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Chronic Herbivory: Impacts on Architecture and Sex Expression of Pinyon Pine

Abstract. *Pinyon pine,* Pinus edulis *(Engelm.), in Northern Arizona is exposed to recurring high levels of herbivory by the moth* Dioryctria albovitella *(Hust.). During a 3-year period, infested trees experienced on average a 30 percent reduction in annual shoot production. This herbivory affects tree architecture, growth rate, reproductive output, and sexual expression. Less infested trees produce 47 percent more trunk wood, 43 percent more branch wood, and are monoecious. Architectural changes in infested trees can result in functionally male plants due to a complete loss of normal female cone-bearing ability. When herbivores are experimentally removed, normal growth and reproduction patterns resume. These strong herbivore impacts should represent a potent selection pressure in the evolution of host traits.*

The demonstration of significant herbivore impacts on ecologically and evolutionarily important plant traits is often lacking data on native plant-herbivore systems (*1, 2*). In the absence of such data, purported plant defenses and adaptationist's arguments in general have been questioned (*3–5*). Furthermore, with herbivores generally consuming less than 3 to 8 percent of the annual foliage production (*6*), examples of herbivory by native pests that is both acute and chronic (that is, repeated high levels of attack) are few (*7*). We examined the impacts of the stem- and cone-boring moth *Dioryctria albovitella* on architecture, growth rates, reproduction, and sex expression of the monoecious conifer *Pinus edulis*. Herbivore-mediated sex expression in plants has been little studied (*8*) because sex expression is thought to be governed by other factors such as plant stress, age, or density (*9–15*).

Studies were conducted from 1982 to 1984 near Sunset Crater National Monument, Flagstaff, Arizona. From a study site of approximately five hectares, 40 trees were selected on the basis of growth form; 20 had a prostrate shrub-like crown and 20 an upright treelike crown. Because tree age may be correlated with resistance to herbivore attack (*16, 17*) and sexual expression (*12–14*), trees were matched for age. Mean counts of tree rings (± standard error of the mean) showed both groups to be nearly identical in age (prostrate, 147 ± 8.5 years; upright, 144 ± 7.9 years). All trees were fitted with dendrometers to measure current year's growth and censused for insect-caused shoot mortality as well as female cone and male strobili production. An average of 205 shoots was collected from all sides and heights of each tree.

Tree architecture is highly correlated with shoot mortality caused by *D. albovitella*. In trees with the prostrate growth form, 28.1 ± 2.52 percent of the current year's shoots were destroyed in 1983, whereas only 7.8 ± 1.28 percent of the shoots of upright trees were destroyed ($t = 7.180$, d.f. = 38, $P < 0.001$). This represents a 3.6-fold difference in shoot loss due to herbivory.

The complex branching architecture of heavily infested trees results from the selective destruction of terminal shoots by the stem-boring larvae of *D. albovitella*. In an examination of 360 shoots from a single tree, 82 percent of the terminal shoots and 10.4 percent of the lateral shoots were killed ($\chi^2 = 175.461$, d.f. = 1, $P < 0.001$). Thus, the probability that a terminal shoot will be destroyed is nearly eight times that for a lateral shoot. Such selective shoot mortality eliminates the normal patterns of apical dominance that are so important in determining tree architecture (*18, 19*).

The selective destruction of terminal shoots stimulates the production and growth of lateral buds, and the plant becomes a dense shrub. Figures 1A and 1B show that as the shoot mortality increases, the production of new terminal buds declines ($r^2 = 68.4$ percent, $n = 40$, $P < 0.01$), and the production of new lateral buds increases ($r^2 = 35.7$ percent, $n = 40$, $P < 0.01$).

When *D. albovitella* is experimentally removed from heavily infested pinyons, tree architecture is affected by an increase and decrease, respectively, in the production of new terminal and lateral buds. Three trees were sprayed with a systemic insecticide (Cygon) to kill stem-boring insects. Shoot mortality and bud production before and 1 year after treatment was compared with that on 20 nearby heavily infested control trees (Table 1). Although control trees showed no statistically significant changes from year to year ($P >> 0.05$), experimental

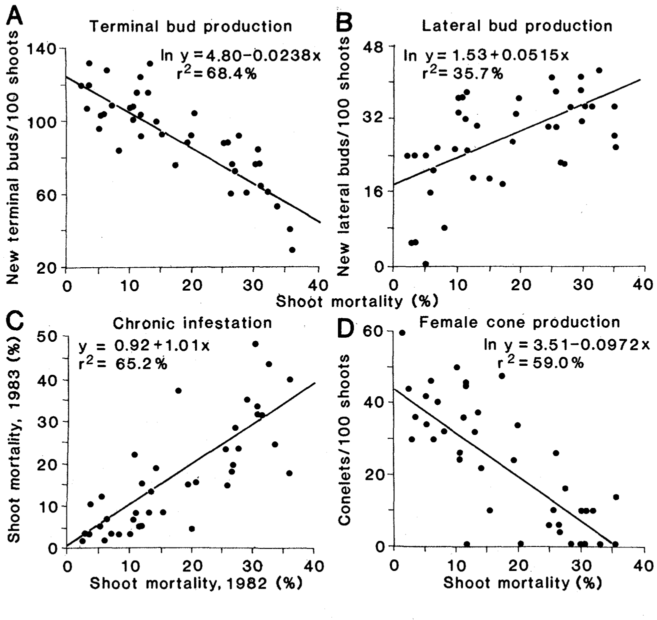

Fig. 1. Herbivory affects the production of terminal and lateral buds, which determines tree architecture and sexual expression. (A) As shoot mortality increases, the production of terminal buds declines, whereas (B) lateral bud production increases. This alters the pattern of apical dominance, and trees eventually become shrubs. Pinyons suffer chronic and acute herbivory (C). Trees with the highest shoot mortality in 1982 also suffered the highest shoot mortality in 1983. With increasing shoot mortality trees change in their sexual expression from monoecious to functionally male plants (D). The production of female cones declines to 0. Mortality percentages are based on average samples of 205 shoots from each of 40 study trees. Variables in Figures A, B, and D are transformed with a natural logarithm. The standard errors of the slopes in A, B, C, and D are 0.00257, 0.0108, 0.01176, and 0.0129, respectively.

Table 1. Comparisons of new lateral and terminal bud production and conelet production before the removal of *Dioryctria albovitella* in 1983 and 1 year after removal in 1984 (*22*). Herbivores removed, $n = 3$ trees; control trees, $n = 20$.

Trees	Shoot mortality (%)		Production (number per 100 shoots)					
			New lateral buds		New terminal buds		New conelets	
	Before	After	Before	After	Before	After	Before	After
Herbivores removed	17.8 (3.13)*	5.4 (1.05)	13.5 (1.70)	5.3 (1.50)	50.6 (5.02)	63.1 (1.52)	2.3 (1.13)	6.6 (1.75)
Control	26.3 (3.09)	25.8 (2.43)	10.5 (0.63)	11.5 (1.44)	41.1 (4.11)	42.2 (3.29)	1.9 (0.80)	2.4 (1.12)

*Numbers in parentheses represent standard errors of the mean.

trees did in both categories. After a 70 percent decline in the damage caused by borers ($t = 3.770$, d.f. = 4, $P = 0.01$), the production of terminal buds increased by 25 percent ($t = 2.380$, d.f. = 4, $P = 0.038$), and production of new lateral buds decreased by 61 percent ($t = 3.622$, d.f. = 4, $P = 0.012$). Presumably, if damage caused by stem borers was prevented for many years, pinyons with shrublike crowns could develop upright, treelike crowns. In association with the experimental removal of stem borers, we also tested the treatment itself to see whether the insecticide has a fertilizing effect that might alter plant growth and negate our findings; no effect was detected (*20*).

Because trees with prostrate, shrublike crowns lost on average 29.8 percent of their shoots during each of the three study years, the growth rates of these trees should be lower than those of trees exposed to less herbivory. Trunk growth rates obtained from dendrometer measurements were on average 47 percent more for trees with an upright growth form than for trees with a prostrate growth form (upright, 1.69 ± 0.15 mm in diameter per year; prostrate, 1.15 ± 0.17 mm per year; $t = 2.381$, d.f. = 35, $P < 0.02$).

Because the herbivory of a single year is not likely to result in a prostrate shrublike growth form, we speculated that these trees were exposed to acute infestations year after year, but trees with upright crowns were not. Figure 1C shows that the percentage of shoot mortality in 1983 was highly correlated with the percentage of shoot mortality in 1982 ($r^2 = 65.2$ percent, $n = 40$, $P < 0.01$). Thus, the same trees are being infested in successive years while nearby trees escape herbivory.

Together with chronic herbivory, infested shrublike trees have a history of slower growth rates than less infested upright trees. The growth rates of 158 small branches averaging 14 mm in diameter and 21 years in age revealed that branches from upright trees grew 43 percent more each year than branches from prostrate shrublike trees (upright, 0.84 ± 0.03 mm per year; prostrate, 0.59 ± 0.02 mm per year; $t = 6.222$, d.f. = 38, $P < 0.01$).

It seems likely that the observed branching patterns of these trees result from the accumulated herbivory of a lifetime. To illustrate the cumulative impacts of herbivory on tree architecture, the needles of two small trees were removed to reveal the underlying branch architecture (Fig. 2). Even though these trees grew only 62 m apart under the same conditions (*21*) and had similar basal trunk diameters, other ecologically important characteristics varied greatly. During 1983 and 1984, tree A, with the shrublike crown and complicated branching system, lost 30.4 and 30.2 percent, respectively, of its current year's shoot production. Tree B, with the upright treelike crown, however, lost only 0.9 and 2.8 percent of its current year's shoot production during the same period. In association with reduced herbivory, tree B produced 59 percent more trunk wood each year during its 63-year life-span than the smaller 91-year-old shrublike tree A. The upright tree also produced both male strobili and female cones, whereas the shrublike tree produced only male strobili (see the legend to Fig. 1 for specific data).

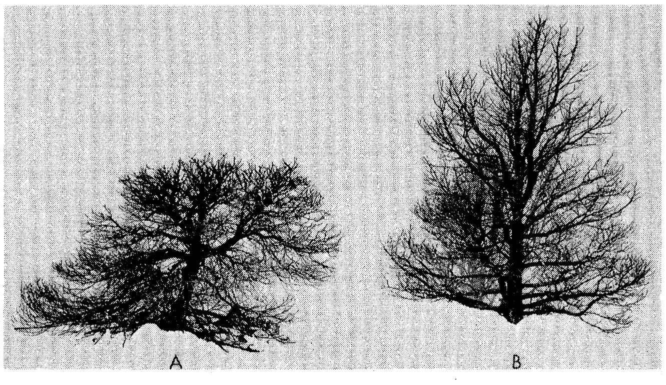

Fig. 2. Photographs of two small defoliated trees show the branch architecture resulting from different levels of shoot mortality caused by *Dioryctria abovitella*. Measurements on trees A and B, respectively, are: 1983 shoot mortality, 30.4 and 0.9 percent; 1984 shoot mortality, 30.2 and 2.8 percent; age, 91 and 63 years; diameter, 10 cm above ground level, 15.3 and 16.8 cm; annual increase in trunk diameter, 1.68 and 2.67 mm; height, 1.74 and 3.20 m; annual increase in height, 19 and 51 mm; total 1984 male strobili bearing shoots, 1332 and 1776; total 1983 conelets, 0 and 209; total 1984 conelets, 0 and 319. [Photographs by Thomas G. Whitham]

Attacks of *D. albovitella* alter tree architecture and affect the sexual expression of host trees in future years. Although *P. edulis* is monoecious and produces both male strobili and female cones on the same tree, they are usually borne on separate shoots. Female cones are produced by the long terminal shoots near the top of the tree, and male strobili are produced by the shorter lateral shoots at the sides and base of the tree. Consequently, selective herbivory that alters the normal ratio of these cone and strobili bearing shoots will affect the sexual expression of the tree in future years. For example, Fig. 1D shows that conelet (cones less than 1 year old) production (*22*) declines to 0 with increasing shoot mortality ($r^2 = 59.0$ percent, $n = 40$, $P < 0.01$). The most heavily infested trees (7 of 20) failed to produce any conelets. Herbivory, by stimulating production of lateral male-bearing shoots relative to terminal female-bearing shoots, indirectly causes pinyons to halt femal cone production and become functionally male plants.

The impact of herbivory on cone production can be reversed experimentally. When stem borers were removed, more terminal cone-bearing shoots were produced, and female cone production once again resumed (Table 1). Although conelet production by control trees showed no significant changes between 1983 and 1984, on experimental trees the conelet production increased by 187 percent after herbivore removal ($t = 2.090$, d.f. = 4, $P = 0.05$).

During the three study years, trees less attacked by *D. albovitella* produced at least five times more surviving cones than heavily attacked trees. In 1983, a mast year, the total number of mature, undamaged cones averaged 20.7 ± 11.90 cones per tree for shrublike trees in comparison to 103.5 ± 30.94 cones per tree for upright trees ($t = 2.499$, d.f. = 38, $P < 0.01$). Although the cone crops in 1982 and 1984 were substantially lower, the same patterns held. Uninfested, upright trees produced 10.3 times more cones in 1982 and 8.2 times more cones in 1984 than infested shrublike trees ($t = 4.236$, d.f. = 38, $P < 0.01$; $t = 2.625$, d.f. = 38, $P < 0.01$, respectively). Since these measures of cone production span both low and mast cone production years, it appears that infested trees do not compensate for previous years of low cone production.

Although the most heavily infested trees lose their female cone-bearing function, they do not compensate for this loss by increasing production of male strobili. No statistically significant relation was detected between male strobili production and shoot mortality ($r^2 = 2.0$ percent, $n = 40$, $P >> 0.05$).

This acute and chronic herbivory by a native pest resulted in significant changes in plant architecture, reduced growth rates and cone crops, and caused a shift in sexual expression. Changes in these traits should have important evolutionary implications for the host (for example, evolution of resistance, allocation strategies for the use of plant defenses, or alteration of the mating system in which the cost of female function has increased relative to male function), the herbivore (for example, counter-adaptations against plant defenses), and the rest of the community (for example, the mutualistic relation between pinyon jay, the major seed disperser, and pinyon may be altered by the reduced cone crop). Since some plants suffer the negative effects of herbivory while others largely escape, the latter should enjoy greater reproductive success and realize a selective advantage.

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20. Because *D. albovitella* is sensitive to Cygon for only a brief time, insecticide applied 2 weeks later than optimum has little control effect. Five trees sprayed after the optimum for herbivore control showed no significant decline in herbivory the next year and no associated changes in bud and conelet production.
21. Analyses of soils (derived from volcanic ash and cinders) from the root zone show no significant differences in soil moisture or particle size between trees with different growth forms or infestation levels.
22. Although *D. albovitella* attacks and kills second-year cones, first-year conelets are not attacked. Thus censuses of conelets should accurately reflect cone initiation in the spring.
23. Author order was decided by a coin toss. We thank A. Mutuura for species confirmation and V. Artman, R. Balda, W. J. Boecklen, S. L. Cohn, D. Conklin, L. Floyd, L. von der Heydt, W. J. Mattson, A. Neas, M. Pederson, P. W. Price, K. Reinhard, A. M. Robinson, D. Takahashi, and M. R. Wagner for assistance in the field and commenting on the manuscript. Supported by USDA grant 84-CRCR-1-1443, NSF grant DEB-8005602, and Organized Research and the Bilby Research Center of Northern Arizona University. We thank the Forest Service for permission to conduct our studies in the Coconino National Forest.

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Major Glycoprotein Antigens That Induce Antibodies in AIDS Patients Are Encoded by HTLV-III

Abstract. *Antibodies from the serum of patients with the acquired immune deficiency syndrome (AIDS) or with the AIDS-related complex and from the serum of seropositive healthy homosexuals, recognize two major glycoproteins in cells infected with human T-cell lymphotropic virus type III (HTLV III). These glycoproteins, gp160 and gp120, are encoded by the 2.5-kilobase open reading frame located in the 3′ end of the HTLV-III genome, as determined by amino terminus sequence analysis of the radiolabeled forms of these proteins. It is hypothesized that gp160 and gp120 represent the major species of virus-encoded envelope gene products for HTLV-III.*

Human T-cell lymphotropic viruses (HTLV) are a group of exogenous retroviruses that have been implicated in a variety of clinical syndromes (*1–5*). HTLV-III, which is the probable etiologic agent of the acquired immune deficiency syndrome (AIDS) (*4, 5*) has several characteristics in common with HTLV-I and -II. These characteristics include an apparent tropism for OKT4$^+$T cells (*4, 6*), a reverse transcriptase with Mg^{2+} preference (*4, 7*), an ability to *trans-*

Table 1. 5′ Nucleotide sequence and predicted amino acid sequence of the HTLV-III envelope gene region. The HTLV-III sequence is derived from Ratner *et al.* (*17*). The dark arrow indicates the site for cleavage of the leader sequence from the envelope glycoproteins resulting in the protein species gp160 and gp120. Asterisks indicate cysteine, leucine, and valine residues determined by radiolabel sequence analysis. The first nucleotide presented corresponds to nucleotide sequence 5802 of the HTLV genome.

ATG	AGA	GTG	AAG	GAG	AAA	TAT	CAG	CAC	TTG	TGG	AGA	TGG	GGG	TGG	AGA	TGG	GGC	ACC	ATG
M	R	V	K	E	K	Y	Q	H	L	W	R	W	G	W	R	W	G	T	M^{20}
CTC	CTT	GGG	ATG	TTG	ATG	ATC	TGT	AGT	GCT	ACA	GAA	AAA	TTG	TGG	GTC	AGA	GTC	TAT	TAT
L	L	G	M	L	M	I	C	S	A ▼	T	E	K	L*	W	V*	T	V*	Y	Y^{40}
GGG	GTA	CCT	GTG	TGG	AAG	GAA	GCA	ACC	ACC	ACT	CTA	TTT	TGT	GCA	TCA	GAT	GCT	AAA	GCA
G	V*	P	V*	W	K	E	A	T	T	T	L*	F	C*	A	S	D	A	K	A^{60}
TAT	GAT	ACA	GAG	GTA	CAT	AAT	GTT	TGG	GCC										
Y	D	T	E	V*	H	N	V*	W	A										