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The buried seeds of *Comptonia peregrina*, the Sweet Fern

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DEL TREDICI, PETER (Harvard Univ., Cabot Found., Petersham, Massachusetts 01366). The buried seeds of *Comptonia peregrina*, the sweet fern. Bull. Torrey Bot. Club 104: 270–275. 1977.—Seedlings of *Comptonia peregrina* (L.) Coult., were observed coming up one year after the clear-cutting of a 100-year old stand of *Pinus strobus* L. in northwest Connecticut. Given that the fruits of *Comptonia* are very dormant and that they lack any obvious means of dispersal, germination from buried fruit is seen as the only satisfactory explanation of their presence. The fruits retained their viability in the soil for a minimum of 70 years. Seedlings of many other species were also noted in the clear-cut, many of which also came from buried seed. The role of seeds buried in forest soils is discussed.

During the summer of 1976, the author watched a forest community, consisting mainly of old-growth white pine (*Pinus strobus* L.), change in response to clear-cutting. Especially noteworthy among the plants coming up were numerous seedlings of *Comptonia peregrina* (L.) Coult., the sweet fern, which, in 4 years of field work by the author, had never before been seen.

This paper is concerned with examining the conditions that led not only to the appearance of the *Comptonia* seedlings, but also to the appearance of seedlings of many other species. Did they come from seeds that invaded the area after the logging operation, or did they come from seeds deposited in the soil during an earlier stage of forest development?

PREVIOUS STUDIES. Weed seeds buried *in situ* in agricultural soils have been extensively studied. See review by Roberts (1972). Controlled seed burial experiments have also been done, most notably, an 80 year test started by Beal (Darlington and Steinbauer 1961), a 40 year test by Duval (Toole and Brown 1946), and a 20 year test by Goss (1924). In Denmark, Ødum (1965, 1974) used a combination of observational, experimental and archeological techniques to study buried seed.

Studies of seeds buried in North American forest soils have been made by Oosting and Humphreys (1940) in North Carolina, Olmstead and Curtis (1947) in Maine woods, Leavitt (1964) in central Massachusetts and Livingston and Allessio (1968), also in central Massachusetts. In these studies, most of the germinating buried seed species were herbaceous. The only arborescent species known to germinate from buried seed is the pin cherry (*Prunus pensylvanica*) (Marks 1974). The dormancy mechanisms of buried seeds have been studied by Wesson and Wareing (1969), and reviewed by Roberts (1972).

Methods. STUDY AREA. Field work was done at the Gold Pines (Housatonic State Forest), located in the extreme northwest corner of Connecticut, a hilly area with peaks averaging 400–500 m. The Gold Pines occupy about 16 ha on the north slope of Green Mountain, 2 km west of the village of West Cornwall on the south side of State Highway 128, (see U.S.G.S. map: Cornwall, Conn. 7.5 min. 1956). The soil in the area is classified as part Hinckley gravelly sandy loam, 3 to 15% slopes, and part Paxton very stony fine sandy loam, 15 to 35% slopes (Soil Survey, Litchfield County, Conn. U.S.D.A., Soil Conservation Service 1970).

Two small plots, totalling approximately 5000 m^2, within the State Forest were clear-cut (except for a few seed trees) during June and July, 1975. After the logging, the whole area was bulldozed ("site preparation") in an attempt to encourage the natural regeneration of white pine. This was done on September 3,

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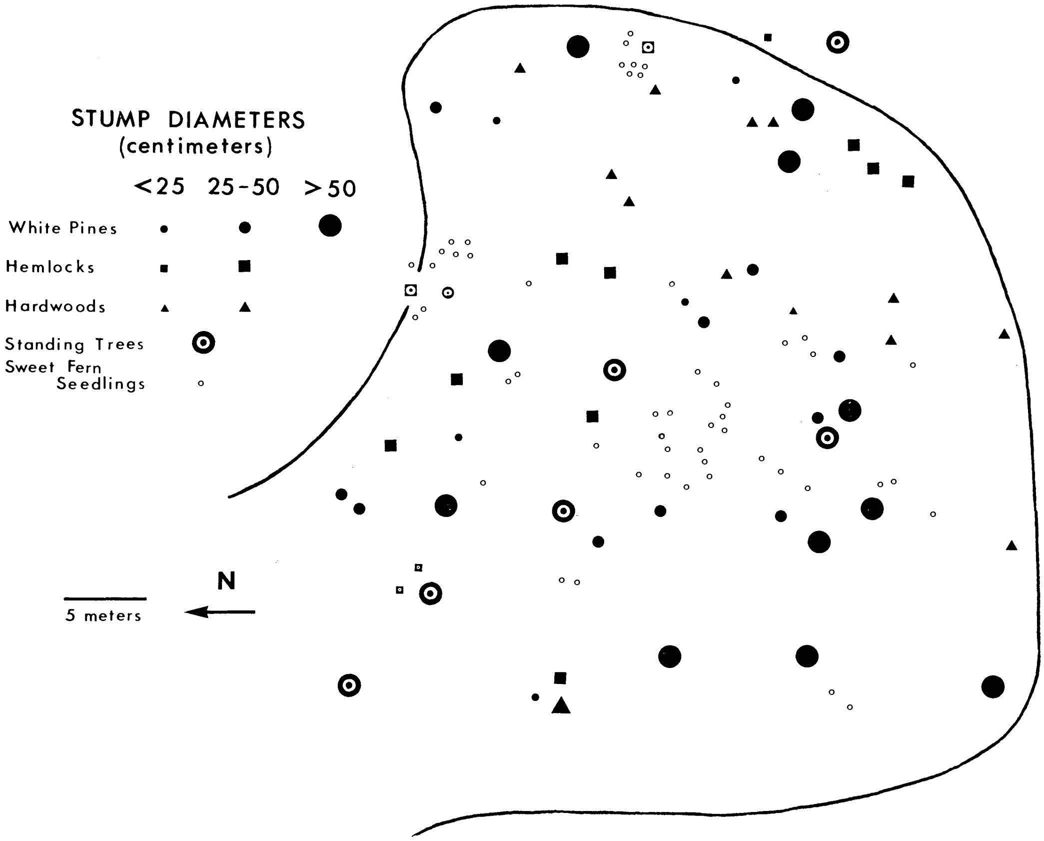

Figure 1. The upper cut in the Gold Pines, between elevation 310 and 320 m, with an area of 2100 m^2. The basal area of the stand, at stump level, was 48.6 m^2/ha.

4, 5, 1976, and involved scraping away a 5–10 cm thick layer of pine and hemlock needles that covered the area, so as to expose mineral soil (G. Brown, personal communication).

The two clear-cut sites have had slightly different histories. The lower cut, between altitudes 270–280 m, was thinned in 1965, without any subsequent site preparation. Consequently, in 1975, there was a preponderance of the stumps of small hardwoods and hemlocks that had been released from suppression by the 1965 thinning. This is the typical New England sequence of hardwoods replacing white pine after logging (McKinnon *et al.* 1935).

In the upper cut (Fig. 1), between altitude 310–320 m, there was a completely closed canopy of old growth white pine, with a minimal hemlock-hardwood understory. The area had been undisturbed for many years prior to the 1975 cutting. The freshly cut stumps showed ages from 96 to 124 years. In general, their first 30 years showed suppression, but rapid growth ensued thereafter, indicating that the canopy has been closed for the last 70 years.

Records show that the Gold Pines were part of a farm started in 1750. A stone wall near the northern boundary of the upper cut indicated that the land was cleared at some point. Since the land is not particularly well suited to farming and ploughing, it was probably once a pasture, then abandoned for woodlot use.

OBSERVATIONS. During the summer of 1976, both clear-cut areas were walked over in a back and forth pattern and all the plants that were coming up as seedlings were counted and listed. Annuals and biennials were assumed to be seedlings; perenials were considered seedlings only if the cotyledons were present.

The plants in the woods surrounding the clear cuts, for approximately 100 m on all sides, were also surveyed. These woods were by no means uniform in their age or appearance. Some stands were 30 to 40 years old while others were well over 100.

Results and discussion. Evidence for the long term survival of *Comptonia* fruits comes from two sources: field observations during the summer of 1976 and laboratory researches with the fruit from 1972 to 1976.

LABORATORY STUDIES. The published laboratory work (Del Tredici and Torrey 1976) will be summarized below and some new data will be added. In *Comptonia* the "seed" is really a nut-like fruit (Elias 1971). The embryo is surrounded by a thin testa and enclosed by a pericarp composed of a soft thin outer layer and a sclerified inner one. 50 viable fruits averaged 5.1 mm in length and 0.017 g in weight. When ripe, in July, the slightest disturbance of the plant, either by animals, wind or rain, will cause the fruit to fall. The heavy fruits always fall straight down into the litter that collects beneath the parent plant (Fig. 2). Their viability can be ascertained by a simple float/sink test, in which fruits with fully developed embryos settle to the bottom of a beaker of water, while empty fruits float to the top. Of 12,373 fruits tested, 63% contained embryos.

Comptonia fruits are difficult to germinate because of a chemical inhibitor localized in the testa. Standard seed treatments failed to yield any germination. Soaking the fruits in gibberellic acid, however, did elicit up to 52% germination in intact fruits. Furthermore, removal of the pericarp and testa and culturing under aseptic conditions yielded 90% germination in the absence of exogenous GA_3. 500 fresh viable fruits planted in sand in a cool greenhouse (a permanent thermostat setting of 4°C) gave 3% germination after one year (or 1.6% taking non-viable fruits into consideration).

FIELD DATA. In 4 years of work, the author never found a wild seedling, despite the fact that thousands of plants across New England had been examined (*Comptonia* usually spreads by means of root suckers). In the Gold Pines' clear-cuts, however, there were 194 of them. Either these seedlings sprang up from buried fruits or from fruits brought in by some dispersal agent. Given its relatively large size and the lack of any specialized dispersal structures, transport by rain or wind must be ruled out. The vast majority of *Comptonia* fruits come to rest within a half meter of the parent that produced them. The only animal ever reported to eat sweet fern fruits is the flicker, *Colaptes auratus,* a ground feeding member of the woodpecker family (*Picidae*). Beal (1911) examined 684 flicker stomachs and found an undisclosed number of *Comptonia* fruits in one of them.

Attempting to explain the presence of the 194 *Comptonia* seedlings by flicker dispersal leads to some implausible conclusions. Given the germination rate of 1.6%, 12,125 intact fruits would have to have been deposited by the birds in July (when the fruits ripen) in order to produce 194 seedlings. The estimate does not take into consideration fruits damaged in the digestive tract or pushed off to one side during the September bulldozing. Clearly, burial, not animal dispersal, provides the better explanation. Given that the canopy in the upper cut was closed for at least 70 years before cutting, this figure serves as a minimum estimate of the duration of the burial period.

Traditionally, sweet fern has been considered a pioneer species. It is not an invasive pioneer in the way that weeds with wind dispersal fruits are. Rather, its fruits persist in the soil for many years until some disaster uncovers them. Over 100 years ago, H. D. Thoreau noted in his journal (Oct. 22, 1860) that sweet fern was one of the first plants to come up in the sand along railroad cuts in the woods, clearly indicating that the plant's fondness for man-made disturbances is nothing new. Nowadays, *Comptonia* is found along highway cuts, where a hill has been intersected and erosion has exposed its buried seeds.

Lutz and Cline (1956), studying the natural regeneration of white pine, found sweet fern coming up in an experimental clear-cut, where the slash had been burned (p. 55). Interestingly, sweet fern was absent from cut-over areas where burning had not occurred. Most likely, burning the slash stimulated *Comptonia* germination by removing the litter layer that covered the seeds and prevented their germination.

One can only speculate as to the mechanism that allows *Comptonia* fruits to remain dormant in the soil for long periods. The chemical inhibition of the fruits wears off after an undetermined length of burial. By that time, however, the seeds are well covered by the litter that collects under a *Comptonia* bush (Fig. 2). The litter may be exerting an inhibitory influence indirectly by excluding light or directly by giving off specific allelotoxins to prevent germination. In either case, the buried fruits will not germinate unless brought to the surface *after* its own internal dormancy mechanisms have been overcome. In *Comptonia,* burial seems to be a requirement for germination.

OTHER BURIED SEEDS. In the Gold Pines' clear cuts, 74 species (nomenclature after Fernald 1950) were coming up as seedlings. These seedlings were counted (for wind dispersal plants, the exact number is in brackets after the name) and organized into the following 5 categories: (A) Species noted in the 100 m of uncut woods surrounding the clear-cut sites—presence most likely due to recent invasion: *Acer pensylvanicum, Acer rubrum, Acer saccharum, Aster divaricatus, Betula lenta, Betula papyrifera, Carex sp., Circaea alpina, Epilobium coloratum, Eupatorium rugosum, Galium triflorum, Liriodendron tulipifera, Lonicera sp., Pilea pumila, Pinus strobus, Prunus serotina, Quercus prinus, Quercus rubra, Rosa multiflora, Rubus sp., Sambucus canadensis, Tsuga canadensis, Viola sp., Vitis labrusca.* (B) Species absent from the surrounding woods with seeeds adapted for wind dispersal: *Anaphalis margaritacea* (1), *Betula populifolia* (1), *Cirsium vulgare* (18), *Erechtites hieracifolia* (309), *Erigeron canadensis* (13), *Eupatorium perfoliatum* (3), *Gnaphalium obtusifolium* (38), *Hieracium pratense* (8), *Taraxacum sp.* (2), *Trifolium agrarium* (2). (C) Species classified are RARE (< 5 individuals) in either the upper or lower cut, and which did not fit (A) or (B)—presence most likely due to random dispersal: *Adlumia fungosa, Chelidonium majus, Cinna arundinacea, Corydalis sempervirens, Houstonia caerulea, Linaria vulgaris, Lychnis alba, Oenothera biennis, Panicum linearifolium, Potentilla argentea, Sphenopholis nitida, Veronica serpyllifolia.* (D) Species classified as FREQUENT (5 to 15 individuals) in either the upper or the lower cut and which did not fit (A) or (B)—presence most likely due to buried seed: *Acalypha virginica, Arabis glabra, Cerastium vulgatum, Chenopodium hybridum, Chrysanthemum leucanthemum, Lechea tenuifolia, Panicum capillare, Polygonum persicaria, Rhus sp., Setaria glauca, Solanum nigrum, Trifolium pratense.* (E) Species classified as ABUNDANT (> 15 individuals) in either the upper or lower cut and which did not fit (A) or (B)—presence definitely due to buried seed (Table 1).

Figure 2. A *Comptonia* clump, in winter, growing in sand along a Massachusetts highway. Note the debris that collects beneath the plant.

It is possible that some of the plants noted in the lower cut in 1975 may have come from seeds of plants that came in with the 1965 thinning. Sizeable openings were created in 1965, but uncut understory trees filled those gaps quickly. Furthermore, there was no site preparation that would have uncovered buried seeds. These facts suggest that invasion by weedy species in 1965 was probably minimal.

A few of the species in Table 1 were susceptible to effective animal dispersal (*Phytolacca americana, Panicum villosissimum, Trifolium sp.*) as well as being capable of long term survival in the soil.

Table 1. Species definitely germinating from buried seed in the clear-cut areas of the Gold Pines. ABS = absent, FREQ = frequent, ABUN = abundant. See text for definitions and explanation.

Species[a]	Frequency in upper cut	Frequency in lower cut	Reference to buried seed habit[d]
Comptonia peregrina	ABUN (52)[b]	ABUN (142)[c]	
Cyperus strigosus	ABUN	RARE (1)	(10)
Hypericum perforatum	ABUN[c]	FREQ	(9), (10)
Juncus tenuis	ABUN	ABUN	(9), (10)
Lobelia inflata	ABUN[c]	ABUN[c]	
Oxalis europaea	ABUN	ABUN[c]	
Panicum villosissimum	ABUN	FREQ	(17)
Phytolacca americana	ABUN	ABUN[c]	(8), (15), (21)
Potentilla norvegica	FREQ	ABUN[c]	(8), (9), (10), (21)
Potentilla simplex	ABUN[c]	ABS	
Rumex acetosella	ABUN	ABS	(9), (10)
Specularia perfoliata	ABUN	RARE (2)	(17)
Trifolium hybridum	ABS	ABUN	(8), (21)
Trifolium repens	ABUN	ABS	(8), (9), (10), (15), (21)
Verbascum thapsus	ABUN[c]	ABUN[c]	(2), (8), (10), (15), (17), (21)
Veronica officinalis	ABUN[c]	ABUN[c]	(9)

[a] Nomenclature after Fernald (1950).
[b] Numbers in brackets indicate an exact count.
[c] More than 100 individuals present.
[d] See numbers in front of references.

While it is impossible to determine which individuals of these species came from fresh seed and which from buried seed, it is clear that an abundance of seedlings on bare ground in the woods cannot be attributed solely to animal dispersal.

Table 1 makes possible some interesting comparisons which strengthen the buried seed argument: (1) In the lower cut, the most abundant wind dispersal plants were *Erechtites hieracifolia* (290 plants) and *Cirsium vulgare* (12 plants). In the upper cut *Gnaphalium obtusifolium* (28 plants) and *Erechtites* (19 plants) were the most abundant. Except for *Erechtites* in the lower cut, *Comptonia* was more abundant than any of the wind dispersed plants, an impressive record, given its total lack of dispersal mechanisms. Many other plants from Table 1, lacking in long range dispersal mechanisms (*Lobelia inflata, Verbascum thapsus, Specularia perfoliata,* etc.), were also more abundant than the wind dispersed plants. (2) Among the various clovers, *Trifolium repens* was ABUNDANT in the upper cut and ABSENT in the lower cut. *Trifolium hybridum* had an opposite distribution. *Trifolium pratense* was FREQUENT in both sites. It is easier to explain these, and other, nonrandom distributions (the two cuts are separated from each other by about 150 m of woods) by assuming different land use histories (and hence different buried seed populations) than it is by assuming different dispersal agents. (3) *Rumex acetosella* was ABUNDANT in the upper cut and ABSENT in the lower cut. All members of the genus *Rumex* that occur in the northeastern U.S., except *Rumex acetosella,* have enlarged sepals (Fernald 1950) that facilitate wind dispersal (Ridley 1930). Thus, in a family well adapted for wind dispersal, the only member lacking such adaptations is the only one found coming up in the Gold Pines.

Conclusions. This paper is the first study of the behavior, under field conditions, of seeds buried in North American forest soils. All earlier studies have limited themselves to the greenhouse behavior of buried seeds. From the study, it is clear that in cases involving large scale, severe disturbance in a wooded area, pieces of rhizomes, buried seeds and seeds from surrounding plants grow up in the area initially. Wind dispersed plants from outside the area are not particularly abundant. After one year, the site is covered with vegetation, and subsequent vegetational change tends to be a reflection of the different growth rates of these initial invaders and survivors. Egler (1954) was the first to propose such "initial floristic composition" as a major factor in old field successions. Drury and Nisbet (1973) extended this basic concept. The situation at the Gold Pines appears to support initial floristic composition, although, after only one year, it is still too soon to be certain.

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