Bulldozers and Bacteria: The Ecology of Sweet Fern

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Comptonia peregrina, a common roadside plant in eastern North America, provides a case study both of how nature copes with disturbance to the land and of just how convoluted the study of this process can be.

Sweet fern, *Comptonia peregrina*, is a shrubby member of the Myricaceae, or bayberry family. Its common name is derived from the pleasing fragrance that its tiny, resin-filled, glandular hairs give off when crushed or rubbed, and from its coarsely lobed, somewhat fern-like leaves. *Comptonia*, a distinctly unprepossessing plant, has a natural range that covers a large portion of eastern North America. Forming a rough triangle, the eastern flank of this range extends from Prince Edward Island and Nova Scotia south into the mountains of north Georgia; the western edge reaches from the southern Appalachians north through Tennessee and Minnesota all the way to central Manitoba; and the northern edge runs from the Canadian plains through central Ontario and Quebec to the Atlantic (Elias 1971). Sweet fern typically grows to three or four feet in height and, over time, forms extensive colonies—up to twenty feet across—from suckers produced by its roots.

As to habitat, sweet fern shows a strong preference for dry, sandy soils with full exposure to the sun. These sites, which include dry, piney woods, exposed mountain slopes, abandoned pastures, pine barrens, highway bankings, gravel pits, weathered mine tailings, and cut-over forested land, have typically experienced some form of disturbance in either the recent or distant past (Schramm 1966; Schwintzer 1989).

Two attributes equip *Comptonia* for the pioneering role of a colonizer of disturbed soils. The first is its use of nitrogen gas from the atmosphere to produce nitrates—a feat it accomplishes by forming root nodules in symbiotic association with nitrogen-fixing bacteria. The second is an ability to propagate itself vegetatively by means of long, thick roots that run an inch or so beneath the soil surface. These shallow roots form numerous buds in the fall that grow into shoots the following spring. Under the right conditions, *Comptonia* behaves as a shrubby groundcover, spreading over large areas by means of these root suckers.

Historical Considerations

Sweet fern's distinctive form and pungent odor made a strong impression on the early European settlers of North America. Nowhere is this more apparent than in a passage from a book written in 1654 by one Edward Johnson, *Wonderworking Providence of Sion's Saviour in New England.* Johnson was presenting a secondhand account of the arduous journey made in 1636 by the first English settlers of Concord, Massachusetts, led by Captain Simon Willard. Starting from Boston, they traveled by boat as far as Watertown and then made their way overland, more or less following the meandering Charles River. Johnson describes (and undoubtedly embellishes) a scene in which the wearied pilgrims confront "a scorching plaine, yet not so plaine, but that the ragged bushes scratch their legs fouly, even to wearing their stockings to

The characteristics that inspired the common name sweet fern—tiny, resin-filled hairs and fern-like leaves—can be seen in this plate from Franz Schmidt's Osterreichs Allgemeine Baumzucht *(Vienna, 1792). The plant we know as* Comptonia peregrina *is labelled under a hybrid of the two names given it by Carolus Linnaeus in his* Species Plantarum. *It was Charles L'Heritier who demonstrated that the plant did not belong in either of the genera suggested by Linnaeus.*

their bare skin in two or three hours." Those without "bootes or buskings . . . have had the bloud trickle downe at every step." And injury was compounded when "the sun casts such a reflecting heate from the sweet ferne, whose scent is very strong, that some herewith have beene very nere fainting, although very able bodies to undergoe much travel."

John Josselyn's reference to sweet fern in his classic work *New-Englands Rarities Discovered*, written in 1672, is considerably more benign: "Sweet Fern, the Roots run one within another like a Net, being very long and spreading abroad under the upper crust of the Earth, sweet in taste, but withal astringent, much hunted after by our Swine: The Scotch-men that are in New-England have told me that it grows in Scotland." Josselyn was an astute observer, as his description of the spreading roots of the plant clearly indicates. His Scottish informants, however, were dead wrong; sweet fern is native only to eastern North America.

It was Carolus Linnaeus who assigned the first modern scientific name to sweet fern, which he did in *Species Plantarum*, published in 1753. Unfortunately, he confused the situation by accidentally giving the plant two names, *Liquidambar peregrina* on page 999 and *Myrica asplenifolia* on page 1024. Subsequent authors were left to choose which name to use. The currently accepted name of sweet fern's genus, *Comptonia*, was established in 1789 by the French botanist Charles L'Heritier, who demonstrated that the plant did not belong in either of the genera suggested by Linnaeus. L'Heritier's name commemorates Henry Compton (1632–1713), Bishop of London, a lover of trees and an early supporter of botanical research and exploration.

Linnaeus' student Peter Kalm, who may well have collected the specimens on which Linnaeus' original description was based, provided a particularly interesting reference to sweet fern in his book, *Travels into North America*, written in 1770. In this work, a report of his travels between 1747 and 1750, Kalm noted the medicinal use of sweet fern by indigenous people: "Among the Iroquois, or Five Nations, on the Mohawk River, I saw a young Indian woman, who by frequent drinking of tea had gotten a violent toothache. To cure it she boiled the Myrica aspleniifolia, and tied it, as hot as she could bear it, on the whole cheek. She said that remedy had often cured the toothache before." The medicinal use of sweet fern must have been widespread, given that later authors and travelers make frequent reference to its use not only by various tribes of Native Americans, but also by European settlers (Erichsen-Brown 1979).

William Bartram mentions sweet fern only once in his *Travels*, but more significantly, he offered it for sale in his famous *Catalogue of American Trees, Shrubs, and Herbaceous Plants*, published in 1783 (Fry 1996). In this broadside, Bartram listed sweet fern under a hybrid of the two Linnaean names, *Liquidambar Aspleni Folia*, noting that it grew on "Light dry sandy Ridges." Two years later, Humphrey Marshall produced the first detailed description of the sweet fern in his book, *Arbustrum Americanum*, also using Bartram's hybrid name, *Liquidambar asplenifolia*. Marshall's publication, which is considered the first book by an American about American trees and shrubs, brings to a close the early history of *Comptonia*. Later botanical authors continued tinkering with the name, but added little original information to the basic understanding of the plant itself.

Desperately Seeking Sweet Fern

My own involvement with sweet fern began in 1971 when I started working for the late Dr. John Torrey at the Harvard Forest in Petersham, Massachusetts, just after he had shifted the focus of his research from root physiology to nitrogen fixation. He selected *Comptonia* as his experimental subject and hired me to grow it in the laboratory. At that time, the symbiosis of legumes with the nitrogen-fixing *Rhizobium* bacteria was well understood, but almost nothing was known about nitrogen fixation by the so-called nonlegumes that form a symbiotic association with a totally different type of bacterium in the genus *Frankia*. When Dr. Torrey's project started, no one, despite seventy years of trying, had succeeded in isolating the causative bacterium from a nonleguminous root nodule or in culturing it independent of its host. This

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Sweet fern is seen with quaking aspen growing along Route 2 in Concord, Massachusetts

failure was the block that held up progress in researching the subject.

With an overabundance of enthusiasm and a dearth of experience, I was hired to bring sweet fern into the greenhouse—domesticate it, if you will—so that we could study the nitrogen-fixation process in a controlled environment. To cultivate *Comptonia* under laboratory conditions, we couldn't just dig up plants from the field because the roots were always contaminated with fungi and bacteria other than the one we wanted to study. No, Dr. Torrey insisted, we had to grow the plant from seed in sterile sand. In central Massachusetts, sweet fern's seeds, technically considered to be fruits, ripen around the fourth of July. They are light brown in color, four-to-five millimeters long, and, as they mature, they become enveloped in a burrlike structure that is covered with long, green bracts. The burrs are soft to the touch and give off a delicious, almost spicy scent when one rubs them between the thumb and the forefinger to extract the seeds.

Once we had managed to collect enough seeds to work with, the next hurdle was to get them to germinate. We tried all the standard techniques for stimulating seed germination in woody plants and all of them failed. Subsequent research with excised embryos grown in a sterile culture demonstrated that the failure resulted from the presence of chemical inhibitors located in the innermost seed coat. These inhibitors are not unique to *Comptonia.* In most temperate plants, however, chilling effectively counteracts the inhibitors—not the case with sweet fern seeds. It was only when Dr. Torrey suggested treating the seeds with gibberellic acid, a naturally occurring plant growth regulator, that we were able to get any of them to sprout. Eventually we learned that soaking scarified seeds in a dilute solution of gibberellic acid for twenty-four hours would produce up to

80 percent germination (Del Tredici and Torrey 1976). While these results were satisfying in that they allowed the research program to move forward, they were also frustrating because we could not relate the gibberellic acid treatment to the way the seeds behaved in nature.

The problem stumped me for some time. In four years of studying *Comptonia* I had examined thousands of plants all across New England but had never found a wild seedling. Invariably, every small plant I found was attached to a root that emanated from an established plant. For whatever reason, I never found *Comptonia* seedlings under an existing clump of sweet fern. In frustration, I stopped thinking about the problem of seed germination in nature until one day in the spring of 1976, on a walk in the woods in northwest Connecticut, I came upon a site where hundred-year-old white pines *(Pinus strobus)* had been clearcut and then bulldozed the autumn before. Among all the weeds and whatnot that were emerging, I was amazed to see seedlings of sweet fern growing, their cotyledons still attached. There were no adult plants to be found, just seedlings. In all, I counted 194 of them in an area of less than an acre (Del Tredici 1977).

According to my reasoning, these seedlings must have arisen either from dormant seeds buried in the soil (the so-called seedbank) or from seeds brought in by some dispersal agent. Given the relatively large size of the sweet fern seed and its lack of any specialized dispersal structures, transport by rain or wind could be ruled out; and its inconspicuous appearance and lack of fleshy coverings make dispersal by animals extremely limited. Indeed, the only animal ever reported to eat the sweet fern seeds is the yellow-shafted flicker *(Colaptes auratus)*, a ground-feeding member of the woodpecker family. One F. E. Beal examined 684 flicker stomachs in 1911 and found an undisclosed number of *Comptonia* seeds in one of them. However, in order to explain by animal dispersal the 194 seedlings that appeared just one year after clearcutting, one would need to postulate a sizeable flock of flickers roaming the countryside, eating sweet fern and defecating exclusively on this one acre in the woods.

The lack of any obvious dispersal mechanism left buried seeds as the only likely explanation for the seedlings in the Connecticut clearcut. The question was, how did they get there? In nature, most *Comptonia* seeds come to rest within a half meter of the parent that produced them and are soon buried in the leaf litter that collects beneath the plant. As I see it, deep chemical inhibition prevents germination for several years, by which time the seeds are well covered. The litter contributes to delayed germination either indirectly, by excluding light, or directly, by giving off specific chemicals that suppress germination. In either case, a buried seed will not sprout unless brought to the surface after its own internal dormant state has been neutralized. In the Connecticut woods where I found my sweet fern seedlings, this resurrection was facilitated, albeit inadvertently, by the state forester who upon completion of the logging operation had the whole area bulldozed to encourage the "natural" regeneration of white pine seedlings.

Clearly bulldozing was just what the sweet fern seeds needed. They had been deposited in the soil before the pines grew up, while the land was in pasture, and then germinated after the logging operation brought them to the surface. On the basis of ring counts of the cut pine trees, I estimated that the canopy of pines had closed about seventy years before I came on the scene, the point when sweet fern would have disappeared from the site because of insufficient sunlight. Seventy years, then, is a minimum estimate of the time the seeds could survive in the soil. I have no idea what the maximum is.

It is clear, however, that soil disturbance is an absolute requirement for the germination of *Comptonia* seeds. Henry David Thoreau made essentially the same observation in his journal on October 22, 1860: "I notice that the first shrubs and trees to spring up in the sand on railroad cuts in the woods are sweet-fern, birches, willows, and aspens, and pines, white and pitch; but all but the last two chiefly disappear in the thick wood that follows." All of the above species, save *Comptonia,* have wind-dispersed seeds that exhibit no capacity for long-term survival in the soil. Clearly sweet fern's buried seed

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Sweet fern in fruit at the height of summer.

strategy, which evolved in response to natural disturbance such as fire and erosion, had adapted well to the human-induced changes of the twentieth century. Sweet fern, as a pioneer species, can play an important role in revitalizing land that has been traumatically stripped of its plant cover.

Nitrogen Fixation

Eventually, after seven years of work, Dr. Torrey's research team succeeded in isolating the bacterium that is responsible for nitrogen fixation in *Comptonia*. Using gibberellic acid to stimulate germination, we were able to produce abundant nodule growth on vigorous seedlings that were grown with their roots dangling in a nutrient mist (aeroponics). This system, unlike water culture (hydroponics), allowed the plant roots to develop the hairs through which the bacteria penetrated the root itself (Zobel et al. 1974). By repeatedly subculturing the nodules from one mist box to the next, we eventually were able to produce "clean" nodules that were relatively free of other microbial contaminants (Callaham and Torrey 1977; Bowes et al. 1977). These nodules were then surface-sterilized, macerated together with special digestive enzymes, and incubated on an elaborately formulated nutrient agar. After three weeks of culture, Dale Callaham, who did the isolation work, observed several small colonies of bacteria with filamentous growth. While the unusual morphology of this organism clearly resembled that of an actinobacterium, it was unlike any that had been previously described. It was not until we had obtained a second generation of functional nodules by re-innoculating fresh *Comptonia* seedlings with a culture of the isolated bacterium that we knew we had the real thing.

This conclusion was corroborated when we isolated the filamentous bacteria from the second-generation nodules and found them to be identical to those of the first generation. It was only by following this elaborate procedure—referred to as fulfilling Koch's postulates—that we could prove that we had the causative organism in hand. These successful results, published

A micrograph of the Frankia *bacteria showing its long, branching filaments under Nomarski phase interference optics at a magnification of 1500x*

in 1978, marked the conclusion of nearly seventy years of frustrated attempts to isolate a *Frankia* bacterium from its host plant.

This breakthrough opened wide the floodgates of research on actinorhizal plants, whose important role in colonizing bare, nutrient-poor ground was just starting to be appreciated. Most of the nitrogen fixed by these plants enters the nutrient cycle slowly through the decomposition of fallen leaves, twigs, branches, and fine roots, but over time the contribution of actinorhizal plants to the total ecosystem nitrogen budget can be substantial. Research on red alder *(Alnus rubra)* in the Pacific Northwest, for example, has shown that pure stands of the tree can add up to 280 pounds of nitrogen per acre per year to the forest (Schwintzer and Tjepkema 1990). It is important to keep in mind, however, that nitrogen-fixing plants can typically hold their own against competition only when soil conditions are poor. On fertile ground they seem to lose some of their competitive advantage to other trees and shrubs. In a very real sense, nitrogen-fixing plants sow the seeds of their own replacement by elevating the nitrogen content of the soil.

Propagation and Cultivation

Sweet fern's ability to propagate itself from root suckers is another important component of its colonization strategy. Once the plant gets a foothold in a location to its liking, it comes to dominate the area by sending up numerous root suckers. The ever-observant Henry Thoreau made note of this on March 18, 1860: "The sweet fern grows in large, dense, more or less rounded or oval patches in dry land. You will see three or four such patches in a single old field. It is now quite perfect in my old bean-field."

William Bartram's 1783 offering of sweet fern notwithstanding, the plant has never made much of an impression in the nursery industry. There are several reasons for this, not least the plant's reputation for being difficult to propagate. Germination from seed, as shown above, is virtually impossible, and digging the plant up from the wild is seldom successful, given the ropy nature of its root system. It wasn't until the early 1970s that a research team at the University of Massachusetts, Amherst, developed techniques that allowed for the plant's commercial production (Hyde et al. 1972).

The authors of that study were seeking to identify plants that would rapidly cover highway bankings, and sweet fern was one of the plants that interested them. They designed an experiment to determine both the best time of year to take root cuttings as well as their optimal size. Two different-sized cuttings were collected twice a month for a period of one year: three inches long by one-quarter-inch diameter and three inches long by one-eighth-inch diameter. Forty-five days after the cuttings had been stuck in individual pots, they were checked to see whether they had produced leafy shoots.

No significant difference was found in the number of shoots produced by the two different cutting sizes over the course of the year, but the time of cutting was highly influential. At least

80 percent of the root cuttings taken between February 24 and May 1 produced shoots, while those taken between May 15 and August 1 produced few or no shoots. Cuttings taken between August 15 and December 10 produced good-to-poor percentages of shoots, depending on the date the cuttings were made. (No cuttings were taken between December 10 and February 24 because the ground was frozen.) Based on these results, the authors recommended that root cuttings be taken before the parent plant started to leaf out, around May in the Boston area. Root cuttings made after the stock plant's leaves emerged produced shoots in very low percentages. Their observations clearly suggest the existence of an inhibitory hormone produced by the leaves that suppressed the development of the root buds into shoots.

Landscape Uses: A Community Approach

Frank Egler, working with researchers at the Connecticut College Arboretum in New London, was among the first to recognize the potential role that sweet fern, as well as other suckering shrubs, could play in the formation of low-maintenance, naturalistic plantings along highway bankings and power company rights-of-way (Kenfield 1966; Niering and Goodwin 1974). In the course of their studies of old-field succession in the Northeast, the authors developed techniques—specifically the use of herbicides to selectively kill trees—to "arrest" the successional process at the shrub stage of development. Their goal was to manage existing vegetation to form a distinctively beautiful, low-growing landscape that would not interfere with power lines or highway sightlines. In New England, these low-maintenance associations commonly include, along with sweet fern, the following woody plants: pitch pine *(Pinus rigida)*, red cedar *(Juniperus virginiana)*, gray birch *(Betula populifolia)*, meadowsweet (*Spirea* sp.), bayberry *(Myrica pensylvanica)*, sumacs (*Rhus* sp.), low and highbush blueberries *(Vaccinium angustifolium* and *corybosum)*, and quaking aspen *(Populus tremuloides)*.

The University of Massachusetts group took the Connecticut College concept further by working out specialized techniques for actually planting—as opposed to simply managing—the shrub cover on fresh roadcuts and bankings. The authors found that root pieces of sweet fern could be stuck directly into a bare bank in early spring. According to recommended procedure, root cuttings of *Comptonia*, which can be anywhere from one-sixteenth to one-quarter of an inch in diameter and four to six inches long, should be planted an inch deep and six inches apart and mulched with two to three inches of wood chips. If this "direct stick" procedure is followed, sweet fern will produce a closed, weed-resistant canopy within three to six years.

A Pathological Problem

The final chapter in the *Comptonia* story pits one plant against another in a battle to the death. It concerns a disease that I became aware of only after publishing an article advocating sweet fern for landscape use. To my surprise, several plant pathologists wrote to chide me for my recommendation. Sweet fern, it turns out, is the alternate host of a fungus, *Cronartium comptoniae*, that causes sweet fern blister rust on hard pines with needles in bundles of two or three. In the Northeast, jack pine *(Pinus banksiana)* and pitch pine *(P. rigida)* can be infected, as well as other introduced hard pines. In the South, shortleaf pine *(P. echinata)* and loblolly pine *(P. taeda)* can be seriously infected.

During the course of its life cycle the blister rust has two hosts, the susceptible pine species and either sweet fern or its swamp-dwelling relative, sweet gale *(Myrica gale)*. The fungus lives one stage of its life on the leaves of the sweet fern and the second inside the stem of the pine tree. Although *Comptonia* is only slightly affected by the fungus, the susceptible pine can be seriously damaged or even killed.

Control of the disease is difficult, given sweet fern's wide natural range, but the forestry literature makes a few simple recommendations, including taking care not to plant infected pine trees and clearing out sweet fern colonies within a quarter mile of any commercial hard pine plantation. In a report on the susceptibility of loblolly pine to sweet fern blister rust, J. D. Artman and T. N. Reeder (1977) observed that sweet fern "may become a major ground cover when dry sites are intensively prepared for planting." What the authors mean by intensive

A few last leaves cling to the stems of Comptonia peregrina *even through the snows of winter.*

site preparation is, of course, bulldozing before planting trees. This observation, buried deep within a technical report, confirmed once again the intimate relationship between *Comptonia* and catastrophic disturbance.

Conclusion

No discussion of *Comptonia* would be complete without saying something about its effect on the human senses. As the first settlers of Concord learned all too well, the scent of *Comptonia* on a warm summer's day can be overwhelming—a thick, resinous pungency that borders on the unpleasant. More spicy than sweet, the warm scent conjures up the fullness of summer, which no doubt explains why *Comptonia* foliage is often dried for use in sachets and potpourris. I suspect, too, that the use of *Comptonia* as tea by Native Americans and Europeans may have had as much to do with its pleasing fragrance as with its supposed medicinal attributes.

A second trait of sweet fern, one that catches the eye rather than the nose, is its tendency to hold onto its leaves late into the growing season. Even in the middle of winter one can find a few leaves clinging to the stems of the plant. Thoreau described this feature in his journal entry for January 14, 1860, along with his response to it: "Those little groves of sweet-fern still thickly leafed, whose tops now rise above the snow, are an interesting warm brown-red now, like the reddest oak leaves. Even this is an agreeable sight to the walker over snowy fields and hillsides. It had a wild and jagged leaf, alternately serrated. A warm reddish color revealed by the snow." And finally, in a passage that moves from mundane detail into emotional description, Thoreau writes of the sweet fern stem, densely covered with fine hairs: "As nature generally, on the advent of frost, puts on a russet and tawny dress, so is not man clad more in harmony with nature in the fall in a tawny suit or the different hues of Vermont gray? I would fain see him glitter like a sweet-fern twig between me and the sun" (October 16, 1859).

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