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THE EFFECT OF FIRE ON THE CALIFORNIA CHAPARRAL VEGETATION[1]

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Abstract

Fire is a very important ecological factor in determining the succession of the California chaparral vegetation. It occurs frequently in the "Mediterranean region" of southern California. The luxuriant growth of herbaceous plants appear in the first growing season after a fire. However, the high toxicity is found in the burned land, this toxic action is primary due to the toxic substance. The quantitative comparison of phytotoxins in the herb, shrub and burned soil is also determined. It has been found that the phytotoxin in the burned soil is much higher than that in the herb and shrub soils. However, the toxicity of burned soil is tremendously decreased after a sequence of rainfalls. The toxicity of the aqueous extract of *Arctostaphylos* leaf litter, heated by a series of temperatures from 60-240°C with 20°C interval, reaches its maximum peak at 160°C, and the toxicity then decreased greatly at temperatures above 180°C and was totally lost at 200°C. The toxin distribution in the treated leaf litter agrees with this bioassay result. It is concluded that phytotoxins in the burned soil is water soluble and can be leached out by rainfall, Apparently fire plays a significant role in enhancing the leachability of toxins by a sequence of rainfalls

Introduction

Fire has been recognized as a significant factor in determining the vegetation of chaparral for many centuries (Cooper, 1922; Clements, 1920; Sampson, 1944; and Sweeney, 1956). The fire cycle phenomenon was early described by Brandegee (1891). Muller, Hanawalt and McPherson (1968) strongly emphasized that this phenomenon occurs in the California chaparral vegetation. Their observations and experiments have centered in Santa Barbara, California, where the climate is typically "Mediterranean" with warm dry summers and cool rainy winters. Annual precipitation averages about 355 mm, mostly occurring between November and April (del Moral and Muller, 1970).

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When a fire occurs it consumes the leaves, twigs and small branches of the shrubs as well as the litter, while the larger branches are killed but remain standing. The ash is deposited on the soil with irregular thickness. Fire recurs about every 25 years due to accidents or lightening and usually occurs in the dry summers. Following a burning numerous annual grasses, broad-leaved herebs and brush seedlings appear on most chaparral lands. Muller *et al.* (1968) found that a large number of native dicotyledonous species of such genera as *Phacelia, Oenothera, Cryptantha, Lotus, Emmenanthe, Chorizanthe* and many others appear in the first growing season following a fire. Many bulb-forming perennials such as *Brodiaea pulchella* appear prominently in two or more than two growing seasons following a fire. They also found that most of the shrub species such as *Adenostoma fasciculatum, Arctostaphylos* spp. and several species of *Ceanothus* produce seedlings in quantity after a fire and fail to do so thereafter.

Chou and Muller (1972) have made extensive studies on the allelopathic mechanisms of *Arctostaphylos glandulosa* var. *zacensis.* They have identified 12 phytotoxic substances present in the aqueous leachate of *Arctostaphylos* leaf litter and its soils. The identifiable phytotoxins greatly inhibit seed germination and radicle growth of *Bromus rigidus* and 4 other herbaceous plants. However, the dynamics of phytotoxic nature of *Arctostaphylos* as affected by fire has not fully been understood. Thus a hypothesis that fire may enhance the disappearance of phytotoxins in the chaparral vegetation was tested. A burned area in the Zaca Lake area, Santa Barbara County, California was consequently chosen as a study site.

Materials and Methods

Study sites

An accidental fire occurred on 12 May, 1970 in the Zaca Lake area. at an elevation of about 1000 meters, located in the San Rafael mountains, Santa Barbara, California. This burned area was previously dominated by the hard chaparral, specially by *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* var. *zacensis.* An area about half mile northeast from the burned area was covered by extensive pure stands of *Arctostaphylos* as previously described by Muller and Chou (1972). An old bulldozer track, receiving run-off from the adjacent *Arctostaphylos* thicket, was barren of any plant species (Chou and Muller, 1972). Another old bulldozer track was located on a knoll receiving no run-off from neighboring thickets and occupied by such annual grasses as *Avena fatua, Bromus rigidus, B. mollis, B. rubens* and *Festuca megalura.* The materials collected from the above sites are hereafter referred to as "burned", "shrub", "bare", and "herb" soil.

Materials

The herb, bare, shrub, and burned soil was sampled by uniformally taking the upper 5 cm layer of mineral soil, each sample being screened through a 2 mm sieve before use. The burned soil samples were collected before rainfall and one week after subsequent rainfall. The fresh fallen leaves of *Arctostaphylos* were also collected and were grounded to powder before use.

Bioassay techniques

To investigate the phytotoxicity of soil and plant materials, four bioassay techniques were conducted in this study. These were called "standard sponge bioassay" (Muller, 1966), "standard sand bioassay" (McPherson, Chou and Muller, 1971), "soil bioassay" (McPherson and Muller, 1969), and "chromatographic bioassay" (Chou and Muller, 1972). Seeds of *Bromus rigidus*, *Avena fatua*, and *Lactuca sativa* var. Great Lake were used as the test materials. The moistening agent was glass distilled water in the control and some aqueous extracts or chromatographic elute in the tests. Each treatment and control was set up at least in triplicate.

The results were taken by measuring the growth of the radicles in millimeters. The data of bioassay results were finally analyzed by means of the Student's *t*-test, and standard deviation as described by Woolf (1968).

Extraction techniques

All extracts of plant materials were initiated by aqueous so that no unnatural process was involved. The aqueous extracts were fractionated by ether extraction and the water fraction was discarded. The ether fraction was then subjected to chromatographic analysis. The details of extraction and isolation were described by Chou (1971). The extract of soil materials was initiated either by aqueous for the purpose of bioassay or by the alkaline ethanol for the purpose of identification. The extraction techniques were also described by Chou (1971).

Chromatographic identification

To identify the responsible phytotoxin in the soil extracts and plant material, paper chromatography was conducted by using 3 developing solvents such as 2% acetic acid, 1-butanol: acetic acid: water (4:1:5, v/v/v) and 1-butanol: ethanol: water (5:1:2, v/v/v) described by Chou and Muller (1972). After the papers were developed with the above solvents, they were examined under short wavelength ultraviolet light and sprayed with two spray reagents: (1) DPNA, diazotized *p*-nitroaniline (Hais and Macek, 1963) followed by 10% sodium carbonate (Wang and Chuang, 1966), and (2) DQC, 0.1% ethanolic 2,6-dichloroquinone chlorimide followed by saturated sodium borate solution (Vásquez, Méndez, Gesto, Seoane, and Vieitez, 1968). Phenolic compounds,

which were thought to be the main toxic substance, appear as absorbing or variously fluorescing spots under short wavelength u. v. light and also appear in distinguishable colors after the spray reagents. A series of 26 known synthetic phenolic compounds were chosen for comparison. Their characteristics, such as Rf values in the 3 solvent systems and their color reagents under the u. v. light and with two different spray reagents, were obtained (Chou, 1971). During the identification of unknown compounds, the synthetic compounds were tested simultaneously with the unknowns.

Results

I. *Bioassay of soils*

Fifty grams of each herb, bare, shrub, and burned soil were placed evenly in a 100 × 80 mm storage dish with cover. Then twenty seeds of *B. rigidus* were planted uniformally in the soil. Different amounts of distilled water used to irrigate the soil; 20 ml for herb soil, 25 ml for bare soil and 30 ml for shrub and burn soil. The herb soil was used as a control for the tests. The results of the bioassay are given in Table 1. It was shown that the growth of *B. rigidus* in the herb soil was much better than that in other 3 soils. The shrub soil always gave 15% to 25% toxicity against the herb soil control, and the toxicity of the bare soil was even higher. Chou and Muller (1972) indicated that the high toxicity found in the bare soil was due to the soil receiving toxic run-off from the adjacent *Arctostaphylos* plants. The highest toxicity of burned soil was found among these soils.

Table 1. *The growth of* ***Bromus rigidus*** *in 4 different soils*
The length of radicle growth was measured in millimeters after incubation at 25°C for 48 hr.

	Radicle growth, mm			
	Herb soil (Control)	Shrub soil	Bare soil	Burned soil
Replicate mean	21.75	16.84	12.35	7.42
	18.65	17.85	9.74	6.15
	19.30	15.52	15.52	5.33
Grand mean	19.90	16.76[a]	12.55[b]	6.33[c]
% of control		84	63	26

a, b, and c represent the significant level at 5%, 1%, and 0.1% respectively, using the Student's *t*-test.

Further investigation of phytotoxicity of aqueous soil extracts was performed by using the sponge and sand bioassay. The aqueous soil extracts were made by combinding 300 ml of water with 100 g of soil and allowing

them to shake for 2 hr. The results of bioassay are given in Table 2. The osmolality of extract was also determined cryscopically by a Fiske G-66 osmometer. The osmolalities of soil extracts and the bioassay results of mannitol solution at the corresponding osmotic concentration are also shown in Table 2. It is shown that the aqueous extract of herb soil exhibits no toxicity at all. However, the shrub soil and burned soil showed significant toxicity in both bioassays. The osmolality determinations of the aqueous extracts of herb soil and shrub soil revealed zero milliosmols. At the concentration of 25 milliosmols of mannitol solution, the growth of *B. rigidus* reached over 92% of the distilled water control.

Table 2. *The effect of aqueous extracts of soils on the radicle growth of* ***Bromus rigidus****, using two bioassay techniques*

Data represent the length of radicle growth in millimeters.

	Sponge bioassay				Sand bioassay			
	Dist. water (Control)	Herb	Shrub	Burned	Dist. water (Control)	Herb	Shrub	Burned
Osmolality					0	0	0	25
Replicate mean	17.6	15.8	14.6	15.5	14 8	17.4	14.2	13
	18.7	19.6	13.1	14.2	16.1	15.0	15.2	13
	19.4	18.8	13.2	15.2	17.1	15.2	13.0	12
Grand mean	18.2	18.1	13.6[b]	15.0[a]	16.0	15.8	14.1	12.6[a]
% of control		99	75	84		98	88	78
Osmotic effect* (% of control)					100	100	100	92

* Muller et al. (1970), unpublished data, based on mannitol equivalents of corresponding extract osmolalities. The symbol of a and b represents the significant level at 5% and 1% respectively by using the Stedent's *t*-test.

Since the natural burned soil, collected immediately after a fire, exhibits significantly toxic effect upon the growth of *B. rigidus*, a study is necessary to determine the dynamics of phytotoxicity of burned soils collected after a sequence of rainfalls. The burned soils sampled before and after the rainfall were bioassayed. The bioassay results are given in Figure 1. The burned soil collected before rainfall showed the highest toxicity, but the toxicity tended to decrease following a sequence of rainfalls. The toxicity decrease was about 40% after the first rainfall, and 70% after the second rainfall. The toxicity of the burned soil was lost completely after the rainy season. This suggests that the toxic substance in the burned soil is water soluble and will be leached out by rainfall or run-off. The soil pH determination for these soils ranged from 6.3 to 6.7. By using the mannitol solution at this pH

range, it has no effect on the growth of *B. rigidus* (Chou and Muller, 1971 unpublished data).

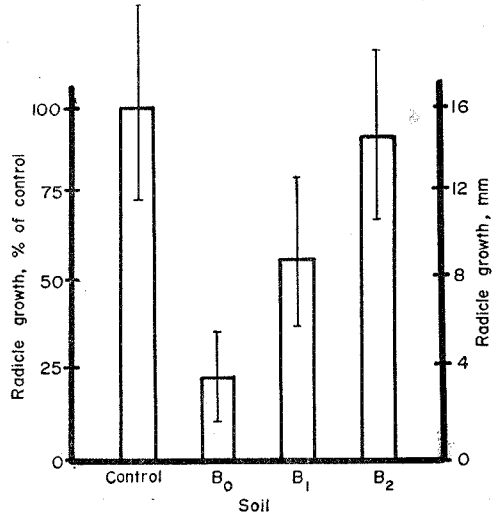

Fig. 1. Bioassay of soils; herb zone soil (control), burned soil before rain (B_0), burned soil after the 1st rain (B_1), and burned soil after the 2nd rain (B_2) against the growth of *Bromus rigidus*. Each bar represents one standard deviation.

II. *Chromatographic bioassay of soil extracts*

In order to find out the responsible toxic spots on the paper chromatogram, a chromatographic bioassay was employed (Chou and Muller, 1972). One percent quantity of the ether fraction of alkaline alcohol extracts of soils; herb soil, shrub soil and burned soil, was chromatographed. The chromatogram was cut into 10 segments according to Rf values, and bioassays were performed on each segment using *Lactuca sativa* var. Great Lake as the test material. An unspotted paper strip was also chromatographed, and then bioassayed as the control. The results of percent growth of the control are given in Figure 3. It is shown that the herb soil exhibited only one toxic spot, the shrub soil revealed 3 toxic spots and burned soil had 5 toxic spots. Obviously the toxicity of burned soil was much higher than that of shrub and herb soil. These results agree with the early findings of soil bioassays (Table 1 and 2, and Figure 1).

III. *Dynamics of phytotoxins in soils*

In the early findings of this study, toxic spots were found on the chromatograms of shrub and burned soils. It is necessary to identify these responsible toxins. The alkaline alcohol extract of each soil was obtained by using a modification of extraction techniques (wang *et al.*, 1967) The equal volume

Table 3. *The growth of lettuce seeds grown on the chromatograms of the ether fraction of alkaline alcohol soil extracts at 25°C for 48 hr incubation.*

Segment (Rf value)	% radicle growth of control		
	Herb soil	Shrub soil	Burned soil
.00-.10	120	82	111
.10-.20	84	87	82
.20-.30	112	97	80
.30-.40	86	101	76[b]
.40-.50	108	118	83[a]
.50-.60	91	85[b]	76[c]
.60-.70	102	100	97
.70-.80	72[c]	73[c]	80[c]
.80-.90	132	60[c]	34[c]
.90-1.0	175	102	108

a, b, and c indicate the statistical significance at 5%, 1%, and 0.1% level respectively, using the Student's *t*-test.

of the ether fraction of these extracts was chromatographed by using 3 solvent systems and then identified by using 2 color reagent sprays and short wavelength u. v. light as described in the earlier section. A quantitative comparison of toxins in the above soil extracts is presented in Table 4. Three compounds were found in the herb soil. These are *p*-hydroxybenzoic, vanillic,

Table 4. *The dynamics and distribution of soil phenolics in different soil extracts obtained by using alkaline ethanol extraction.**

Compound	Toxin comparison		
	Herb soil	Shrub soil	Burned soil
o-Coumaric acid	−	++	++
p-Coumaric a.	−	+	++
cis-Ferulic a.	−	+	++
trans-Ferulic a.	+++	+	++
p-Hydroxybenzoic a.	++	++	+++
Syringic a.	−	++	+++
Vanillic a.	+	++	+++
Unknown	+	+++	+++
Total (+)	7	14	20

* The data of chromatographic identification were described by Chou (1971), and the toxin comparison was based on the size of spot on paper chromatogram after the color reaction of DPNA followed by 10% sodium carbonate (*e.g.*, +++>++>+>−).

and *trans*-ferulic acids. In addition, *p*-coumaric, syringic, *cis*-ferulic and *o*-coumaric acids were found in the extracts of shrub and burned soil. One unknown toxic compounds was found in all soil extracts. The concentration of toxins in the burned soil was significantly higher than that in the shrub and herb soils. It was thought that the concentration of each responsible toxin was, at least, above 100 ppm. It has been reported that these toxins could inhibit the seed germination and plant growth at that concentration (Börner, 1960; Chou and Muller, 1972; McPherson, Chou and Muller, 1971; Wang *et al.*, 1967). It is concluded that the toxicity of burned soil is due to these above mentioned toxins.

IV. *The effect of temperature on the* ***Arctostaphylos*** *leaf toxins*

In attempting to understand the effect of fire on the dynamics of phytotoxins present in the *Arctostaphylos* stands, an experiment, simulate to the field situation, was designed to determine the dynamics of phytotoxins as affected by temperature. Twenty grams of leaf power of *Arctostaphylos* was placed in a 200 ml beaker and was heated with a series of temperatures from 60–240°C with a 20°C interval for 2 hr in an oven. Then 400 ml of distilled water was added to make a 5% aqueous extract solution, and another 5% aqueous extract of unheated leaf powder was also obtained. Each aqueous extract was then divided into two parts; one part for bioassay and another one for chromatographic identification. The glass distilled water was used as the control in the bioassay. The bioassay results of the above extract solutions and the distilled water control were obtained by using *B. rigidus* as the test material and were given in Figure 2. It was found that the toxicity was

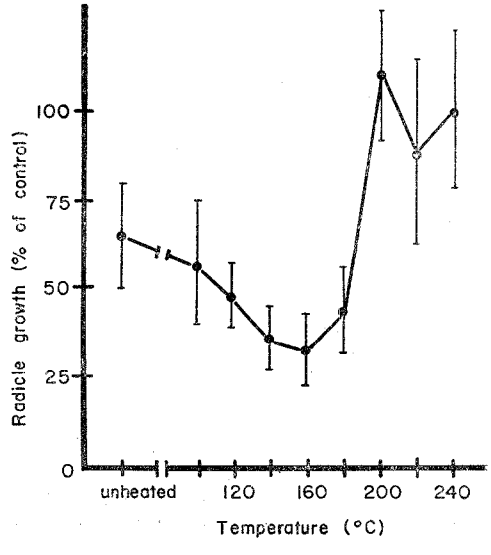

Fig. 2. The effect of temperature upon toxicity in *Arctostaphylos* leaf litter, shown by radicle growth of ***Bromus rigidus***. Each bar represents one standard deviation.

increased with increase of temperature up to 160°C, and then decreased at the temperatures above 180°C. Finally the toxicity was completly lost at 200°C. It is suggested that *Arctostaphylos* leaf toxins were more leachable when the leaves were treated at the temperatures around 160°C.

Furthermore, a study parallel to the bioassay was performed by the chromatographic identification mentioned in the earlier section. Thus the dynamics of phytotoxins as affected by temperature treatment was studied. The identity of phytotoxin is given in Table 5. The results of toxin identification are quite similar to the results shown in Figure 2 that the amount of toxin reached its maximum at the temperatures between 60°C and 140°C, and then was almost lost at the temperatures above 180°C. This indicates that *Arctostaphylos* toxins accumulated in soil can be released in great guantity when the soil temperature does not go above 140°C during a fire.

Table 5. *The change of* ***Arctostaphylos*** *leaf toxins as affected by various temperatures.**

Compound	Toxin comparison					
	Unheated	60	100	140	180	220
Arbutin	++	++	++	+	−	−
Chlorogenic acid	++	++	++	++	−	−
Gallic a.	++	++	++	++	−	−
p-Hydroxybenzoic a.	++	++	++	++	++	−
Hydroquinone	++	++	++	++	++	−
Protocatechuic a.	++	++	++	++	−	−
Tannic a.	++	++	++	++	−	−
Unknown 1	++	++	++	++	−	−
Unknown 2	+	+	+	++	−	−
Total (+)	21	24	23	21	5	0

* The original data of chemical indentificantion were described by Chou (1971). After spraying DPNA and 10% sodiun carbonate, the color reaction was blue green for Unknown 1 and yellowish gray for Unknown 2.

Discussion and Conclusion

It is obvious from the above experiments that the *Arctostaphylos* burned soil exhibits toxicity higher than that of the shrub soil, and more toxic spots are found in the burned soil than in the shrub soil, although Chou and Muller (1972) had clearly demonstrated that the *Arctostaphylos* shrub soill exhibited significant toxic effect on the growth of herbaceous plants. It was indicated that the toxic substance present in the burned soil was water soluble and most of them were phenolic acids in nature. The quantity of the toxic

phenolics present in the burned soil was shown higher than that in the shrub soil. However, after 2 subsequent rainfalls following a fire the toxicity of the burned soil was tremendously decreased. Therefore, in the first growing season following a fire, a great amount of *Emmenanthe penduliflora* and many herbaceous plants occurred (Sweeney, 1956; McPherson and Muller, 1972). Sampson (1944) stated that the loss of soil toxicity was primary due to heavy loss of potassium and carbonates and low pH values. However, in this study the osmolality determination of the burned soil extracts was low as 25 milliosmols. At this concentration of Hoagland's solution, the growth of *Bromus rigidus* is not significantly affected. In addition, the pH determination among these soils showed no significant difference from each other. The pH values of soils collected before rainfall and after each subsequent rainfall varied from 6.3 to 6.7, and at these pH values vagetation is not affected significantly. It is obvious, therefore, that the loss of toxicity after rainfall was not due to the loss of nutrients or lower soil pH but due to the toxic substancs leached out by rainfall.

Muller *et al.* (1968) proposed that the fire could denature the phytotoxic substance of chaparral vegetation. The evidence shown here does not fully agree with their suggestion. Because the phytotoxicity was greatly increased after a fire, it was believed that the soil temperature was not high enough to denature the toxic substance. Beadle (1940) indicated that during a natural forest fire the soil temperature below 2.5 cm would be approximately 112°C. At this temperature, the identifiable water soluble toxins present in the burned soil below 2.5 cm layer could not be denatured and most of seeds present in in soil could survive (Sweeney, 1956). In fact the *Arctostaphylos* leaf litter heated at temperatures of 60–140°C released lerge amounts of toxic substances, the toxicity was decreased at temperatures above 180° and was totally lost at 200°C.

Wang *et al.* (1971) reported that phenolic acids added to soil disappeared differentially, *p*-hydroxybenzoic acid being more persistent than ferulic, syringic, *p*-coumaric and vanillic acids. They showed that addition of small amounts of one acid resulted in the release of others. Addition of large quantities of phenolic acids in the soil resulted in the fixation of extractable acids, apparently by the incorporation of humic acid. Muller and Chou (1972) also found that the rate of diminution of extractable compounds greatly increased with the increase of the humus content in the soil. Apparently soil phenolics can be easily fixed with humic substances and converted into phenolic-humic acid complex substances. This complex structure is thought to be unstable, and free phenolic acids can be released under some conditions. Wang and his associates (personal communication, 1973) have made an extensive

study along this line to find out the mechanism of polymerization and depolymerization of phenolic acid with humic acids. It is highly possible that phenolic-humic acid complex can be depolymerized by fire, this may result in free phenolic acid being more leachable. Consequently, fire may not play a direct way in denaturing phytotoxic substances, but play an indirect way in enhancing the soil phenolic acids which are eventually leached out by rainfalls. When the toxin in the chaparral soil disappears, herbaceous plants will be seen in the first growing season following a fire. This study, further, supports the concept that allelopathy plays a significant role in the fire cycle of chaparral vegetation (Muller, Hanawalt and McPherson, 1968).

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火災對美國加州荊棘植物羣落的影響

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美國加州的荊棘植物羣落 (chaparral vegetation) 常因火災而破壞。火災過後，雖然 *Arctostaphylos* 所分泌的植物毒物質在土壤中的含量大增，但它在土壤中的可濾性 (leachability) 却增加，致使這些毒物質容易被雨水冲掉。*Arctostaphylos* 落葉中的植物毒物質經過溫度處理後，其毒性隨溫度增高到 160°C 爲最高峯，在溫度 180°C 時毒性急劇下降，到200°C 以上時毒性完全消失。實驗證明火災並不能直接破壞土壤中的毒物質，而是使其可濾性增高。導致在火災過後的第一個生長季裏，大部份的草本植物因而復生。