a particular damage level was kept constant, as damage distribution within a single leaf can affect photosynthesis rates [F. R. Hall and D. C. Ferree, *J. Econ. Entomol.* **69**, 245 (1976)].
13. Small plants, 20 to 33 leaves; medium plants, 34 to 55 leaves; and large plants, 56 to 120 leaves.
14. A minimum of 35 plants per treatment was used.
15. Analysis of covariance (with original leaf number as the covariate), followed by Tukey means comparison, was performed separately for each plant size class for the dependent variables, shoot growth and seed production. The growth measurement reported is the total length of new shoots produced over the entire plant. Individuals suffering subsequent appreciable damage, due to further herbivory, or damage due to tree or branchfalls, were omitted from analysis.
16. The fruiting structure in *P. arieianum* is a spike of tightly packed, single seeded fruits [W. C. Burger, *Fieldiana Bot.* **35**, 5 (1972)]. Seed output was determined by measuring the length of all infructescences on a plant and multiplying by the mean number of seeds per unit of infructescence.
17. Viability was determined by germinating freshly collected seeds in petri dishes with moistened filter paper. The dishes were placed on the forest floor in the understory of primary forest. Mean viabilities and standard deviations of seeds of the first year's fruit crop for the 0, 10, 30, and 50 percent defoliation treatments were 87.43 ± 5.76, 84.99 ± 63, 88.22 ± 10.52, and 54.62 ± 10.98 percent, respectively ($P < 0.01$; Kruskal-Wallis test; $\chi^2(3)= 12.26$).
18. The flowering peak of the fully defoliated plants occurred in April 1982, while that of plants of all lower defoliation levels was in mid-February.
19. H. V. Eck *et al.*, *Crop Sci.* **15**, 421 (1975); E. A. Bernays and R. F. Chapman, *Symp. Biol. Hung.* **16**, 41 (1976); G. R. Waller and E. Nowacki, *Alkaloid Biology and Metabolism in Plants* (Plenum, New York, 1978), p. 116.
20. I thank S. Hendrix, H. Howe, S. Koptur, R. Black, K. Grove, C. Kelly, E. Trapp, D. Feener, S. Hermann, B. Minor, S. Hubbell, and J. Howard for manuscript comments; O. Vargas R., and I. Chacon G. for help in data collection; the Organization for Tropical Studies staff for logistical support; and J. Ewel and B. Brown for use of the area meter. Supported by the University of Iowa, two grants-in-aid of research from Sigma Xi, grant DEB 81-10197 from the National Science Foundation, and a Jessie B. Noyes predoctoral fellowship.

* Present address: Department of Ecology, Ethology, and Evolution, University of Illinois at Urbana–Champaign, Merrill Hall, 505 South Goodwin Avenue, Urbana 61801.

9 March 1984; accepted 11 July 1984

Elemental Anomalies at the Cretaceous-Tertiary Boundary, Woodside Creek, New Zealand

Abstract. *Iridium and 26 other elements were determined in shale from the Cretaceous-Tertiary boundary at the* locus classicus *(for iridium anomalies) at Woodside Creek, New Zealand. Iridium, gold, copper, cobalt, chromium, nickel, arsenic, molybdenum, and iron were enriched in the basal 2 millimeters of the 8-millimeter shale parting as compared with the rest of the stratigraphic column. No other shale partings in the column had anomalous concentrations of any element when the data were expressed on a carbonate-free basis. The boundary material showed striking compositional similarities with the Stevns Klint Danish boundary shale. Elemental concentrations were in general much higher in the New Zealand material than in nonboundary shales from elsewhere in the world. The high concentration of iridium (153 nanograms per gram) in the basal layer of the boundary, together with the enrichment of other siderophile elements supports the idea of an extraterrestrial source for much of the material. The iridium/gold ratio of 2.1 is also in accordance with such a source. The iridium content of the basal layer is higher than for any other marine boundary shale obtained on land. The integrated iridium value is 187 nanograms per square centimeter of boundary surface.*

In a benchmark paper, Alvarez *et al.* (*1*) proposed that mass extinctions at the end of the Cretaceous had been caused by the impact of a large asteroid. As evidence of this, they reported a very large iridium anomaly at the Cretaceous-Tertiary (K/T) boundary in marine shales at Gubbio in northern Italy, Stevns Klint in Denmark, and Woodside Creek in New Zealand. No data were reported from New Zealand beyond the statement that the iridium concentration in the K/T shale was about 20 times that in the adjacent limestone. Alvarez *et al.* (*2*) later reported an integrated iridium excess of 120 ng cm^{-2} for this site.

Iridium is a siderophile element that is rare in terrestrial material but much more abundant in chondrites and other extraterrestrial bodies. Thus its presence at relatively high concentrations may well indicate an extraterrestrial source for the material studied. The report by Alvarez *et al.* (*1*) sparked a lively and continuing debate, which resulted in a conference at Snowbird, Utah (*3*), devoted entirely to this topic. In the ensuing debate a number of different sources for the iridium anomaly have been proposed: chondritic meteorites or asteroids (*4*), metal sulfide–cored meteorites (*5*), comets (*6*), and terrestrial nonimpaction sources (*7–10*).

We have determined the elemental content of a suite of marine carbonate rocks from the Woodside Creek section in South Island, New Zealand, in the course of which 27 elements were quantified. The purpose of this work was to determine similarities between the K/T boundary shale of this New Zealand formation and a K/T boundary shale from Denmark, and to compare a variety of shales from other parts of the world with our material in order to determine whether the Woodside Creek material did indeed have an anomalous composition and was not merely reflecting the usual composition of marine shales.

The K/T boundary in the narrow gorge of Woodside Creek in northeastern Marlborough Province, New Zealand, was