MW. Unless there is an intermediate relatively oxidized horizon, these oxidation states probably persist into the upper mantle and down through the depleted lithosphere (*26*); thus native iron may also exist below the Moho. If so, then it must be temperature and the αFe-γFe crystallographic phase boundary, rather than temperature and the αFe-γ'Fe Curie point transition, that are the significant controls on the lower depth limit for iron ferromagnetism in the lithosphere. The αFe-γFe phase boundary (*27*) intersects the typical geothermal gradient of the continental shield at 75 to 80 km, but the deepest limit may be defined by a very low gradient geotherm—for example, the Sierra Nevada geotherm (*28*)—which intersects the αFe-γFe phase boundary at 90 to 95 km.

The granulites described here contain metallic iron, along with sulfides and graphite. These components, mitigated by grain contact and temperature (*29*), could contribute to the supposed high electrical conductivities of the lower crustal or upper mantle, explained (*30*) as being due to hydrous minerals or partial melting. The mafic granulite character, specific gravities, and the temperature, pressure, and V_p estimates correspond to model parameters (*31*) of the continental lower crust, but the extent to which native iron is present remains to be established, as does the precise mechanism that induced decomposition of iron-rich almandine garnet and ilmenite. Decomposition is not due directly to inclusion into the kimberlite because these gas-charged, CO_2-rich eruptives are moderately oxidizing and because mantle metasomatism is typically potassic (*32*), whereas the native iron–bearing granulite xenoliths are highly reduced and are sodium-enriched.

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33. Fieldwork was supported by the Weasua Mining and Development Corporation. Logistical support was provided by the Ministry of Lands, Mines, and Energy, Liberia, and by the embassies of the United States and the United Kingdom. NSF grant EAR83-08297 and NASA contract NAS5-26414 supported the analytical study.

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Ecological Effects of Salicin at Three Trophic Levels: New Problems from Old Adaptations

Abstract. *Salicin, a toxic phenol glycoside, is used by larvae of the beetle* Chrysomela aenicollis *as a substrate for producing defensive secretions. In the east-central Sierra Nevada mountains of California, salicin concentrations ranged from 0.05 percent to over 5 percent of dry weight in leaves of different plants of* Salix orestera, *the Sierra willow. Beetles produced more secretion and suffered less predation on willows containing more salicin. In addition, leaf damage due to herbivory among 16 willow clones ranged from 0 to 20 percent of leaf area and was linearly related to salicin content. These results illustrate how a plant secondary chemical can become a problem for the plant when herbivores are adapted to use the chemical for their own benefit. The results also show the effect of a plant chemical on three trophic levels—the producer, a herbivore, and the predators of the herbivore.*

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Secondary plant chemicals—those not necessary for primary metabolism—often serve as agents of plant defense, although they may solve other adaptive problems for plants as well (*1*). The repellent or toxic properties of these chemicals are well known (*2*) and have been shown to confer protection against herbivory under field conditions (*3*). Many insect herbivores effectively exploit secondary plant chemicals, using them to repel or poison their own predators (*4, 5*), to attract mates (*6*), and perhaps to exclude competitors (*7*). It is possible that some secondary plant chemicals are so useful to insect herbivores that the chemicals become a problem for the plant that produces them. Such a process may be very important in insect-plant coevolution, since it favors novel defensive compounds in plants and may thereby generate the tremendous diversity of compounds we see in present-day plants (*7, 8*). Here we report an increase in herbivory caused by salicin, a toxic phenol glycoside, in plants that produce large quantities of the compound. We also report the benefits of salicin for the herbivores under field conditions.

The evolution and ecology of salicin-exploiting chrysomelid beetles in the tribe Chrysomelini have been reported elsewhere (*9–12*). These beetles prefer food plants rich in salicin (primarily willows of the genus *Salix*), which is metabolized in dorsal glands to salicylaldehyde, which is stored and secreted by the glands, and glucose. The salicylaldehyde secretions are an effective deter-

rent against attacks by some ants (*9, 13*), and, like other volatile irritants, are probably effective against a wide range of arthropod predators (*5*).

We investigated a salicin-exploiting beetle, *Chrysomela aenicollis* (Shaeffer), at 2500 to 3500 m in the Sierra Nevada mountains of California (*14*). The beetles were feeding on several species of *Salix* and *Populus*, but were most common on *Salix orestera* and *Salix lasiolepis*, the most abundant willow species in the area. Most willows at this elevation grow in clumps. Individual branches in a clump were more similar in morphology and coloration than branches from different clumps (*15*), and we assumed that all the branches in a clump were from the same clone. Estimated salicin concentrations in leaves of *S. orestera* and *S. lasiolepis* clones ranged from 0.05 percent of dry weight to over 5 percent, a hundredfold range, whereas the standard deviation within clones varied less than twofold on average (*16*). Salicin production in individual clones remains constant or declines slowly during a season.

To investigate the possibility that a high salicin content could cause increased herbivory by *C. aenicollis*, we studied *Salix* plants in September 1983 along a 9-km trailside transect from 2660 to 3300 m above sea level. By this date, *C. aenicollis* had completed larval development at all but the highest elevations. Every 200 m along the transect, the nearest willow clone was examined for leaf damage and foliage was collected for chemical analysis. If no willows grew adjacent to the trail, no sample was taken. Our final sample consisted of 28 different willow clones, 21 from *S. orestera* and 7 from *S. lasiolepis*. To ascertain leaf damage, we collected ten twigs at random from the sampled clone and estimated the area of leaf damage (expressed as a percentage) for each. Feeding by *C. aenicollis* was easily quantified, and other damage was minimal. Collected foliage was dried and preserved for chemical analysis. Salicin content was determined by thin-layer chromatography (TLC) (*17*) and the results were checked by comparison with quantitative high-performance liquid chromatography (HPLC) (*18*). We also detected an unknown compound ("PG2"), probably a phenol glycoside, which we arbitrarily scored against our salicin standards (*19*). Proanthocyanidins (tannins) were also found (*20*).

Salicin content and leaf damage along the transect are compared in Fig. 1. For 3.8 km between 2700 and 3000 m elevation, herbivory was linearly related to salicin content (n = 16, b = 5.6, standard error = 1.6, $P < 0.0001$) (*21*). This zone contained dense willow populations growing along the valley floor. Above this elevation to 3200 m, the creek drainage was interrupted by a series of lakes and the willow stands were isolated into small patches. In this zone no linear relation between salicin content and herbivory was seen, suggesting that other factors, such as isolation and patch size, may override the effects of salicin content. Above 3200 m the willows were abundant in large patches, but *C. aenicollis* were few and had not completed their feeding owing to an extremely late snowmelt at that elevation (*22*). No statistically significant relation was observed or expected under these conditions. The two species of willow were equally variable in leaf damage and chemical content, and Fig. 1 indicates that herbivory in both species was similarly related to salicin content.

Between 2700 and 3000 m elevation, the relative amounts of PG2 were linearly related to salicin content (b = 0.93, standard error = 0.26, P = 0.0025). Since PG2 is probably a phenol glycoside related to salicin, it may also act as a substrate for salicylaldehyde production.

To determine the effects of a high salicin content on the survival of *C. aenicollis*, without the confounding effects of different physical and biotic environments, we located two clones of *S. orestera* growing side by side in boggy soil at 2850 m. One clone (R) had more reddish twigs and considerably less defoliation (2.1 percent, n = 20 branches) by *C. aenicollis* than the other clone (Y) with yellowish twigs (18.8 percent, n = 30 branches). The average salicin contents were <0.6 percent and 3.3 percent of dry weight, respectively. In August 1984 we isolated two branches of each willow clone using a commercial preparation of castor oil and natural gum resins (Tree Tanglefoot, Tanglefoot Company) to prevent ingress or egress by larvae of *C. aenicollis*. This procedure did not affect flying predators, such as *Ancistrocerus* species (Hymenoptera: Eumenidae), which we have observed to avoid salicylaldehyde secretions when attacking larvae. We then obtained ten intermediate-sized third-instar larvae of *C. aenicollis* from a willow clone at 3200 m, emptied them of salicylaldehyde se-

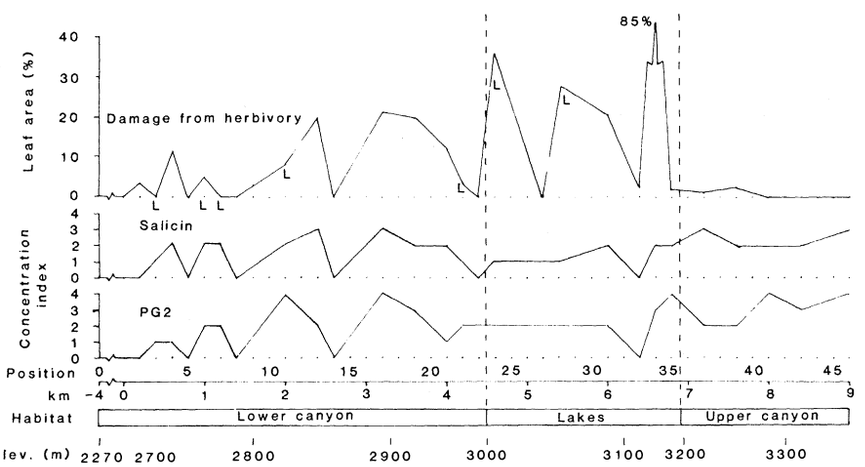

Fig. 1. Leaf damage and chemical content of willows growing along an elevation gradient in the east-central Sierra Nevada mountains. Sampling points were at 200-m intervals numbered 0 to 46; if no foliage was present none was collected. Data points indicated by L represent *S. lasiolepis*; otherwise they represent *S. orestera*.

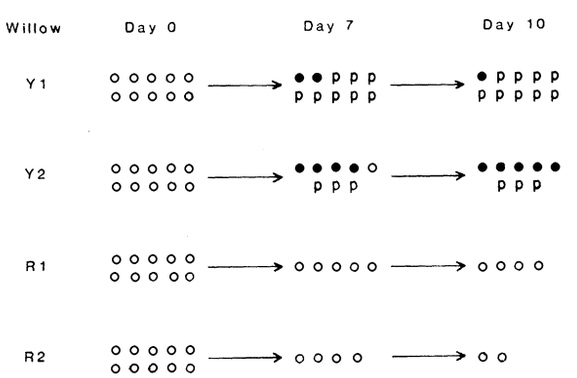

Fig. 2. Survival, developmental stage, and salicylaldehyde secretions of *C. aenicollis* on two clones of *S. orestera* at 2780 m. On each clone, two sets of ten third-instar *C. aenicollis* were emptied of salicylaldehyde, isolated by Tree Tanglefoot, and examined after 7 and 10 days for salicylaldehyde droplets (●), empty glands (○), or pupation (p). Absent larvae were probably taken by flying predators.

cretion by prodding gently with a needle, and placed ten of them on each of two branches of clones R and Y. After 7 and 10 days we counted the survivors, some of which had pupated. For surviving larvae we recorded whether or not they produced salicylaldehyde droplets when prodded gently with a needle. The results (Fig. 2) indicate that by day 10 more *C. aenicollis* larvae had produced the defensive secretion (100 percent versus 0 percent, $P = 0.0011$, Fisher's exact test), more had pupated (12 versus 0, $P = 0.0069$), and more had survived (90 percent versus 30 percent, $P = 0.0001$) when feeding on willows high in salicin (Y1 and Y2) than on those low in salicin (R1 and R2).

These results demonstrate the direct effects of salicin, a plant-produced secondary chemical, on the plant and herbivore trophic levels. The observed effect of salicin on salicylaldehyde production also suggests a strong effect on the predator trophic level. Salicin enhanced survivorship of the herbivores while having a negative effect on the plants and, presumably, the predators. This illustrates that, as predicted, chemical defenses can become a problem for plants that produce them.

It is not surprising that the negative effects of salicin were seen only at certain elevations. We predict such a situation to be evolutionarily unstable, favoring plants that have deleted the chemical from their defensive repertoire.The reson why some clones of *Salix* maintain high concentrations of salicin is not known. Our results suggest that one of the costs of salicin production is increased herbivory by *C. aenicollis*, and that these localized selective agents may be responsible for some of the observed variability in salicin content. Clones with low salicin occurred largely where beetle numbers are not restricted by cold environmental conditions, suggesting that these phenotypes may have been selected by prior bouts of intense herbivory. Willow clones live for very long periods but are nonetheless variable and can undergo intraclonal selection (*22*). Interclonal variation in salicin content was not observed at high elevations with reduced numbers of *C. aenicollis*. Salicin may defend plants against generalist herbivores (*9*), including deer (*23*), or may act as an antibiotic (*24*). The variability of the herbivore response to salicin concentrations at different elevations and the variability among willow clones in salicin content suggest a means for evaluating the evolution and ecology of certain plant-herbivore-predator interactions.

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14. Field sites were located along the north fork of Big Pine Creek, west of the town of Big Pine, Inyo County (37°7'N, 118°29'W), between 2200 and 3400 m above sea level.
15. There was great variation in twig coloration, stipule size, and bud size and coloration.
16. We measured salicin concentration in four clones of *S. orestera* and one clone of *S. Lasiolepis*, totaling 35 individual branches. Analysis of variance indicated that most of the variation present was between clones ($P < 0.0001$). Within clones, the standard deviation in salicin content averaged 36 percent of the mean.
17. Portions (200 mg) of dried leaves were extracted in 2 ml of distilled water for 24 hours. Serial 1:2 dilutions of extract were applied to silica gel TLC plates with microcapillary tubes. Plates were run in a solvent of methylene chloride and methanol (80:20), sprayed with potassium dichromate (3 mg/ml) in dilute sulfuric acid, and baked for 5 minutes at 120°C. Salicin was found at 0.32 relative to the solvent front (Rf). Quantitative estimates were obtained by comparing serial dilutions of extract and salicin standards (Sigma).
18. M. Rowell-Rahier analyzed two samples of *S. orestera* using HPLC and salicin standards. The quantities of salicin found (0.36 percent and 0.08 percent of dry weight in clones Y and R, respectively) were in agreement with our TLC estimates (0.32 percent and <0.24 percent, respectively).
19. The quantities of compound PG2 were similar to those of salicin, and PG2 migrated farther (Rf, 0.49) than salicin on our TLC plates. We estimated PG2 concentrations by comparison with the salicin standards.
20. This was determined by the gelatin precipitation and ferric chloride test. Proanthocyanidin contents were not correlated with salicin contents or with herbivory by *C. aenicollis*.
21. Leaf damage was regressed against concentrations of salicin and PG2, scored on a logarithmic scale: 0 (<0.63 percent), 1 (1.25 percent), 2 (2.5 percent), 3 (5 percent), and 4 (10 percent).
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Discovery of Sodium in the Atmosphere of Mercury

Abstract. *The spectrum of Mercury at the Fraunhofer sodium D lines shows strong emission features that are attributed to resonant scattering of sunlight from sodium vapor in the atmosphere of the planet. The total column abundance of sodium was estimated to be* 8.1×10^{11} *atoms per square centimeter, which corresponds to a surface density at the subsolar point of about* 1.5×10^5 *atoms per cubic centimeter. The most abundant atmospheric species found by the Mariner 10 mission to Mercury was helium, with a surface density of* 4.5×10^3 *atoms per cubic centimeter. It now appears that sodium vapor is a major constituent of Mercury's atmosphere.*

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Before the Mariner 10 mission to Venus and Mercury, it was expected that Mercury might have a thin but appreciable atmosphere. Argon, derived from potassium decay, and carbon oxides were favored species (*1, 2*). However, these expectations were not realized when Mariner 10 flew by Mercury. Broadfoot and colleagues (*3*) measured the Mercury atmosphere using the ultraviolet airglow spectrometer on Mariner 10. The only definite line emissions they found were from helium and atomic hydrogen. No other constituents were observed, with the possible exception of atomic oxygen, for which a signal at the limit of detection was found. Upper limits were derived for the densities of neon, argon, and carbon, which would have been detected had they been present in sufficient amounts. Final analysis of the spectrometer data yielded a value of 2×10^{-10} millibars (*4*) as the upper limit for the surface pressure of any atmospheric constituent.

We now report the discovery of sodium vapor in the atmosphere of Mercury. This element does not have strong resonance lines in the range of the Mariner 10 ultraviolet spectrometer, and consequently it was not detected by that in-