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ON THE GERMINATION OF SEEDS OF COMPTONIA PEREGRINA, THE SWEET FERN

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Fruits of the sweet fern, *Comptonia peregrina* (L.) Coult., possess a hard, resistant, sclerified pericarp which surrounds a membranous seed coat or testa which in turn encloses the embryo. Scarification of the fruit, low-temperature treatment of moistened fruits, and a variety of chemical treatments failed to elicit seed germination. Treatment of the whole fruit with 500 ppm gibberellic acid (GA_3) for up to 24 h elicited 20% germination, which increased to as high as 80% when combined with scarification. Mechanical removal of the pericarp did not allow germination; removal of both pericarp and the seed coat membranes resulted in good germination. Best germination was obtained with isolated embryos treated with 1–10 ppm GA_3. The age of the fruit in storage had no effect on development of the isolated embryo but did affect the response of intact seeds to treatment with GA_3. Fruits of *Myrica gale* L. and *M. cerifera* L. showed improved germination following GA_3 treatment. An inhibitor in the seed coat of *Comptonia*, possibly abscisic acid, was believed to be responsible for fruit dormancy in this plant.

Introduction

Comptonia peregrina (L.) Coult., the sweet fern, is a perennial shrub of the family Myricaceae. It is a common roadside plant throughout eastern and central North America. In the field, the plant is characterized by its highly aromatic leaves and its marked preference for growing in poor soils and full sun. The plant is used to stabilize sloping banks of fresh or badly eroded road cuts (Hyde, Troll, and Zak 1972). *Comptonia* sprouts readily from its wide-ranging horizontal roots; it can spread quickly and easily over a large area. Further, because of a symbiotic relationship with an unidentified actinomycete that forms root nodules, the plant can fix atmospheric nitrogen (Ziegler and Huser 1963), which is responsible for its ability to grow well in poor soils. In this character, *Comptonia* resembles its close relatives of the genus *Myrica*.

Comptonia is propagated commercially by root cuttings, a relatively easy and efficient method, because the seeds of sweet fern are notoriously difficult to germinate. Repeated efforts by numerous investigators, reported to us informally, have failed to yield a significant degree of success with seed germination. Over a period of 4 yr we have never found seedlings in the field, indicating that germination in nature is uncommon. Heino (1961), working with *Comptonia* in Minnesota, succeeded in germinating excised embryos grown in sterile nutrient medium. She found that seed germination was inhibited by the seed coats. Attempts to achieve germination by prior soaking of seeds in concentrated sulfuric acid, a solution of zinc chloride in concentrated hydrochloric acid, hot water treatment, or prolonged low-temperature stratification failed. Heino (1961) found that by dissection, after soaking seeds for 1–2 days in water, fruit and seed coats could be removed and the excised embryo would grow readily in nutrient culture. She concluded that the inner seed coat was impervious to water and prevented seed germination.

As a result of class experiments with difficult-to-germinate seeds of woody species, we found that seed germination could be achieved in *C. peregrina* by treating the fruit with gibberellic acid (GA_3). Studies of this hormone-dependence for seed germination are reported.

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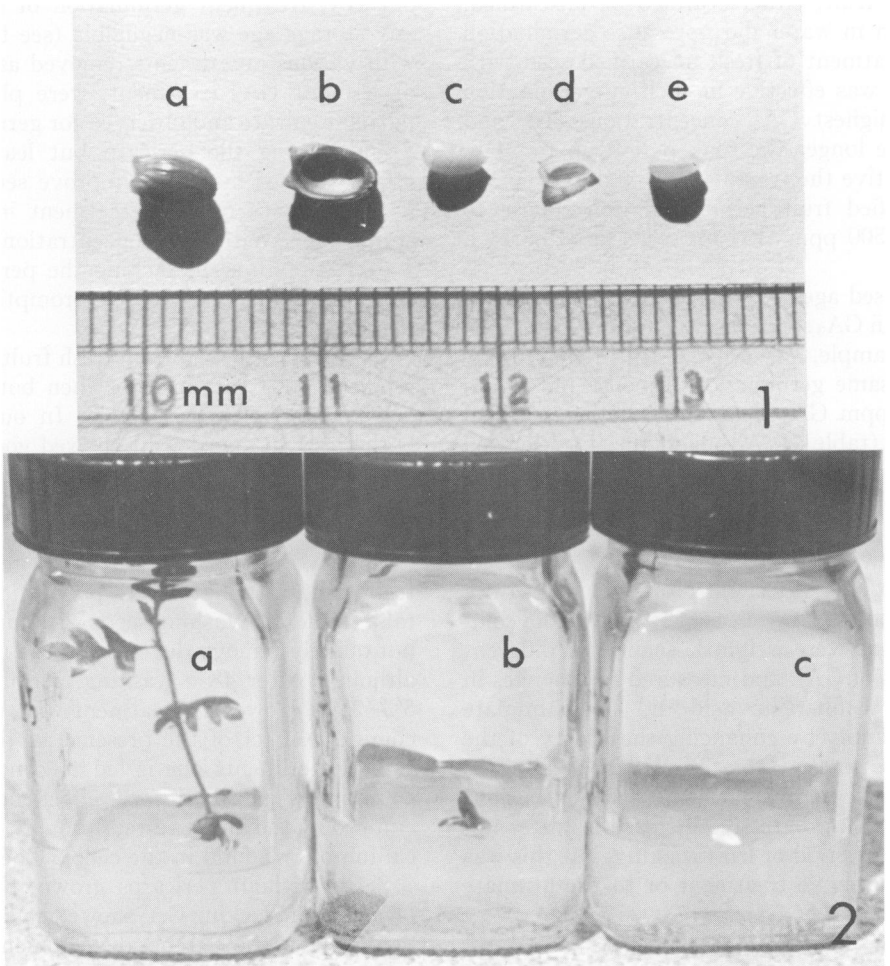
Terminology

In *Comptonia*, the structure commonly referred to as the seed is a nutlike fruit (Elias 1971). The embryo itself is surrounded by a thin seed coat (the testa) which in turn is surrounded by a sclerified pericarp composed of a thin, fleshy, outer layer and a hard, thick inner layer (fig. 1). The term "fruit" indicates the intact reproductive structure as it comes from the plant; "seed" refers to a fruit with the pericarp removed; and "embryo" refers to a seed with its testa removed.

Material and methods

General methods.—Fruits of *Comptonia peregrina* were collected from plants along New England roadsides during July when ripe fruits start to turn brown at the area of attachment to persistent secondary bracts that form a burrlike structure. Viable fruits are golden, show a distinct cusp at their attachment end, and sink when placed in water. Nonviable fruits are black, pinched at the point of dehiscence, and float in water. Viable fruits abscise soon after maturity and must be collected as soon as ripe. Nonviable and hollow fruits tend to remain firmly attached to the plant for many months. Only viable fruits with a potential germination of 100%, as determined by the float-sink test, were used. Approximately 60% of all seed collected sank when placed in water. In the scarification experiments, the attachment end of the fruit was excised with a razor blade until the embryo was just barely visible. All fruits were sown in washed sand and placed in



FIGS. 1–2.—Fig. 1, *Comptonia peregrina; a*, the intact fruit; *b*, the sclerified pericarp removed by dissection; *c*, the intact seed; *d*, the excised testa; *e*, the isolated embryo. Fig. 2, *Comptonia peregrina; a*, normal seedling developed from seed with testa removed; *b*, abnormal seedling developed from seed with intact testa (note extensive cotyledon expansion but total lack of radicle elongation); *c*, a seed with intact testa, which failed to undergo any change. All cultures 51 days old; × 1.

the greenhouse with minimum 21 C daytime and 16 C nighttime temperatures. All germination percentages were determined after 2 mo.

EMBRYO CULTURE PROCEDURES.—*Comptonia* embryos were cultured to determine the contributions of the various fruit and seed coats to seed dormancy. Fruits from cold-dry storage, refrigerated at 4 C in snap-top film cans, were cultured with and without GA_3 and with various parts of the fruit present or absent. After soaking the fruits for 20 min in 20% Clorox solution, the sclerified pericarp was removed aseptically with sterile forceps and a razor blade. The excised embryo was sterilized in a 6:1 Clorox/water solution for approximately 1 min, rinsed in sterile water for 2–3 min, and then planted in 2-oz French square culture bottles. In those experiments in which the testa was not removed, the excised seeds were soaked 1 h in sterile water, sterilized in the 6:1 Clorox solution, and rinsed before planting in the culture bottles. The culture bottles with embryos were placed in a controlled environment chamber at periods of 16-h light, 27 C, and 8-h dark, 19 C. The root culture medium of BONNER and DEVIRIAN (1939) was used for most experiments with cultured excised embryos or isolated seeds. In early experiments Knudsen's orchid embryo medium (FENNELL 1959) was also used.

Results

EFFECTS OF STRATIFICATION.—Fresh unscarified fruits stored in moist sand at 4 C in the dark without GA_3 treatment were tested at various intervals for their ability to germinate under favorable conditions in the greenhouse. Lots of 50 fruits sampled after 60, 90, 120, 160, and 245 days of stratification showed no germination. Scarified fruits treated in the same fashion also failed to germinate. Clearly, stratification alone or combined with scarification was completely ineffective in eliciting germination in *Comptonia*.

EFFECTS OF GA_3 TREATMENT ON SCARIFIED AND UNSCARIFIED FRUITS OF DIFFERENT STORAGE AGES.—

Soaking fresh fruit, either scarified or unscarified, for up to 24 h in water did not cause germination (table 1). Treatment of fresh unscarified seed with GA_3 solutions was effective in eliciting germination only at the highest GA_3 concentrations (100 and 500 ppm); the longer the soak period up to 24 h, the more effective the treatment. A high percentage of fresh scarified fruit germinated in response to soaking with 500 ppm GA_3 for 3 h (46%) or 24 h (80%).

With increased age in dry storage, soaking of unscarified fruit in GA_3 solutions became more effective. Thus, for example, 90-day-old fruit showed essentially the same germination response (48% and 40%) to 100 ppm GA_3 treatment whether scarified or unscarified (table 1). Although the data showed considerable variability, it would appear that dry storage tends to cause age changes affecting the fruit and seed coats which in turn affect their permeability properties.

EFFECTS OF GA_3 TREATMENT ON WATER UPTAKE BY UNSCARIFIED FRUITS.—Lots of 50 fruits from cold-dry stored seeds were weighed, soaked in different concentrations of GA_3, and measured for changes in fresh weight. Gibberellic acid did not stimulate germination simply by enhancing the ability of the fruit to imbibe water (table 2). Water uptake was essentially similar in all treatments, with or without GA_3. There was a progressive increase in water uptake during the period of fruit soaking, but this was unrelated to hormone treatment or to the ultimate germination response.

EFFECTS OF REMOVAL OF INVESTMENTS.—Without GA_3 treatment germination of whole fruits of any storage age was negligible (see table 1). Fruits with various investments removed aseptically, with or without GA_3 treatment, were placed in sterile nutrient culture and observed for germination (table 3). Removing the pericarp but leaving the testa intact did not markedly improve seed germination in the absence of GA_3 treatment in seeds of any storage age. With GA_3 concentrations varying from 1 to 100 ppm, seeds lacking the pericarp but with the testa intact germinated promptly and in high percentages (50%–98%).

In embryos excised from fresh fruit, HEINO (1961) reported 80% germination when both the pericarp and the testa were removed. In our experiments, both fresh and aged fruit showed good germination without hormone treatment if both the pericarp and testa were removed (36%–71%; see table 3). One can conclude that the testa is responsible for dormancy in *Comptonia* fruit. The effect of the testa is not attributable to prevention of water uptake (table 2). Washing seeds with intact testas does not quickly remove the effect of the testa (table 3B) although, after 48 h washing, germination reached 5%–25%. However, treatment with GA_3 does overcome the effect of the presence of the testa. From these experiments one is led to conclude that GA_3 counteracts an inhibitory effect imposed on the embryo by the intact testa, probably due to a chemical inhibitor bound in the cells of the testa.

Seeds without pericarps grown in sterile culture on a medium lacking GA_3 showed a variable response. Some seeds showed no development while others

TABLE 1

EFFECT OF GA_3 CONCENTRATION AND SOAKING TIME ON THE PERCENTAGE GERMINATION OF SCARIFIED AND UNSCARIFIED COMPTONIA FRUITS OF DIFFERENT STORAGE AGES[a]

			Aged seed (days in dry storage)			
	Fresh seed		90 days		150 days	
Soaking time and treatment	Unscarified	Scarified	Unscarified	Scarified	Unscarified	Scarified
3 h:						
H_2O	0	0	0	0	0	0
1 ppm GA_3	0	...[b]	0	0	...	...
10 ppm GA_3	0	...	0	2%	...	...
100 ppm GA_3	0	...	16%	16%	...	...
500 ppm GA_3	6%	46%[c]	13%	14%	0	2%
8 h:						
H_2O	0	0	0	0	0	0
1 ppm GA_3	0	...	0	0	...	...
10 ppm GA_3	0	...	0	4%	...	...
100 ppm GA_3	2%	...	13%	30%	0	8%
500 ppm GA_3	8%	...	40%	14%	4%	10%
24 h:						
H_2O	0	0	0	0	0	0
1 ppm GA_3	0	...	2%	0	0	0
10 ppm GA_3	0	...	8%	4%	0	0
100 ppm GA_3	12%	...	48%	40%	4%	10%
500 ppm GA_3	20%	80%	52%	12%	8%	16%

[a] 50 fruits were used in each test, except as noted.
[b] Denotes not tested.
[c] 610 seeds used.

TABLE 2

EFFECT OF GA_3 TREATMENT ON WATER UPTAKE OF UNSCARIFIED FRUIT OF COMPTONIA, EXPRESSED AS PERCENTAGE OF ORIGINAL FRESH WEIGHT[a]

Soaking time and treatment	% Fresh weight increase
3h:	
H_2O	16.7
1 ppm GA_3	16.7
10 ppm GA_3	16.0
100 ppm GA_3	17.0
500 ppm GA_3	16.3
8h:	
H_2O	22.5
1 ppm GA_3	23.0
10 ppm GA_3	22.9
100 ppm GA_3	23.4
500 ppm GA_3	24.7
24 h:	
H_2O	30.5
1 ppm GA_3	29.0
10 ppm GA_3	30.5
100 ppm GA_3	25.5
500 ppm GA_3	28.2
48 h:	
100 ppm GA_3	32.1
500 ppm GA_3	31.2

[a] Fruits had been stored for 84 days and were weighed in lots of 50.

grew in a curious manner—that is, the cotyledons enlarged to twice or more their normal size, ruptured the testa, and turned a red-green color. The radicle either failed to elongate or elongated only slightly, and no shoot elongation occurred. The seeds remained swollen for many months and eventually died. Such seeds were scored as not germinating. The difference between these abnormal embryos and the normal ones that developed when the testa was removed or when the intact seed was exposed to GA_3 was striking (fig. 2).

THE POSSIBLE ROLE OF LIGHT IN SEED GERMINATION IN COMPTONIA.—In none of the experiments with seed germination tests with *Comptonia* (pericarp removed aseptically and seeds with intact testas placed in sterile nutrient culture) was there any suggestion of light inhibition of seed germination or of a light requirement. All tube cultures (e.g., table 3) were maintained in a controlled environment chamber with 16 h light periods alternating with 8 h dark. In experiments in which seeds on the nutrient medium suitable for successful embryo culture were placed in total dark for 4 wk, no seeds germinated. More extensive tests of different light regimes were not undertaken.

THE POSSIBLE ROLE OF INHIBITORS IN SEED GERMINATION.—Chemical inhibitors in seeds are a common cause of seed dormancy in plants, especially woody species grown in temperate climates. The inhibitor may occur in the pericarp, testa, or embryo itself, as has been reported (SONDHEIMER, TZOU, and GALSON 1968) for seeds of *Fraxinus*

TABLE 3

EFFECT OF STORAGE AGE OF FRUIT, PRESENCE OR ABSENCE OF TESTA, AND WASHING ON GERMINATION OF SEEDS OF COMPTONIA

Storage age and treatment[a]	Germination response: Testa intact	Germination response: Testa removed
	A. Unwashed seeds	
0 days:		
0 ppm GA_3	0/33 (0%)	29/51 (57%)
10 ppm GA_3	15/23 (65%)	4/5 (80%)
100 ppm GA_3	8/10 (80%)	...
45 days:		
0 ppm GA_3	0/30 (0%)	...
1 ppm GA_3	5/10 (50%)	...
10 ppm GA_3	10/14 (71%)	...
100 ppm GA_3	6/10 (60%)	...
60 days:		
0 ppm GA_3	0/20 (0%)	12/33 (36%)
142 days:		
0 ppm GA_3	2/16 (12%)	...
1 ppm GA_3	8/10 (80%)	...
10 ppm GA_3	9/10 (90%)	...
100 ppm GA_3	8/10 (80%)	...
219 days:		
0 ppm GA_3	1/10 (10%)	9/17 (53%)
10 ppm GA_3	27/28 (96%)	5/7 (71%)
250 days:		
0 ppm GA_3	0/15 (0%)	10/14 (71%)
10 ppm GA_3	202/206 (98%)	...
Storage age and washing time	B. Washed seeds	
0 days:		
24 h	0/12 (0%)	9/12 (75%)
48 h	3/12 (25%)	11/13 (85%)
60 days:		
24 h	0/19 (0%)	11/19 (58%)
48 h	1/20 (5%)	12/20 (60%)

[a] All fruits had pericarp removed aseptically. Seeds with or without testa were cultured in tubes on BD medium (BONNER and DEVIRIAN 1939) in a growth chamber at 27 C for 16 h light alternating with 19 C for 8 h dark.

TABLE 4

EFFECTS OF ABA AND GA_3 ON THE GERMINATION OF EXCISED COMPTONIA EMBRYOS[a]

Treatment	Germination response
0.001 ppm ABA	14/18 (78%)
0.01 ppm ABA	17/19 (89%)
0.1 ppm ABA	15/20 (75%)
1.0 ppm ABA	2/15 (13%)
Control	13/15 (87%)
1.0 ppm GA_3	12/15 (80%)
10.0 ppm GA_3	9/9 (100%)
1.0 ppm ABA + 1 ppm GA_3	14/15 (93%)

[a] All fruits had a storage age of 90 days.

americana L. which contain abscisic acid (ABA). Excised embryos of *Comptonia* were cultured on nutrient agar medium containing various concentrations of ABA and ABA combined with GA_3 (table 4). At 1 ppm, ABA markedly inhibited germination of the isolated embryos; lower concentra-

tions were ineffective; GA_3 at 1 ppm completely counteracted the inhibition to germination caused by 1 ppm ABA.

In preliminary experiments, isolated testas collected from dormant seeds of *Comptonia* were extracted with ethanol, purified by thin-layer silica gel chromatography, and tested for ABA-like activity using the wheat coleoptile assay. Considerable amounts of inhibitor were found which co-chromatographed with a bonafide sample of ABA, suggesting that the native inhibitor in *Comptonia* fruit may be ABA.

EFFECTS OF GA_3 ON OTHER MEMBERS OF THE MYRICACEAE.—Seed germination in three species of *Myrica* was studied since these species are the closest relatives of *Comptonia*. Fresh unscarified fruit of *M. gale* L. showed behavior similar to *Comptonia* (table 5) in response to GA_3. Unlike *Comptonia*, however, fruits of *M. gale* respond to a natural cold period. In one test, fruits which had overwintered on the plant in the field showed 28% germination without any other treatment. This response to cold treatment was observed also by BOND (1949).

In *M. cerifera* L., the wax myrtle, a tree of distinctly southern distribution in Northern America, fresh dewaxed fruit from Florida germinated well in the absence of GA_3 treatment. The percentage germination was more than doubled when the seeds were soaked in 500 ppm GA_3 for 24 h (table 5).

Fresh dewaxed fruits of the bayberry, *M. pensylvanica* Loisel., were tested for germinability. The unscarified fruits showed a slight response to GA_3 treatment (table 5). Some scarified fruits germinated without GA_3 treatment, but the percentage germination was enhanced by hormone treatment. Even with dewaxing, scarification, and GA_3 treatment, the germination percentages were low. As in *M. gale*, fruit dormancy in *M. pensylvanica* is reported to be overcome by cold treatment (BARTON 1932).

TABLE 5

EFFECT OF GIBBERELLIC ACID TREATMENT ON THE GERMINATION OF FRESH FRUITS OF MYRICA GALE, M. CERIFERA, AND M. PENSYLVANICA

Species and treatment	% Germination
M. gale:	
3 h H_2O	2[a]
3 h GA_3 (500 ppm)	60
20 h GA_3 (500 ppm)	58
M. cerifera (dewaxed):	
3 h H_2O	36
3 h GA_3 (500 ppm)	44
6 h GA_3 (500 ppm)	60
24 h GA_3 (500 ppm)	76
M. pensylvanica (dewaxed):	
24 h H_2O	0[b]
24 h GA_3 (500 ppm)	5[c]
M. pensylvanica (dewaxed and scarified):	
3 h H_2O	16
3 h GA_3 (500 ppm)	30
24 h GA_3 (500 ppm)	18

[a] In each treatment 50 fruits were tested unless otherwise specified.
[b] 100 seeds tested.
[c] 82 seeds tested.

Discussion

From the data presented here, we can eliminate the following as causes of seed dormancy in *Comptonia* (CROCKER and BARTON 1953; STOKES 1965): (1) impermeability of the sclerified pericarp or of the testa to water, (2) physical constriction imposed by the pericarp on the embryo, (3) immaturity of the embryo, (4) physiological state of the embryo itself requiring "afterripening," (5) a chemical inhibitor localized in the pericarp, or (6) a light requirement.

Conceivably, the lack of germination in seeds with an intact testa could be due to interference with gaseous exchange, to the mechanical resistance it affords the embryo, or to its impermeability to water. While these factors may play a role in delaying germination in intact fruits, it is unlikely that they are the primary causes of dormancy in *Comptonia*, because (1) in removing the pericarp, the testa was often lacerated rather severely, yet germination was not promoted, and (2) embryos with an intact testa imbibed water and ruptured the testa, but still failed to develop normally. The abnormal embryo development shown by these seeds clearly indicates that factors other than simple mechanical resistance or interference with gas exchange are involved.

A large percentage of isolated embryos placed in sterile cultures on an appropriate nutrient medium developed quickly. The presence of the thin membranous testa around the embryos was sufficient to impose dormancy. Treatment of the seed after removal of the pericarp with low levels of GA_3 allowed good germination even with an intact testa. This response might have two explanations: The seed has a requirement of GA_3 for growth, or GA_3 counteracts a chemical inhibitor in the testa. Since isolated embryos do not require GA_3 in order to grow, we conclude that dormancy in *Comptonia* is attributable to a chemical inhibitor in the testa and that GA_3 destroys or counteracts its inhibitory action. Since washing the seeds (pericarp removed) in distilled water for 48 h did not stimulate germination, it is clear that the inhibitor is bound in the testa and is not readily leached. Low-temperature stratification was not effective in eliciting germination, apparently having no effect on the inhibitory action of the testa.

One of the most thoroughly studied seed dormancy systems involves hazel, *Corylus avellana* L., in which ABA occurs in the seed. Low-temperature stratification overcomes seed dormancy and treatment of dormant seed with GA_3 results in prompt germination (FRANKLAND and WAREING 1966; BRADBEER 1968). According to WILLIAMS, ROSS, and BRADBEER

(1973), ABA occurs especially in the testa of the seeds of hazel with lower concentrations in the pericarp and embryo. Upon imbibition either at 5 C or at 20 C, the ABA level in the seed was reduced by about 60%. Only after treatment at the lower temperature did germination occur, suggesting that loss of the inhibitor was not the only change necessary for overcoming dormancy.

Endogenous gibberellin levels increased slightly in the hazel seed during stratification (BRADBEER 1968), but the low-temperature treatment stimulated changes in the seed which allowed gibberellin synthesis to proceed at a high rate when the seed was placed at favorable temperatures for germination. Thus, in hazel, dormancy is attributable first to an accumulated inhibitor (ABA) and secondarily to existing or developed blocks to gibberellin synthesis, which are released by low-temperature treatment or are bypassed by treatment of the seed with exogenous GA_3. The mechanism of action of gibberellin in this system has been studied by PINFIELD (1968), PINFIELD and STOBART (1969), and JARVIS, FRANKLAND, and CHERRY (1968), but the molecular basis for its action remains unclear.

In another temperate tree species, *Acer saccharum* Marsh., WEBB, VAN STADEN, and WAREING (1973) demonstrated that ABA is associated with seed dormancy. This seed, which germinates after stratification at 5 C, showed a loss of 98% ABA during stratification, and changes in gibberellins (first increase, then decrease) and in cytokinins (early increase, then decrease). Other species have a high ABA content associated with dormancy. These seeds respond to GA_3 treatment by germinating or by showing an increase in gibberellin content during or after stratification, followed by germination (see review by WAREING and SAUNDERS 1971).

Seeds of *Comptonia* have features of each of these examples. *Comptonia* is unusual in that the seed does not respond to stratification, nor does the inhibitor leach readily from the seed coat. Treatment of the seed with GA_3 directly counteracts the effect of the chemical inhibitor. As yet, no measure of changes in the seed of endogenous ABA or gibberellins associated with effective germination procedures have been made.

Thus far we do not know why *Comptonia* germinates in nature. It is important to keep in mind the ecological niche that *Comptonia* occupies. It is an early successional species that thrives best in disturbed areas with sandy soil and full sunlight. *Comptonia* is never found growing in good soil or in shade. For different reasons, the seeds of many such "sun-loving weeds" are dormant. They are capable of persisting in the soil for many years and germinate when they are brought to the surface and exposed to the light. Perhaps the fruits of *Comptonia* behave in a similar way. Assuming that a germination inhibitor is localized in the testa, the sclerified pericarp acts to prevent the leaching of the inhibitor into the environment, thereby allowing the inhibitor to exert its influence on the embryo for as long as the pericarp remains intact or for as long as the inhibitor retains its effectiveness.

Because sweet fern does not remain in any given site very long, and because any established individual relies almost completely on root sprouts for extending its range, its fruits function more as an insurance of survival than as the unit of annual reproduction; that is, the type of dormancy seen in *Comptonia* may not have evolved so much to protect the embryo from the severity of its first winter as to ensure the establishment of new plants at some point in the more distant future when a major disturbance has eliminated the parental population. Conceivably, *Comptonia* fruits deposited in the soil during early succession might be capable of surviving a very long time, awaiting some disaster to destroy the late successional vegetation that had replaced the original sweet-fern population.

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