HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 26 DECEMBER, 1956 NUMBER 6

TRANSLOCATION OF HERBICIDES

I. THE MECHANISM OF TRANSLOCATION: METHODS OF STUDY WITH C^{14}-LABELED 2,4-D

ALDEN S. CRAFTS

II. ABSORPTION AND TRANSLOCATION OF 2,4-D BY WILD MORNING-GLORY

ALDEN S. CRAFTS

III. UPTAKE AND DISTRIBUTION OF RADIOACTIVE 2,4-D BY BRUSH SPECIES

OLIVER A. LEONARD and ALDEN S. CRAFTS

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

THE MECHANISM OF TRANSLOCATION

Tracer studies with radioactive 2,4-D in bean, cotton, and cucumber plants confirmed previous findings that 2,4-D penetrates the cuticle of sprayed leaves, migrates to the phloem, and is transported in that tissue along with food materials in the plant. Freeze-dried plants were radioautographed to determine the rate and direction of translocation and the amount of chemical moved to various parts of the plant.

WILD MORNING-GLORY RESPONSE TO RADIOACTIVE 2,4-D

Radioactive 2,4-D was applied first to greenhouse-grown morning-glory seedlings to compare various formulations. Emulsifiable acid and heavy ester formulations proved superior to the older salts and light esters, and the addition of a surfactant was found to increase absorption and translocation.

Field studies revealed that 2,4-D moves most actively in plants growing in moist soil, that movement is most rapid and extensive in plants in the seedling stage, and that 2,4-D moves where foods are moving.

BRUSH SPECIES AND RADIOACTIVE 2,4-D

Further evidence of the correlation between 2,4-D movement and food movement in plants was provided by tracer studies in seven species of woody plants common to California: coyote brush, arroyo willow, wedge-leaf ceanothus, manzanita, toyon, blue oak, and live oak. In addition to detailed analyses of the tracer studies in these species, the following general conclusions are presented:

Contact injury is a major hindrance to the uptake and transport of 2,4-D.

Soil moisture and root growth are important to 2,4-D transport and response.

In evergreen species the chemical may move throughout the plant for many months, whereas in deciduous species it may move only for relatively short periods.

Different species require different treatments; a single application cannot be expected to control mixed brush populations under California conditions.

The research reported in these papers was made possible by A.E.C. Contract AT(11–1)–34 Project No. 9.

III. UPTAKE AND DISTRIBUTION OF RADIOACTIVE 2,4-D BY BRUSH SPECIES[1]

OLIVER A. LEONARD[2], ALDEN S. CRAFTS[3]

BRUSHY SPECIES of plants occupy millions of acres of land in California. Some of this land is rough, rocky, and unsuited for the growth of grass. Much of it, however, is well suited to the growth of forage species, and only the cover of brush prevents its use for grazing. Vigorous efforts are being made to reclaim this valuable land (Love and Jones, 1952) by controlled burning, reseeding, and improved range-management practices. The weak link in this program is the control of seedlings and resprouting stumps of certain brush species. Although reburning and proper grazing management are useful, chemical control is proving most valuable in this final clean-up process.

For successful chemical control of brushy plants, the chemical must penetrate the leaves or bark and move through the stem into the roots. Most resprouting occurs from a band of meristematic tissue at or somewhere below the ground line. In young seedlings this tissue is rather easily destroyed; in old plants it becomes more difficult to kill. Although 2,4-dichloro- and 2,4,5-trichlorophenoxyacetic and propionic acids are now in use, further studies of these four basic molecules must be carried out in many localities to determine the effects of differences in species, habitats, seasonal responses, and methods of application.

Obviously, a radioactive tracer that can be followed after it is applied to leaves or bark can be a valuable tool in studies on absorption and translocation. This report deals primarily with the absorption, translocation, and toxic action of 2,4-D. The carboxyl group of the 2,4-D used in these experiments was labeled with C^{14}. This tracer, hereafter referred to as 2,4-D*,[4] was applied to several California species of brushy plants. In conjunction with the tracer studies, branch tips were treated with nonradioactive 2,4-D to determine the extent of die-back in the various species. Two related studies were also undertaken: one a comparative analysis of the penetrative capacities of two formulations of 2,4-D*, the other a comparison between radioactive urea (urea*) and 2,4-D*.

STUDIES IN ABSORPTION AND TRANSLOCATION

Two areas representing different soil and climatic conditions were selected—one west of Davis in the foothills of the Coast Range, the other to the east in the Sierra. The growing season in the west area is early; that in the east is about a month later. The west area has rather low rainfall, the east has more. By making periodic treatments and samplings in both areas, it was possible to cover many growth stages, several species, several sites, and rather distinct differences in humidity and temperature.

Seven species were studied: blue oak, *Quercus douglasii;* wedge-leaf ceano-

[1] Received for publication June 10, 1955.

[2] Associate Botanist in the Experiment Station, Botany Department, Davis.

[3] Professor of Botany and Botanist in the Experiment Station, Davis.

[4] Supplied by Tracerlab.

thus, *Ceanothus cuneatus;* coyote brush, *Baccharis pilularis;* manzanita, *Arctostaphylos manzanita;* live oak, *Quercus wislizenii;* toyon, *Photinia arbutifolia;* and arroyo willow, *Salix lasiolepis.* The results with the different species are considered in the order of decreasing sensitivity to herbicidal concentrations of 2,4-D.

Treatment. Preliminary treatments started on February 17, 1953, and continued into September. The last collection of samples was taken on October 22. Each treatment involved applications to one leaf on each of three or four plants, and bark samples were collected at various distances from the treated leaf, ranging from a few inches to 4 or even 5 feet in a few cases (figs. 1, 2, 4, 5, 6, 7, and 8).

During the summer of 1954 a series of tests was undertaken in which an effort was made to apply more of the radioactive tracer. Instead of treating just one leaf, 10 leaves near the tip of a branch were treated on their under surfaces, and bark samples were taken at various levels below. These tests gave excellent radioautographs (figs. 9–14).

The treatment in 1954 was standardized at 50 μg of 2,4-D* (1.24 millicuries per millimol) applied in a 50 per cent solution of ethyl alcohol and containing 0.1 per cent Nonic 218. Treatment consisted of applying 0.01 ml of this solution to the leaf surface and spreading it over a sufficient area that the liquid would not drip off. Applications were made to upper leaf surfaces on some plants, to lower surfaces on others. All applications were made around 10 A.M. and samples were taken one day, one week, and three weeks later from each set of treatments.

Samples consisted of bark, leaves, stem tips, and inflorescences of the treated plants. The bark was sampled by girdling the stem in two places and slipping off the ring of bark between the girdles. When the bark ceased slipping in late summer, satisfactory samples could no longer be obtained.

Radioautographing. Each bark sample was fastened flat to thick blotters by pinning it around the edges. When this preliminary drying had removed the bulk of the moisture, the samples were pressed flat between warm, dry wooden slats with C-clamps to hold them flat. Leaves, shoots, and inflorescences were dried between blotters. After complete drying, all samples from a given treatment were cemented to a piece of paper, the bark samples being oriented with the cambium side out (fig. 1). They were then placed on Eastman No-screen X-ray film and autographed for four weeks (fig. 2).

In order to obtain good contact between the samples and the film, the materials were arranged in the following order. The film was placed on a hard, flat surface (¼-inch plywood) and the sheet of samples was placed face down on the film. Next came a piece of heavy paper, then a ¼-inch sheet of sponge rubber, another heavy paper, a second sheet of samples, a film, and a second plywood sheet. This sequence was repeated until a complete set of samples was ready, then the whole pile was squeezed between clamps with sufficient pressure to insure good contact between samples and films. If the materials are reversed, so that the samples are backed by the boards and the films by rubber, the samples are pressed into the film, which becomes indented, and dark pressure spots occur along all borders where the film is curved by the pressure (fig. 3).

The problems of radioautographing have still not been completely eliminated, and efforts are currently being made to find satisfactory solutions.

Means of overcoming certain difficulties were devised during the study. For example, films are spotted when strongly radioactive treated leaves are used, so treated leaves were omitted after the first samplings. The method of backing the film with a hard, smooth surface was developed after it was found that the film bent from the pressure necessary to insure close contact with the specimen. In other cases pseudoautographs were produced. Some were caused by the reaction of chemical constituents of certain species, notably willow, with the film (compare figures 2 with figures 5 and 8). These we learned to recognize by comparison with the untreated controls. Other difficulties inherent in the photographic procedure have been eliminated, and we feel that the data recorded in the tables represent a true picture of the uptake and movement of radioactive 2,4-D.

General Observations. The first autographs were the result of leaf applications made in February, 1953, when only upper surfaces were treated. These autographs suggested that the 2,4-D* was not penetrating the cuticle in leaves lacking stomata on their upper surfaces, and so all later applications that season were to the lower surfaces. Later, however, more detailed study of many autographs proved that absorption may take place from either surface. Leaves that had no stomata on the upper surface were protected against a sudden influx of high concentrations of 2,4-D*, but this protection was not afforded when the applications were made to the lower surface. Penetration is therefore likely to be rapid in leaves that have stomata on both surfaces.

The sensitivity of leaves to contact injury by 2,4-D varies with species, age of the leaves, and air temperature. Other factors influencing absorption and translocation will be considered later.

Since single leaves were treated, except as otherwise noted, the translocation of 2,4-D* was confined for the most part to a narrow strip of the bark, the portion directly connected to the treated leaves (figs. 2 and 5). When 10 leaves in a group were treated, the entire area of the bark sample produced autographs, especially within 6 inches below the lowest treated leaf (figs. 9–12); however, below the junction of the treated branches with one or more untreated branches, the radioactivity became confined to narrow portions of the bark, which appeared to be in a line of flow in the bark from the treated branch. There was some indication that 2,4-D* is less apt to be in streaks in bark above treated leaves than below them.

Branch tips treated with herbicidal concentrations of nonradioactive 2,4-D frequently died back to their connecting branches and no farther (especially noted on easily killed plants, such as coyote brush). From this reaction, plus the findings of the tracer studies, it may be inferred that if the branches are to be killed, the 2,4-D must be well distributed throughout the entire bark.

Coyote Brush

This is a moisture-loving, erect, compactly branched evergreen shrub, which grows to a height of 2 to 10 feet. It occupies vast areas in the Coast Range of California. The test plants were located in Putah Canyon in Yolo County, the inner limit of the normal range of this species. Occasional infestations occur in the Sacramento Valley and the foothills of the Sierra. The leaves are quite porous, having stomata on both the upper and lower surfaces. Some shoot growth may occur in the winter season, but the main activity starts in April and continues into early summer, varying considerably with soil-moisture conditions. The flowering period is from August to October.

Coyote brush is successfully controlled by aircraft applications of 2,4-D (either amine or ester forms), which are generally applied from April through July, the time varying somewhat in different areas. Like certain other species, coyote brush responds much more strongly to 2,4-D than to 2,4,5-T.

Tracer Studies. There were marked seasonal differences in the absorption and translocation of 2,4-D* from treated leaves (figs. 15 A and B). In February only one third of the branches showed radioactivity outside of the treated leaves. Applications in April, at the time of vigorous new shoot development, resulted in an intense absorption and translocation of 2,4-D*. The intensity decreased slightly in May and June. No absorption or translocation was evident in July. No 2,4-D* was detectable in the bark of plants treated on a single leaf on July 31, 1953. However, treatment on August 5, 1954, when 10 leaves were treated on each branch, resulted in readable autographs as far as 12 inches from the nearest treated leaf.

The treatment time necessary to obtain the darkest autograph of the bark also appeared to vary with the season. A three-week period was apparently best in February, but one week was enough in the following months. Some 2,4-D* was present in bark one day after the applications were made, but in no case were the autographs as dark as those taken one week after treatment.

In February and March, only downward movement was evident, although in March there was also some movement into new branch tips quite close to the treated leaves. In April, on the other hand, movement was almost entirely upward; in only one case did 2,4-D* penetrate into a branch below the treated leaves; the movement upward from the treated leaves was into growing tips within 2½ inches or less from the point of application. After the month of April translocation appeared to be entirely downward.

The tests were not designed to give clear-cut information regarding the rate of translocation; however, 2,4-D* seemed to be farther down the stems one week after application than one day after. There is apparently a continuous redistribution of the radioactivity (probably 2,4-D*) within the plants. As used in these experiments, the degree of radioactivity depends upon such factors as the quantity of 2,4-D* applied and the physiological state of the plants.

Branch-Tip Treatments. Branch tips were sprayed with an emulsifiable acid formulation of 2,4-D (table 1). Appreciable die-back beyond the point of spray occurred at all times of the year, confirming field experience that coyote brush is always sensitive to spray applications with 2,4-D. However, this plant is most sensitive to sprays applied during the periods of active growth and is much harder to kill (especially by aircraft application) after the soil has become dry. The reduced die-back of branch tips in the summer accords with this observation, as well as with the reduced intensity of autographs obtained during this period.

Translocation behavior and spraying experience indicate ready absorption of 2,4-D by coyote brush leaves, active transport to the roots, and a high susceptibility to its toxic action. The periods of highest susceptibility may reflect active root growth, which is, in turn, a response to soil moisture. When the growth is young and succulent, the amine salts are superior to the esters. Stomata on the upper surfaces of the leaves allow a rapid influx of 2,4-D into the leaves; such rapid influx of the esters brings about contact injury. The acid formulation used in these experiments resulted in some contact kill, which was evident three weeks after the applications were made; however, fewer instances of contact injury were noted on coyote brush leaves than on any other plant, except manzanita. This lack of contact injury is

TABLE 1

BRANCH-TIP TREATMENTS OF COYOTE BRUSH WITH A 0.5 PER CENT 2,4-D ACID (EMULSIFIABLE) FORMULATION IN WATER CONTAINING 0.5 PER CENT NONTOXIC OIL.* READINGS MADE JULY, 1954

Date of application	Percentage of tips killed by the spray	Average die-back of branch beyond the part sprayed
1953	*per cent*	*inches*
February 18	100	12
April 3	100	20
May 18	100	10
June 5	100	11
July 23	100	8
August 19	100	5
September 24	100	6
October 31	100	5
October 31	100	5

* Shell Mineral Seal Oil; viscosity 46 SUS, UR 90 per cent.

probably a factor in its successful control by aircraft applications of 2,4-D. Another factor is the excellent absorption by petioles and stems, as can be noted in figure 21.

Arroyo Willow

Arroyo willow is one of the most common willows of the valleys and foothills throughout California. Like coyote brush, it is favored by a moist environment, at least for its roots; it also responds definitely to 2,4-D treatment.

Tracer Studies. Marked seasonal differences in absorption and translocation were observed between arroyo willow, a deciduous plant, and coyote brush, an evergreen. In contrast with coyote brush, little, if any, translocation occurred in arroyo willow before April 15 (fig. 16 A, B, and C). Beginning in late April, when some leaves had reached full size, translocation of 2,4-D* appeared to take place and continued without any outstanding change throughout the summer and fall; this was associated with continuous shoot growth, which, in turn, is related to the presence of adequate soil moisture (figs. 7 and 8).

Translocation both downward and upward from the treated leaves occurred from late April until September; the date of application had little effect on either the concentration of 2,4-D* in the bark or the distance moved. However, the most intense autographs of the branch tips above the treated leaves were made from April samples; furthermore, this was the only time that autographs were produced by branch tips from branches located below the treated leaves. Applications made in October showed no evidence of upward movement of 2,4-D*, but the movement downward was as good as or better than that during any previous month.

Seven days after treatment seemed to be the optimum time for obtaining autographs. High concentrations of 2,4-D* were not found in the willow bark, although the bark samples of other woody plants, such as toyon and live oak, sometimes had very high concentrations of radioactivity. Arroyo willow, however, is much easier to kill with 2,4-D than either toyon or live oak.

TABLE 2

BRANCH-TIP AND WHOLE-PLANT TREATMENTS OF THE ARROYO WILLOW USING 0.5 PER CENT 2,4-D ACID (EMULSIFIABLE) IN A WATER SOLUTION CONTAINING 0.5 PER CENT NONTOXIC OIL. READINGS MADE DECEMBER, 1954

Date of application	Average die-back of branch tips beyond the part sprayed	Percentage kill of sprayed plants
1953	*inches*	*per cent*
February 17	0	0
March 30	16	0
April 23	50	40
May 15	30	80
October 21	46	60
November 25	..	0

Branch-Tip and Whole-Plant Treatments. The results in table 2 on the die-back of branch tips treated with 2,4-D indicate that the greatest effect was produced after the leaves had become fully expanded in April and that considerable die-back occurred from all treatments, ending with that of October 21. Because the amount of die-back varies considerably among branches, seasonal changes cannot be further evaluated.

Sensitivity of the entire plant to 2,4-D parallels in a general way the responses of branch tips. 2,4-D sprays applied too soon after the leaves have first appeared in the spring result in a poor plant kill. Plant kill may not correlate very well with 2,4-D* translocation in April because the young leaves are too quickly injured by herbicidal concentrations of 2,4-D. Translocation is thus limited. In contrast, nonherbicidal concentrations, such as those used in the tracer studies, may bring about extensive translocation. This does not, however, prove that killing will be extensive.

Some contact injury resulted from the applications of 2,4-D to the lower leaf surfaces. This was evident three weeks after application in March, but in April and later months it was evident only one week after.

Wedge-Leaf Ceanothus

This plant is a common evergreen shrub of the California chaparral. Shoot growth is most active in April and May. Flowering starts in February and continues into March at the Putah Creek location. The leaves are

½ to 1 inch long and do not have stomata on the cutinized upper surface. The under surface has numerous stomata and is covered with microscopic hairs. Spray droplets applied to the upper surface spread rapidly over the surface, while applications made to the under surface spread very little and appear to be quickly absorbed through the stomata into the intercellular spaces. This plant does not sprout after a fire and is not considered a vigorous stem sprouter.

This species is quite susceptible to aircraft sprays, especially to applications of esters of 2,4,5-T in diesel oil; it is only slightly less sensitive to similar sprays with 2,4-D. Oil emulsions are appreciably less effective than applications in straight oil, and applications with only water as a diluent are poor. Available evidence points to a penetration problem, related either to the leaves or to the stem. The leaves are subject to contact injury when applications are made to the lower surface, but in airplane applications the spray is deposited mostly on the cutinized upper surface. This type of deposition may largely explain the plant's susceptibility to aircraft sprays, since a slow diffusion of 2,4-D through the cuticle would minimize contact kill.

Tracer Studies. Radioautograph studies yielded very little information on the absorption and translocation of 2,4-D* by this plant (fig. 17 A and B). Only the February treatments, when upper leaf surfaces were treated, resulted in positive autographs, with the exception of a single branch showing positive movement of 2,4-D* in the bark in May and the occasional appearance of 2,4-D* in leaves opposite the treated leaves. Most of the translocation in the bark was downward, although close to the treated leaves there was some movement upward, perhaps associated with the onset of flowering. The 2,4-D* was much farther down the bark one week after application than one day after.

Applications to the lower surfaces resulted in killing some of the treated leaves within one week after treatment. This may have been one factor contributing to the negative autographs obtained after February 17, the only date when applications were made to the upper surface. However, even treatment of the upper surface resulted in some spread of the solution over the surface and leaf margins, causing marginal burn one week after application.

Branch-Tip Treatments. These treatments were relatively ineffective at all times of the year, very few of the branches being killed farther than ½ inch beyond the sprayed portion. In many cases only 25 to 50 per cent of the sprayed part (bark and wood) was killed. The poor kill of the branches with the acid formulation may have been due to poor penetration of leaves or bark. Although some delayed kill may be anticipated, this does not explain the complete and quick killing of this plant by aircraft application when esters are applied in oil (5 gallons to the acre).

Common Manzanita

This evergreen shrub flowers in midwinter; vegetative growth starts in March and is most active in April and early May. The leaves are broadly ovate; they are 1 to 1¾ inches long and ¾ to 1½ inches wide and have stomata on both the upper and lower surfaces. Being quite pervious, either surface absorbs sprays quickly. This shrub does not sprout after a fire and is not considered a vigorous stem sprouter. The bark is red and very thin; it peels off each year, starting in May.

Aircraft applications often produce a partial top kill, although if the plants are well covered by the sprays, complete kills result. A partial top kill the first year often becomes complete the second or third year after spraying. Delayed kill of manzanita is common, even with the sprouting species.

Tracer Studies. One day was not enough for absorption and translocation of 2,4-D* into any of the sampled parts (fig. 18 A and B). Even seven days did not seem to be enough, better autographs generally being obtained 21 days after application.

Translocation of 2,4-D* occurred in manzanita from February through May; later bark samples could not be obtained. Downward translocation was predominant, although in March and April some upward movement occurred into young leaves and stem tips close to the treated leaves. The 2,4-D* had moved farther down the stems three weeks after application than seven days after. There appears to have been a slow but continuous flow of 2,4-D* downward, indicating a gradual but continuous absorption of 2,4-D* by the treated leaves. These treatments did not cause injury to the leaves.

Branch-Tip Treatments. The die-back of manzanita branch tips beyond the sprayed portion was only 0.9 inch, even one and a half years after treatment. Death of the sprayed portions was very slow, often taking more than a year. Kill may not be complete until three or four years after treatment.

It is clear, however, that 2,4-D* moved much farther down the stems than the branch-tip treatments indicate. The tracer studies explain why delayed kill is commonly observed following aircraft applications to this plant. Manzanita leaves were the only ones that showed no evidence of contact injury from applications of 2,4-D, even though they are the most pervious of any studied and the solutions were rapidly absorbed into the intercellular spaces.

Toyon

This evergreen shrub is 6 to 10 feet high; its leaves are 2 to 4 inches long and ¾ to 1½ inches wide. It is abundant in the lower Sierra Nevada, in the Coast Ranges, and elsewhere. Some shoot growth may occur at any time, but active growth does not start until April. Flowers develop in June or July, and the fruit matures about Christmas time, hence its common name, Christmas berry.

There are no stomata on the heavily cutinized upper leaf surface. The lower surface is pervious to applications of oil, the mesophyll appearing oil-soaked within a few minutes after the application of an oil droplet. No penetration is visible from similar applications made to the upper surface.

Toyon is only moderately sensitive to broadcast applications of 2,4-D. One- and two-year sprouts (developing after a fire), however, appear to be quite easily killed, especially when the sprays are applied from February to mid-April; effectiveness seems to decrease gradually after this time.

Tracer Studies. Autographs made seven days after application were generally stronger than those made one day after (fig. 19 A, B, and C). Excellent autographs were still obtained 21 days after treatment. The most intense autographs were produced by applications made in April, May, and June (figs. 2, 5, and 8), while the faintest were those from the September and October treatments.

Movement appeared to be primarily downward in February and March, but 2,4-D* appeared in the young tips and leaves directly above the treated leaves from April through July (fig. 8). Autographs obtained three weeks after the March 17 application gave the only evidence of radioactivity in side branches below the treated leaves. This result indicates a shift in the direction of translocation during the three-week period that coincided with the beginning of active shoot growth in the spring. Translocation appeared to be entirely downward in the fall, but the total radioactivity in the bark was less than at previous times.

TABLE 3

BRANCH-TIP TREATMENTS OF TOYON AND LIVE OAK WITH 0.5 PER CENT 2,4-D ACID (EMULSIFIABLE) IN WATER CONTAINING 0.5 PER CENT NONTOXIC OIL. READINGS MADE JULY, 1954

Date of application	Average die-back of toyon branch tips beyond sprayed part	Average die-back of live oak branch tips beyond sprayed part
1953	*inches*	*inches*
February 17	7	3
March 30	8	0
April 23	10	2
May 15	3	3
June 17	1	3
July 16	1	0

Branch-Tip Treatments. The average kill of branch tips beyond the part actually sprayed was never very great (table 3). This suggests one reason why toyon is readily killed by 2,4-D sprays only when the sprouts are sprayed within one or two years after a burn. Leaves are quite close to the roots at this time so that translocation of lethal concentrations for only a few inches may be enough to kill the underground parts that have dormant buds. The die-back of branches beyond the sprayed portion was greatest in the winter and early spring and then decreased.

The treated area of toyon leaves turned red 21 days after treatment in April. Dead spots were present seven days after applications in June and July. It is clear that toyon leaves can suffer contact injury from 2,4-D and that this factor is more important in late spring and summer than in winter and early spring.

It should be emphasized that branch-tip treatments may require more than a year to be effective. Hence, some delayed kill may occur, which is quite common on toyon sprayed with 2,4-D. It should also be emphasized that the ultimate distribution of 2,4-D* within the plant cannot be determined within 7 or even 21 days after application.

Blue Oak

Blue oak is a deciduous tree common in the foothills of the Sierra Nevada and in the Coast Ranges. The best kill of this species by aircraft application was 25 per cent with a single application (Leonard and Harvey, 1956). Sprouts are susceptible to ground applications with 2,4-D amines or esters applied in May. Reaction to the 2,4,5-T esters appears to be poor at this time of the year; however, in late June or July 2,4,5-T esters are much more effective than when applied earlier, and 2,4-D is less so. These differences are probably related to at least two factors: (1) 2,4,5-T is a better penetrating agent than 2,4-D; and (2) contact injury to leaves decreases with age or maturity.

Tracer Studies. Tracer studies were negative for the most part. Sampling started March 24 and continued until June 23, when all of the season's leaves were fully expanded; shoot growth had ceased and the bark no longer slipped. Out of 42 samples autographed—including tests run one day, one week, and three weeks after application—only five showed any movement of 2,4-D* out of the treated leaf, and the average distance in which discernible autographs were produced was 5.2 inches. Two of these were three-week samples treated in April and collected April 28. Three were one-week samples treated May 19 and May 26 (approximately the optimum season for treatment with 2,4-D).

Blue oak leaves are quite sensitive to the contact action of 2,4-D, whether in acid, amine, or ester form, and the small quantities of 2,4-D* applied to leaves in the above tests frequently killed them. It seems entirely possible that this is the principal reason for the limited translocation that was observed.

These findings corroborate the experience that spray treatment on blue oaks seldom results in more than local response. Small trees may occasionally die, but in large ones movement seldom extends beyond the main trunk. In the season of treatment, after the sprayed leaves have died, dormant buds along the branches may develop, and their leaves may be large and misshapen. Also, ridges of callus may form beneath the bark, and the smaller branches are often killed. Usually, however, the trees recover during the year following treatment. Blue oak is one of the species least responsive to aircraft spray treatment with the phenoxyacetic acid herbicides.

Live Oak

This species is an evergreen tree with oblong leaves 1 to 2½ inches long and ¾ to 1½ inches wide. The glabrous upper surface is well cutinized and contains no stomata; the under surface is not heavily cutinized and has numerous stomata.

Live oak sprouts vigorously after a fire or after being cut. Aircraft application has not yet killed a single tree; consequently, most attention has been given to the reaction of sprouts to complete coverage with foliage sprays. Sprouts have been killed by one or two applications of a mixture of 2,4-D and 2,4,5-T esters in 1 per cent diesel oil emulsion applied in May or June. Trees, also, can be killed by placing the amine salt of 2,4-D in a ring of deep cuts around the bottom of the stems.

Tracer Studies. Autographs obtained one week after application were generally more intense than one day after (fig. 20 A, B, and C). From February to May, autographs were as intense three weeks after application as one week after; however, in May and later, the one-week period was the most satisfactory.

Translocation was entirely downward in February, but there were traces of 2,4-D* in new leaves, bark, and stem tips above the treated leaves after growth started in March (fig. 5), and there were occasional traces of 2,4-D* above the treated leaves even in July; however, 2,4-D* movement upward was never very intense. The detectable distance of movement of 2,4-D* was not great in any case, usually less than 13 inches; the greatest movement seemed to occur from February through May.

Branch-Tip Treatments. As may be seen in table 3, the kill of live oak stems beyond the sprayed portion was slight. The 2,4-D* studies show that the chemical moves in rather high concentrations for at least 6 inches beyond the point of application, and it seems likely that fairly high concentrations may at times be present at least a foot or more down the stems from the treated leaves. The actual kill of live oak by 2,4-D is extremely slow, however, and may not take place for two and a half years or more after treatment. In many cases delayed kill of live oak has followed application of the amine salt formulations of 2,4-D (Emrick and Leonard, 1954).

Live oak leaves appeared to be uninjured by the contact action of 2,4-D until May 14, when dead areas were produced within seven days after treatment; some injury resulted from treatments applied in July. Young leaves are more apt to be injured by the contact action of 2,4-D applied to the under surface than are old leaves. This may be related to the more extensive and thicker cuticle that is present on the undersides of old live oak leaves.

PENETRATION STUDIES

Two different solutions were used in studies on penetration. One solution (A) consisted of 0.5 per cent 2,4-D* acid, plus 1 per cent Vatsol OT (dioctyl ester of sodium sulphosuccinate, an anionic surface active agent), plus about 1 per cent Amine 220 (1-hydroxyethyl-2-heptadecenylglyoxalidine, a cationic surface active agent), plus 2 per cent of a paraffinic oil (viscosity 46 SUS and a UR of 90 per cent), plus water. The second solution (B) consisted of 0.5 per cent 2,4-D* acid, plus 45 per cent of tetraethyl orthosilicate, plus 45 per cent of a dimethyl silicone having a viscosity of 40 centistokes. Leaf treatment clearly showed solution B to be much more penetrating than solution A.

An 0.01-ml droplet of each of these solutions (50 μg of 2,4-D* acid) was applied to the upper and lower surfaces and to the petioles of young and old toyon and live oak leaves and to young coyote brush leaves. Samples were collected one week after the applications were made. The autographed results are shown in figure 21 A, B, and C.

Most solutions of 2,4-D result in some contact injury to leaves, regardless of formulation; however, solution A was slightly more toxic than the standard 2,4-D* formulation because it included Vatsol OT, which has appreciable contact toxicity. Solution B, containing tetraethyl orthosilicate, was considerably more toxic than A; the dimethyl silicones appear to have no contact toxicity. The results, especially with solution B, should be considered in the light of the above-mentioned toxicity. The spreading and penetrating properties of solution B were unusually good, and it appeared to be better in this respect than any of the oils with which it was compared (for example, n-tetradecane, n-decane, n-dodecane).

Applications to the upper surfaces of live oak and toyon leaves gave no visible evidence of penetration during the one-week experimental period; these observations were in contrast to the rapid penetration of the mesophyll when applications were made to the lower surfaces. With coyote brush leaves, the solutions penetrated rapidly when applied to either upper or lower surfaces. Petiole applications were not confined to the petioles; there was some rundown into the axillary buds.

Results with young toyon leaves indicate that with solution A there was little difference in the absorption and translocation of 2,4-D* whether upper or lower surfaces were treated; however, with solution B (silicone) the upper-surface application resulted in effective absorption and translocation of 2,4-D*, while applications to the lower surface were completely ineffective. The negative results from treating young toyon leaves with solution B were anticipated and were due to the sensitivity of the young tissues to contact injury by the tetraethyl orthosilicate.

Old toyon leaves responded somewhat differently than the young leaves. This may be because of the increased thickness of the cuticle (reduced cuticle penetration) and because of an increased resistance of the older tissues to contact injury. When solution A was applied to the upper surface of old toyon leaves there was no detectable penetration of the cuticle by 2,4-D* within the experimental period, but good autographs were produced from applications made to the lower surfaces. In contrast, applications of solution B to either upper or lower leaf surfaces resulted in good autographs; solution B was evidently not toxic enough to the tissues of mature toyon leaves to prevent translocation from applications made to the lower surfaces.

Live oak leaf responses differed slightly from those of toyon. The differences can be interpreted as indicating that live oak leaves are more sensitive to contact injury than toyon leaves. Other lines of evidence also support this belief.

Young live oak leaves, like young toyon leaves, absorbed and translocated solution A to about the same degree from upper- or lower-surface applications; however, solution B, when applied to the upper surface, resulted in good autographs, but when applications were made to the lower surface, the autographs, if any, were faint. Results with old live oak leaves followed the same general pattern as that obtained with the young leaves; however, with solution A absorption was poor, while solution B resulted in excellent absorption, especially when applied to the upper surfaces.

With coyote brush the responses were similar. Absorption and translocation were excellent from solution A applied to either surface, but very little took place with solution B. In the case of solution B, contact injury prevented the leaves from functioning.

Petioles usually responded rather well to applications of either solution A or B; however, for the most part, the strongest autographs were obtained with solution B. Actually, petiole applications represent applications to the axillary buds and to the stems, and most of the absorption probably takes place here. This is especially true with coyote brush, which has practically no true petiole; the droplets applied near the leaf base were observed to spread to the buds and up and down the stems for perhaps an inch.

TRANSLOCATION OF UREA* AND 2,4-D*

Radioactive urea and radioactive 2,4-D were made to the same specific activity in 50 per cent alcohol. The purpose was to compare these two different chemicals as to penetration and translocation. It is well known that when urea enters the leaf cells, it is decomposed to ammonia and CO_2 by the enzyme urease (Kuykendall and Wallace, 1954; Sumner and Myrback, 1951). Most of the radioactive carbon dioxide is possibly converted into sucrose and translocated in this form.

A 0.01-ml droplet of solution was applied to the underside of each of 10 adjacent leaves near the ends of the branches of toyon, live oak, and coyote brush. One week later the bark was sampled as previously described and autographed for 30 days. On each plant, one branch was treated with 2,4-D* and another with urea.*

Data from these tests are presented in figures 10 and 22. The 2,4-D* appeared to be absorbed slightly better than the urea* by all three plants. There was no appreciable difference in the translocation of either the 2,4-D* or the urea*; however, there is some suggestion that in live oak urea* moves more freely than 2,4-D*, which may indicate some chemical binding of the 2,4-D either in the sieve tubes or in other cells. Such binding has been indicated as possible in some plants with MCP (2-methyl-4-chlorophenoxyacetic acid), according to Brian and Rideal (1952).

The radioactivity was, for the most part, well distributed throughout the bark within 6 inches of the treated leaves, but at greater distances it was commonly restricted to certain parts of the bark. A uniform distribution in the bark near the treated leaves would be expected; as the treated branch joined other branches, the radioactivity would automatically be confined largely to those portions of the bark directly connected to the treated branch. This is apparently what occurred. However, the distribution in the bark was not always confined to streaks, nor was it always present in general or uniform concentrations. Thus it is clear that there is some lateral migration and utilization of the 2,4-D* or urea*, probably as a result of intense cambial activity in the shoot. This may be one explanation for the decrease in concentration of radioactivity, even within the "streaks" or the limited portions of the bark responsible for translocation. The urea* tended to be more generally distributed in the bark than the 2,4-D*, indicating a greater lability of urea or products derived from its radiocarbon, such as sucrose.

DISCUSSION AND CONCLUSIONS

A number of points of interest have arisen since the last report on this project (Crafts and Stewart, 1954). The early autographs indicated that little 2,4-D* was penetrating the cuticle on the upper sides of hypostomatal leaves, and subsequent treatments were therefore confined to the lower surfaces. Careful study of the original autographs and a number of later ones, however, showed that the tracer will penetrate the cuticle in the absence of stomata. In the penetration studies it was apparent that the intact cuticle may protect the mesophyll from too rapid absorption of the toxicant, which would result in rapid injury and an inhibition of translocation. This effect may explain the excellent results of airplane application of an oil formulation of 2,4-D ester on wedge-leaf ceanothus (Leonard and Harvey, 1956), whereas a similar treatment on young leaves of blue oak fails because of the contact injury to the leaves.

This finding re-emphasizes the significance of the whole problem of the penetration of herbicides into leaves and the relation of contact toxicity to uptake and transport. Possibly many of our present failures result not from lack of absorption but rather from too rapid and great an uptake, resulting in injury and failure to translocate.

The relation of 2,4-D transport to food movement in the plant is evident throughout this work. Also important is the fact, borne out by much experimentation, that only growing cells and tissues respond to 2,4-D. These facts emphasize the importance of thoroughly understanding the physiology of the plants to be treated and the difficulties of meeting all the requirements for success.

Translocation takes place throughout a fairly long portion of the year, particularly in evergreen species. As long as the plants are synthesizing foods and using them in growth, flowering, fruiting, and storage, transport is possible within the plant. Failure to kill active plants with green foliage apparently seldom results from the toxicant's failure to translocate. It may, rather, result from lack of absorption, from translocation to the wrong tissues (flowers, fruits, or vegetative shoots), or from the roots' inability to respond. Because root response to 2,4-D involves active root growth, available soil moisture is essential to successful treatment. Inadequate soil moisture is one of the greatest obstacles to successful use of hormone herbicides in brush control in the West.

The period for successful treatment of many brushy species is apparently a relatively brief time in the spring or early summer when the leaves have fully expanded but have not become too heavily cutinized. If chemicals are to be effective, soil moisture must still be available for root growth. Weather conditions, too, should be favorable for treatment (moderate temperature and a humidity above 20 per cent). In seasons of low rainfall such periods may last only a few days; in extreme cases there may be no such time at all. This has been the case with respect to mesquite control in Texas and Arizona during a succession of dry years.

Continued spray programs on many species have proved that, in contrast to blue oak, arroyo willow, which thrives only in moist habitats, may be treated throughout a rather long period from the time the leaves have fully expanded until late in the autumn (Leonard and Harvey, 1956). And, in contrast to these two deciduous species, several evergreen species may be treated in late winter or early spring while the previous season's leaves are still green and active and during the rainy season when soil moisture is amply available. Toyon and wedge-leaf ceanothus are such species.

It would be wrong to imply that absorption, translocation, and root activity are the only factors involved in successful treatment of brushy plants with 2,4-D. Species susceptibility, temperature, nutrition, secondary invasion by fungi and bacteria, and many other factors are undoubtedly important. But, for successful results, at least four physiological factors must be favorable: (1) The herbicide must be absorbed. (2) Photosynthesis must provide assimilates for movement through the phloem. (3) Translocation from active, photosynthesizing leaves to the roots must be going on. (4) Root activity must involve meristematic activity and growth, not just storage.

In California these four functions may not coincide in a number of brushy species within a given locality. For example, manzanita, wedgeleaf ceanothus, toyon, live oak, and coyote brush are perennials with green leaves throughout the winter. Arroyo willow, blue oak, and poison oak, on the other hand, are deciduous, and the time between leaf maturation and the depletion of soil moisture may be short.

Blossoming in the seven species used in this study may occur as early as January (manzanita) or as late as July or August (coyote brush). Hence, budding or blossoming cannot be used as a criterion for determining time of treatment as it can in many herbaceous perennials (Crafts, 1956). A further consideration involves the stage of growth and the conditions of growth in the brushy plants. Oaks, for instance, may be treated as young seedlings in their first year's growth, as small trees or shrubs, or as old, mature trees with trunks several feet in diameter. The method of treatment varies, of course, according to each stage of growth. Brush seedlings may be growing in competition with forage species such as grasses and clover, or they may be in competition with themselves and other brush species in dense stands of brush. The availability of soil moisture, and hence the optimum time for treatment, may vary widely under these different conditions. Obviously, there can be no optimum time for treating mixed stands of brush under these western range conditions, and even in pure stands conditions may be such that the optimum time may vary according to the age and nature of the plant stand. Years of research will be required to study all the variables concerned, and radioactive isotopes will be valuable tools.

It seems quite obvious that fire will be the primary tool for brush clearance on ranges in many western states. Chemicals will provide a supplementary, but an essential, method for eliminating seedlings and killing stumps of resprouting species. They are a primary tool in treating trees in woodlands where fire, for many reasons, is undesirable.

Where fire is used, reseeding with tested forage varieties is essential (Love and Jones, 1952), and management must be aimed at the establishment and maintenance of successful stands of forage. Reburning may be used in many places to control brush seedlings and to suppress resprouts. However, after the initial burning and seeding, chemicals provide a valuable method for eliminating seedlings and resprouts. Chemical control of brush may provide the best and most useful method in many situations on almost every range.

SUMMARY

After suitable methods had been devised, studies on the absorption and translocation of radioactive 2,4-D (2,4-D*) were carried out on seven species of woody plants common to California.

Coyote brush (*Baccharis pilularis*): 2,4-D* was absorbed and translocated slightly in February, intensely in April, less intensely in May and

June, and not at all in July. In February and March movement was downward from treated leaves, in April almost entirely upward.

Arroyo willow (*Salix lasiolepis*): Little translocation of 2,4-D* occurred before April 15; from late April until late summer translocation of the tracer was continuous. Translocation both upward and downward from treated leaves occurred from late April until September. Upward movement was predominant in April; in October all movement was downward.

Wedge-leaf ceanothus (*Ceanothus cuneatus*): little translocation of 2,4-D* was observed. Application to the lower surfaces of leaves resulted in rapid killing of the treated leaves; this may explain the failure of uptake and transport of the tracer.

Manzanita (*Arctostaphylos manzanita*): 2,4-D* was absorbed and translocated throughout May; after this time bark samples could not be obtained. Some upward movement took place in March and April; in general, downward translocation was predominant.

Toyon (*Photinia arbutifolia*): Absorption and translocation of 2,4-D* were prominent from February through October; transport was primarily downward in February and March, upward in midspring and summer, and downward again by fall. Radioautographs obtained from treatments in September and October were faint.

Blue oak (*Quercus douglasii*): Tracer studies were mostly negative. Starting in March and continuing until June 23, only 5 out of 42 samples showed any movement, and the average distance of transport was only 5.2 inches. Blue oak leaves are very sensitive to contact action by 2,4-D. This probably explains the poor results of the tracer tests and the similar poor response or blue oak trees in the field to 2,4-D treatment.

Live oak (*Quercus wislizenii*): Translocation of 2,4-D* was active from February through September. Movement was entirely downward in February, somewhat upward after new growth started in March, but largely downward through the rest of the season.

These studies emphasize the deleterious effect of contact injury on the uptake and transport of this herbicide. They strengthen the evidence for a correlation between food movement and 2,4-D movement in plants. They show that the chemical may move in evergreen species for many months, whereas in deciduous species it may move only during relatively short periods. They pinpoint the importance of soil moisture and root growth to 2,4-D transport and response. And finally, they prove that different species require different treatment and that a single application cannot be expected to control mixed brush populations under California conditions.

LITERATURE CITED

BRIAN, R. C., and E. K. RIDEAL
1952. On the action of plant growth regulators. Biochem. et Biophys. Acta **9**:1–18.

CRAFTS, A. S.
1956. Studies on the absorption and translocation of 2,4-D by wild morning-glory. Hilgardia **26**(6):335–365.

CRAFTS, A. S., and DOUGLAS N. STEWART
1954. Use of radioactive isotopes of 2,4-D in brush control. Research Progress Report 14th Western Weed Control Conf. pp. 131–134 (Mimeo.).

EMRICK, WALTER E., and OLIVER A. LEONARD
1954. Delayed kill of interior live oak by fall treatment with 2,4-D and 2,4,5-T. Jour. Range Management **7**(2):75–76.

KUYKENDALL, J. RICHARD, and ARTHUR WALLACE
1954. Absorption and hydrolysis of urea by detached citrus leaves immersed in urea solutions. Proc. Amer. Soc. Hort. Sci. **64**:117–127.

LEONARD, OLIVER A., and C. E. CARLSON
1955. Chemical brush control techniques on California range lands. Progress Report California Div. Forestry. 12 p. (Mimeo.).

LEONARD, OLIVER A., and WILLIAM A. HARVEY
1956. Chemical control of woody plants in California. California Exp. Sta. Bul. **755**: 1–39.

LOVE, R. MERTON, and BURLE J. JONES
1952. Improving California brush ranges. Revised by R. Merton Love, Dorman C. Sumner, and Victor P. Osterli. California Agr. Exp. Sta. Cir. **371**:1–38.

SUMNER, J. B., and K. MYRBACK
1951. The enzymes. (See Vol. 1, Part 2, Chapter 24.) Academic Press, Inc., New York, N.Y.

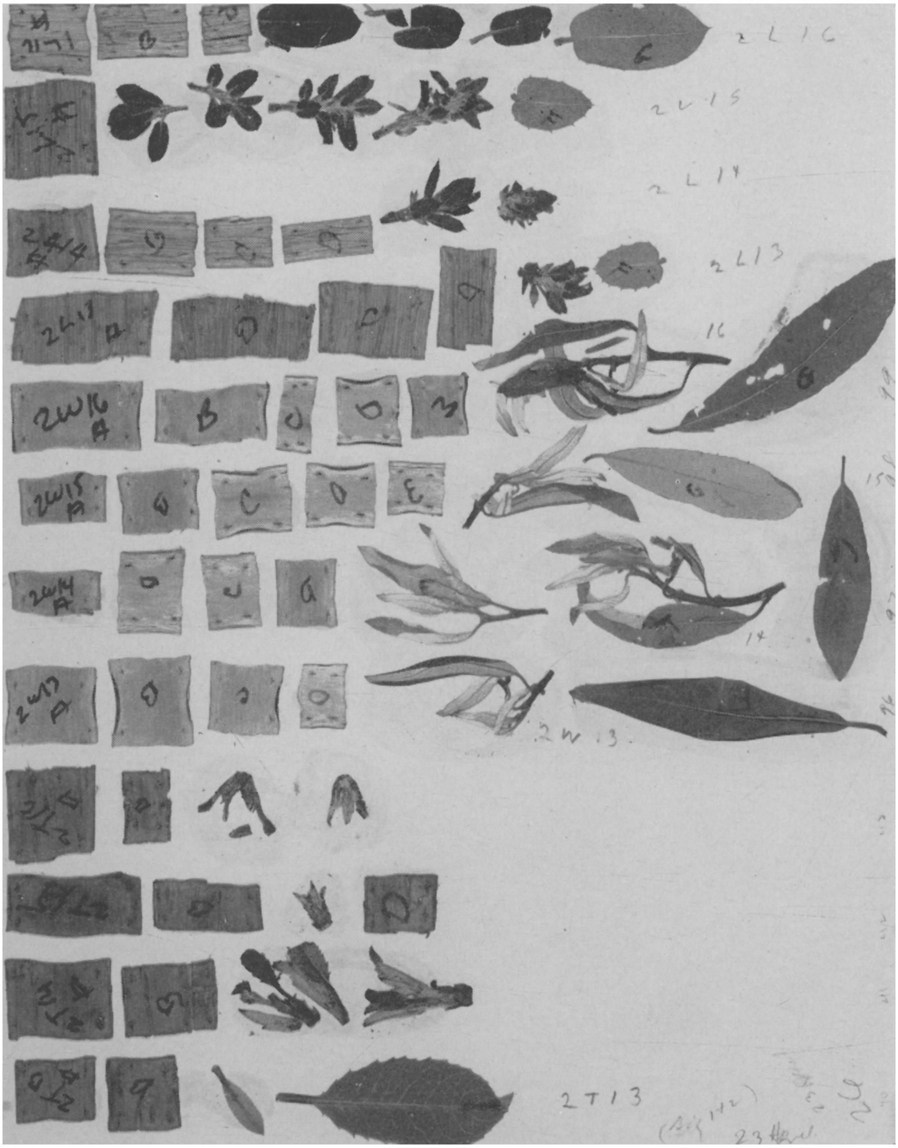

Fig. 1. Samples of bark, stems, and leaves of toyon, arroyo willow, and live oak cemented to a sheet of paper and ready to be placed, face down, on the X-ray film.

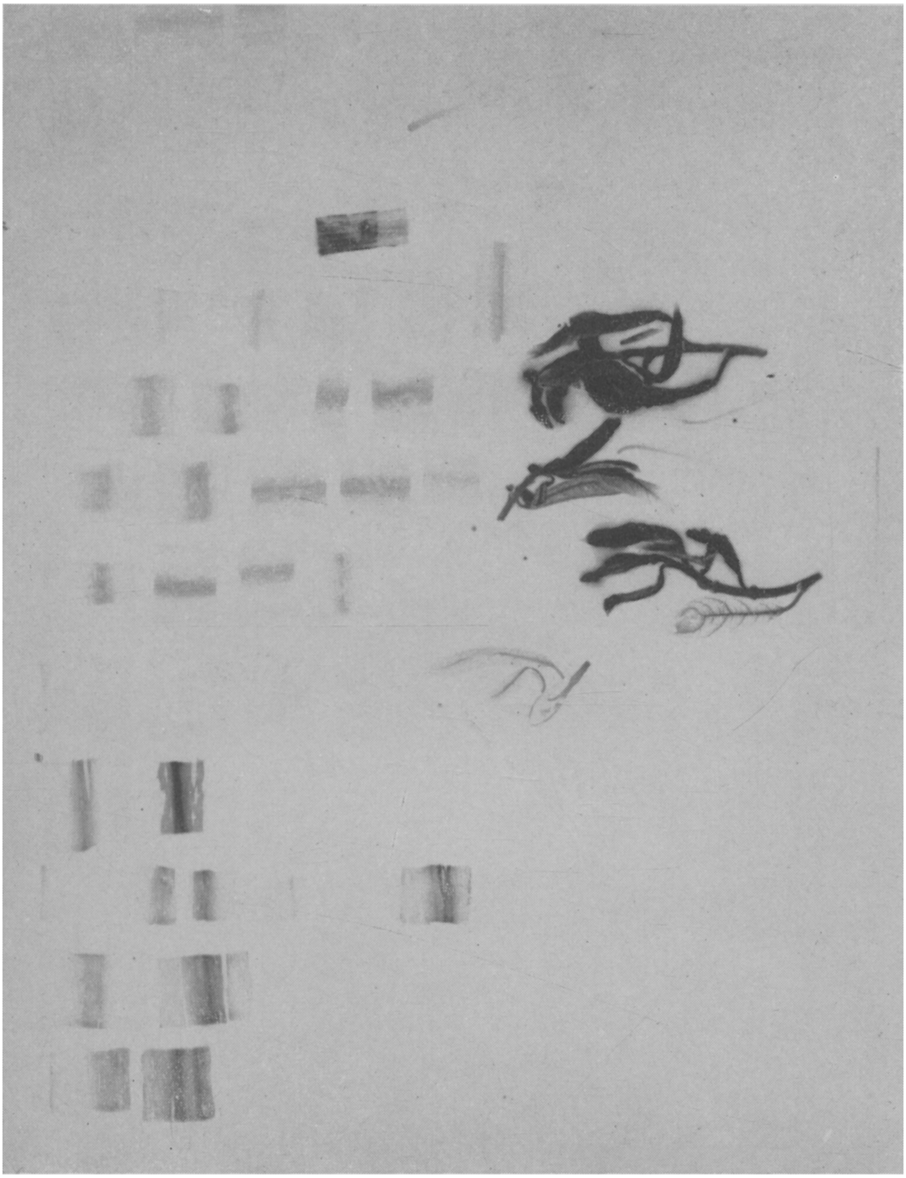

Fig. 2. Radioautograph of the plant samples shown in figure 1. The plants were treated on April 15. Samples were taken April 24. Exposure on the film was four weeks. Movement has been upward and downward in willow, downward in toyon and live oak.

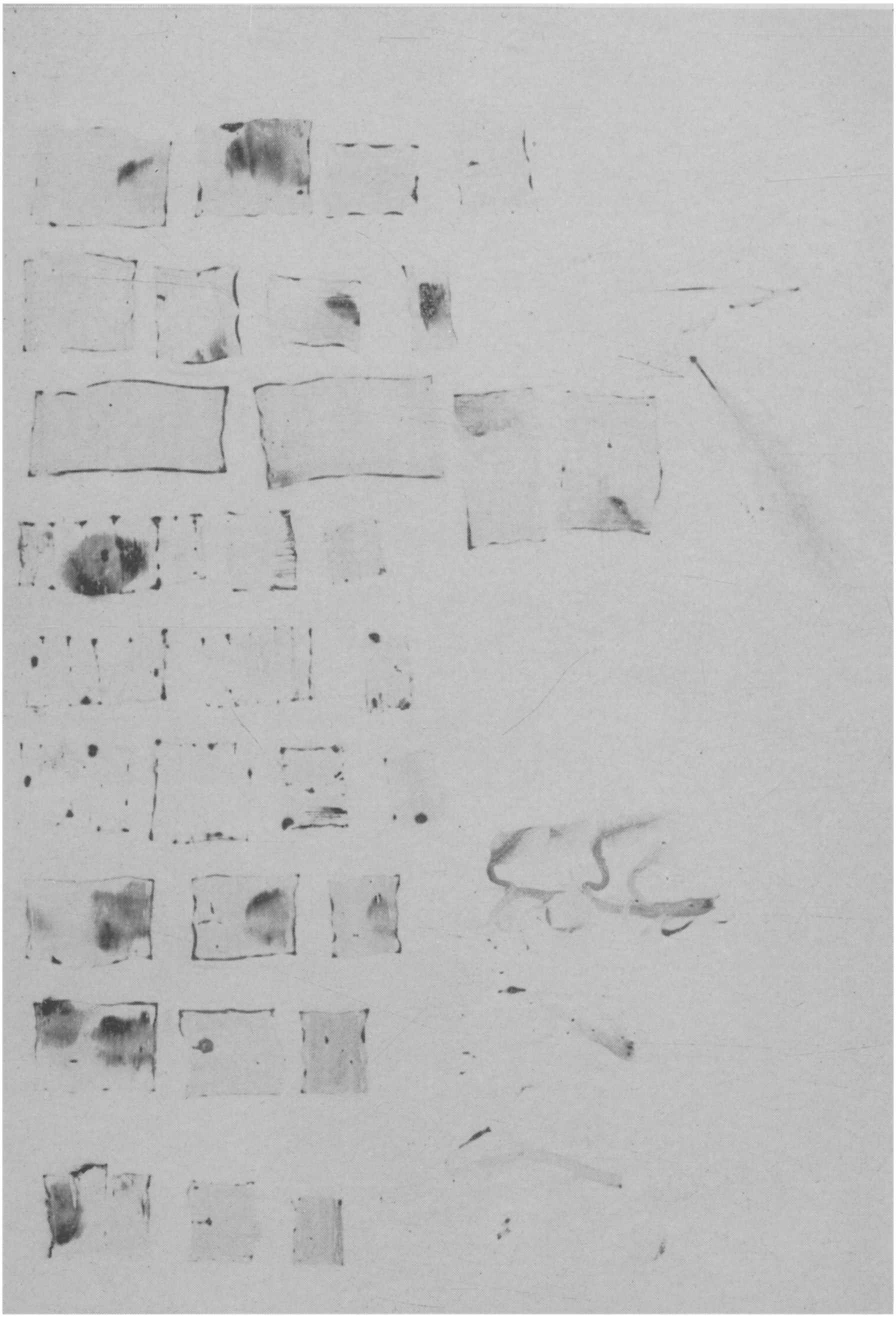

Fig. 3. Radioautograph made with high pressure and soft backing for the film. Compare with figure 2, obtained with less pressure and a firm backing.

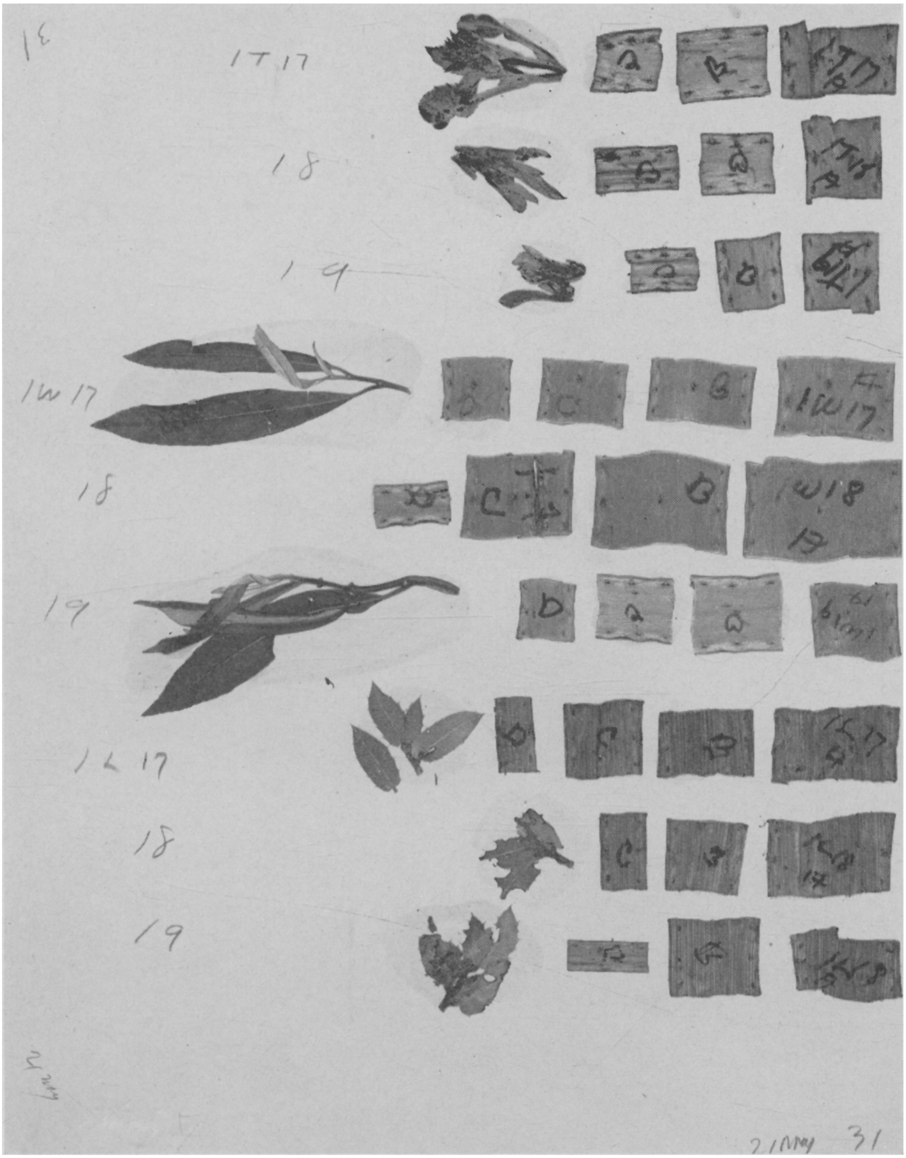

Fig. 4. Samples of live oak, arroyo willow, and toyon from plants treated May 14 and sampled May 21.

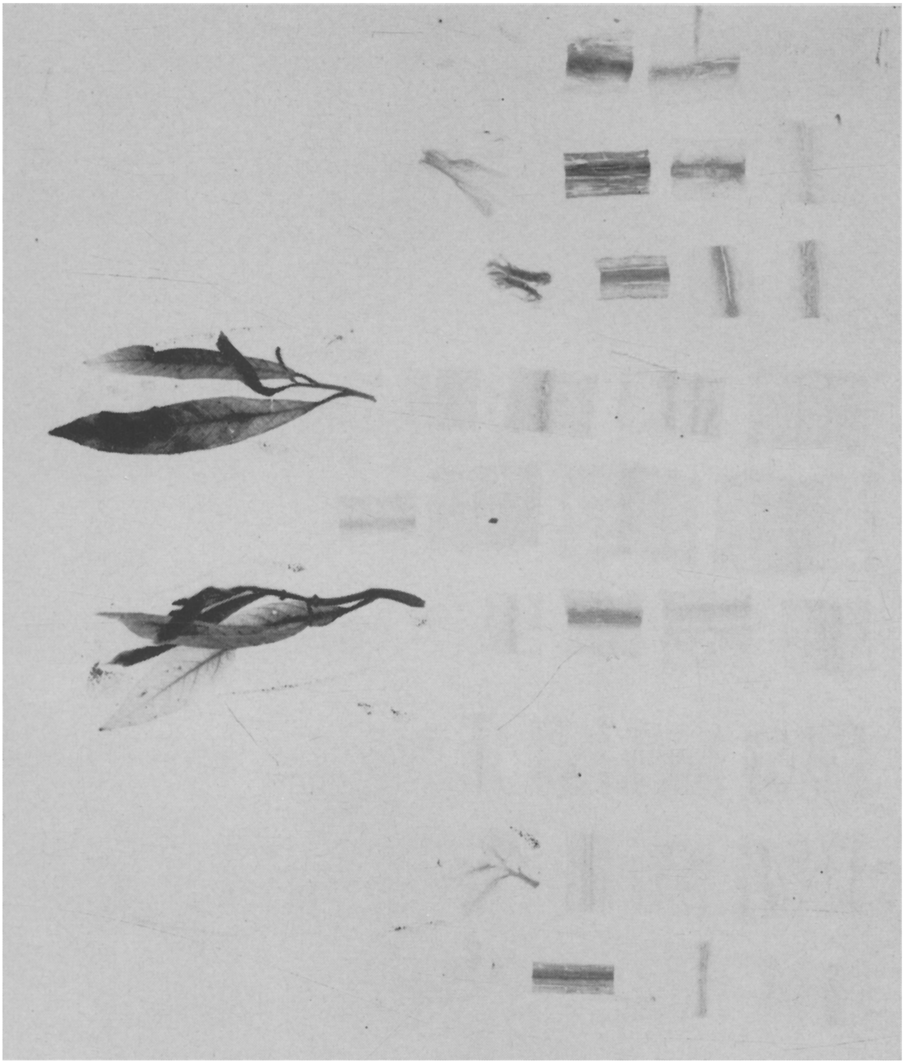

Fig. 5. Radioautograph of the samples of figure 4. Note that movement has been upward in the two willow tips sampled and upward in two of the three toyon shoots and one (middle) of the live oak shoots. All three show some downward movement.

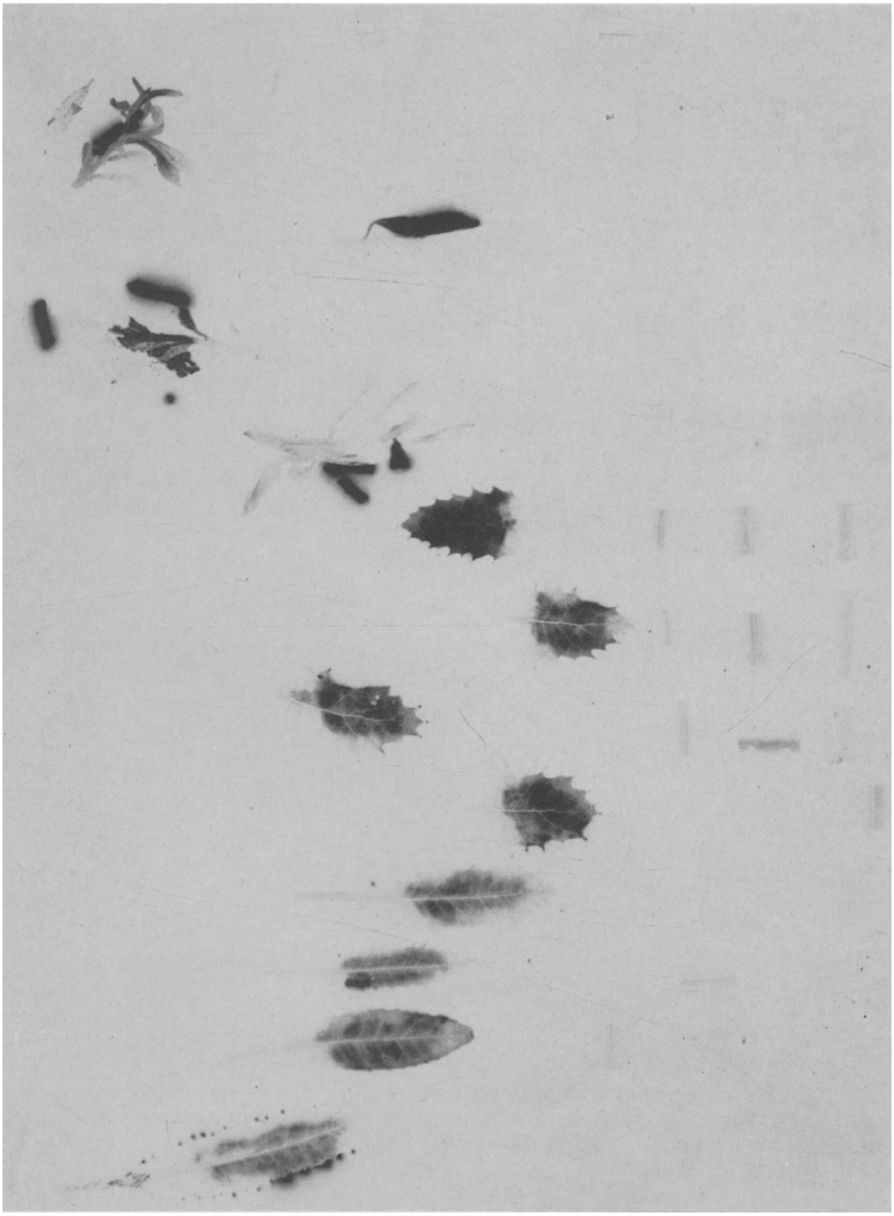

Fig. 6. Radioautograph of one of the first collections. The species are toyon, arroyo willow, and live oak, and the treated leaves as well as bark are shown. These treated leaves were so high in radioactivity that they caused spots on other films in the bundle being exposed. In subsequent samplings, treated leaves were omitted.

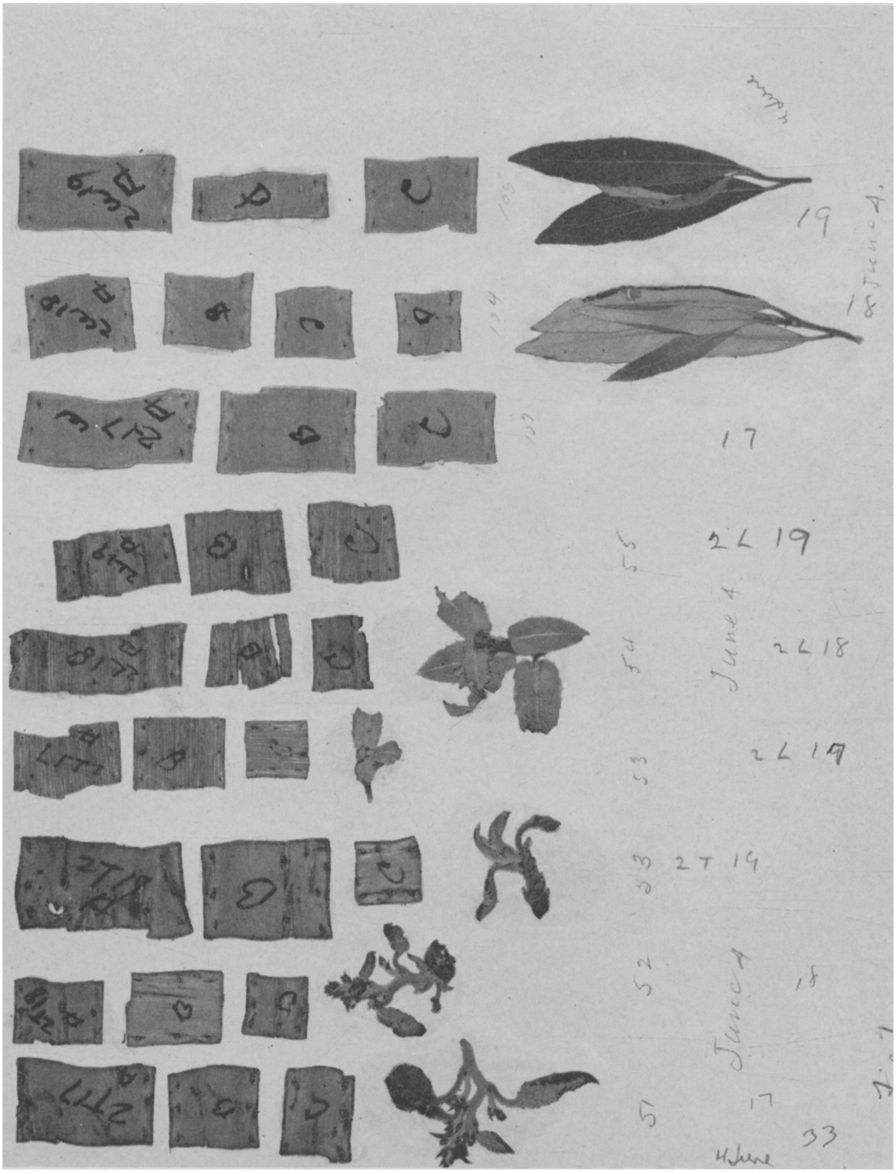

Fig. 7. Samples of live oak, arroyo willow, and toyon from plants treated May 14 and sampled June 4.

Fig. 8. Radioautograph of the samples of figure 7. Movement after three weeks in this willow plant has been slight and in both directions; in live oak it has been downward only; in toyon some downward movement has occurred, but it is strong in an upward direction into the inflorescences. Live oak at this time had formed terminal buds and there was no shoot growth.

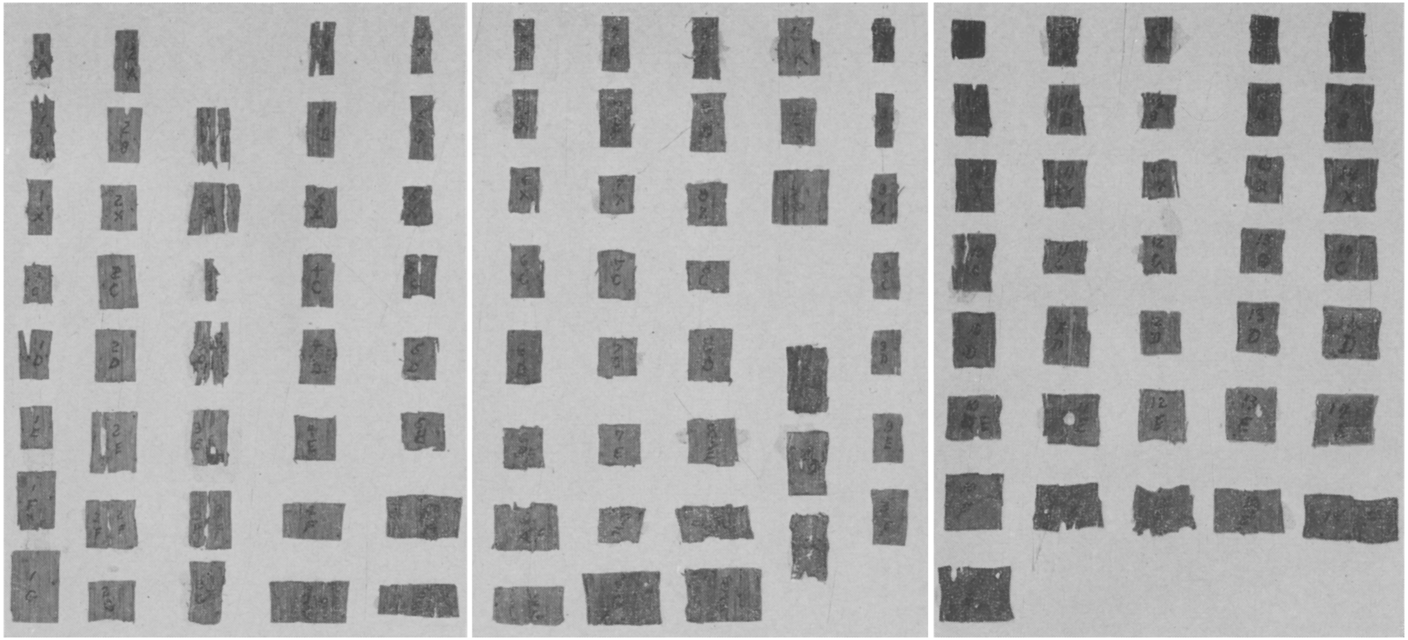

Fig. 9. Samples of live oak, toyon, and coyote brush plants treated April 5, 1954, and sampled April 13, 1954. The plants received two radioactive tracers, 2,4-D* and urea*. Ten leaves near the tips of branches were treated, each receiving 0.01 ml of a 50 per cent alcohol solution containing the isotope at a concentration that gave 400 counts per minute when 0.01 ml was dried on a planchet 26 mm in diameter. The two top bark samples were taken within the treated region on the shoot. The third sample was taken 1 to 2 inches below the treated region; the fourth sample, 3 to 4 inches below; the fifth sample 6 to 7 inches below; the sixth sample, 12 to 13 inches below; the seventh sample, 24 to 25 inches below; and the eighth sample, 36 to 37 inches below. The first vertical row in each group received 2,4-D*, the second urea*, the third 2,4-D*, the fourth urea*, and so on. Row 9 is a control.

Fig. 10. Radioautographs of samples shown in figure 9.

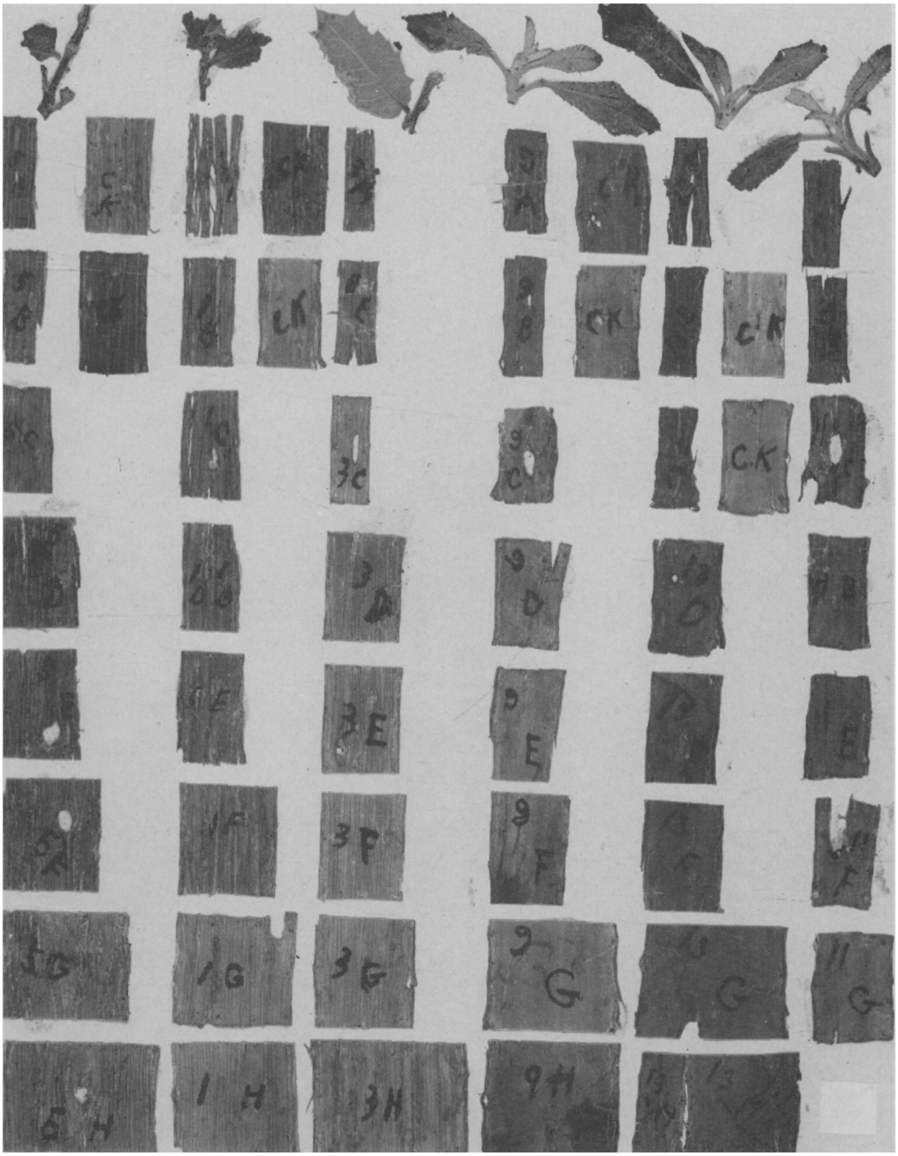

Fig. 11. Bark and shoot samples of live oak and toyon plants treated June 1, 1954, and sampled June 8. The plants received 2,4-D* at the same rate as in figure 9. Shoot tips shown were taken immediately above the treated region. Growth at the tips of these plants was slowing down, and the top 10 fully expanded leaves were treated. The first, third, and fifth vertical rows represent the treated samples, rows 2 and 4 are controls. There was no upward movement in live oak but strong upward movement in toyon. Downward movement was pronounced in one shoot of each species but not extensive. Note the streaking in the downward movement.

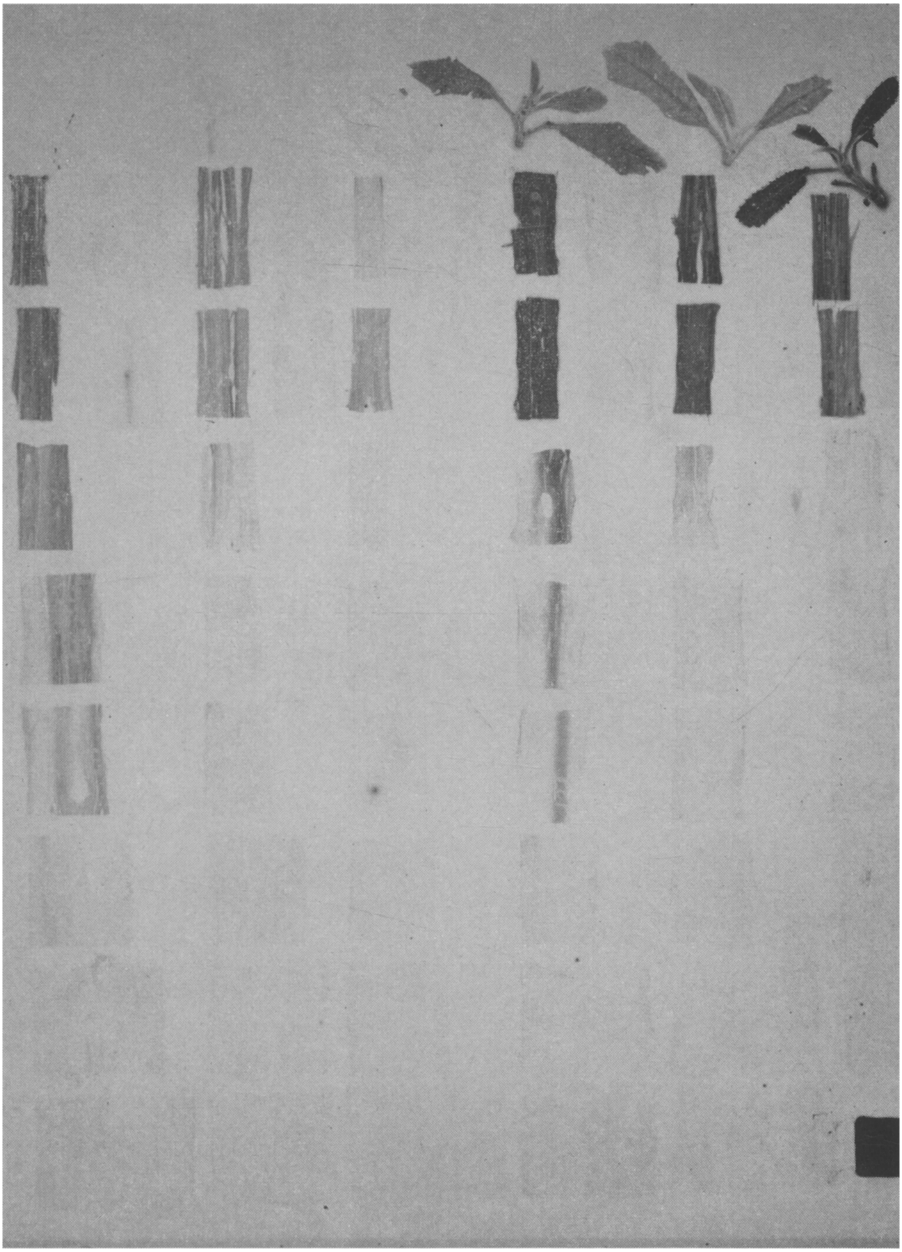

Fig. 12. Radioautographs of samples shown in figure 11.

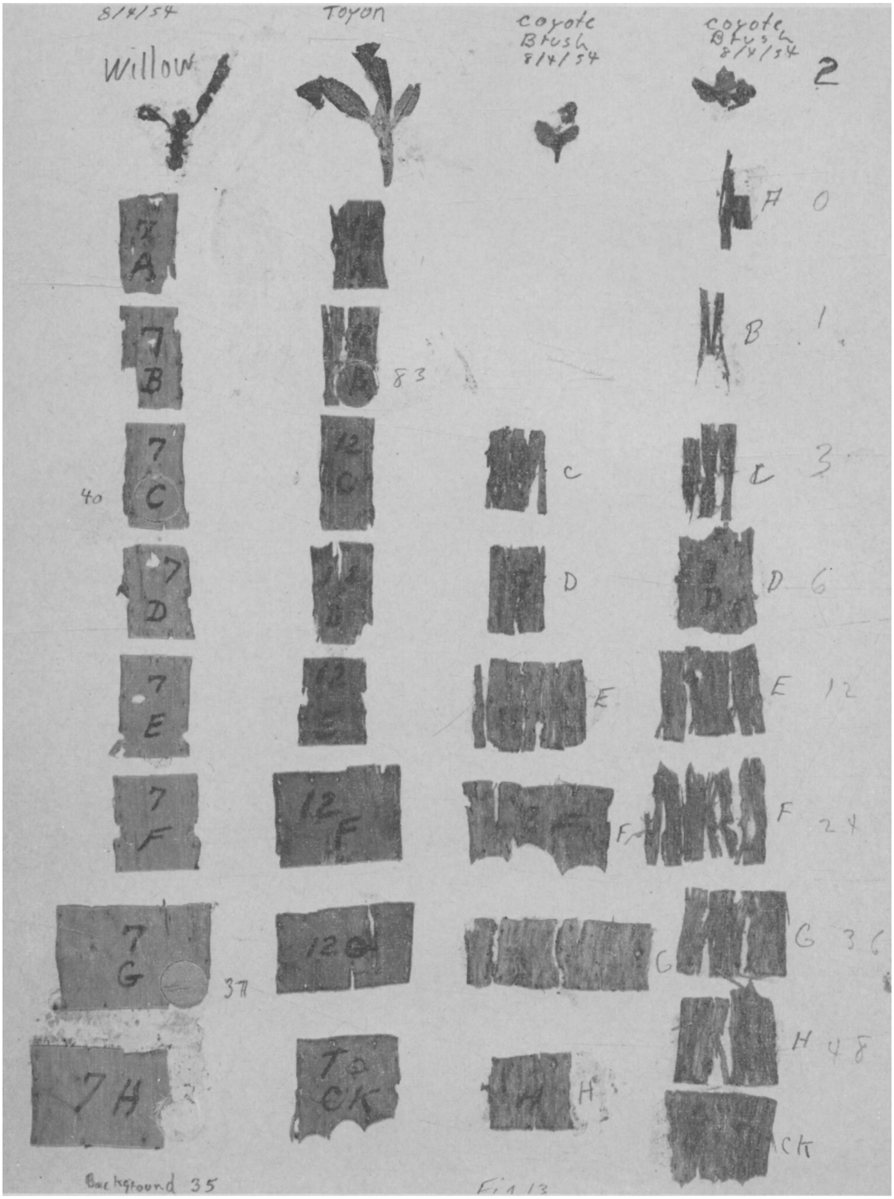

Fig. 13. Bark and shoot samples of arroyo willow, toyon, and coyote brush plants treated August 4, 1954, and sampled August 15. Treatments were as in figure 10, and sampling was the same. There was both upward and downward movement in willow and toyon, but only downward movement in coyote brush. Bark of the latter was starting to stick and hence difficult to sample. A few counts were made on these samples. On willow, sample C had a count of 40, G a count of 37, and both H and the background a count of 35. On toyon, sample B had a count of 83.

Fig. 14. Radioautographs of samples shown in figure 13.

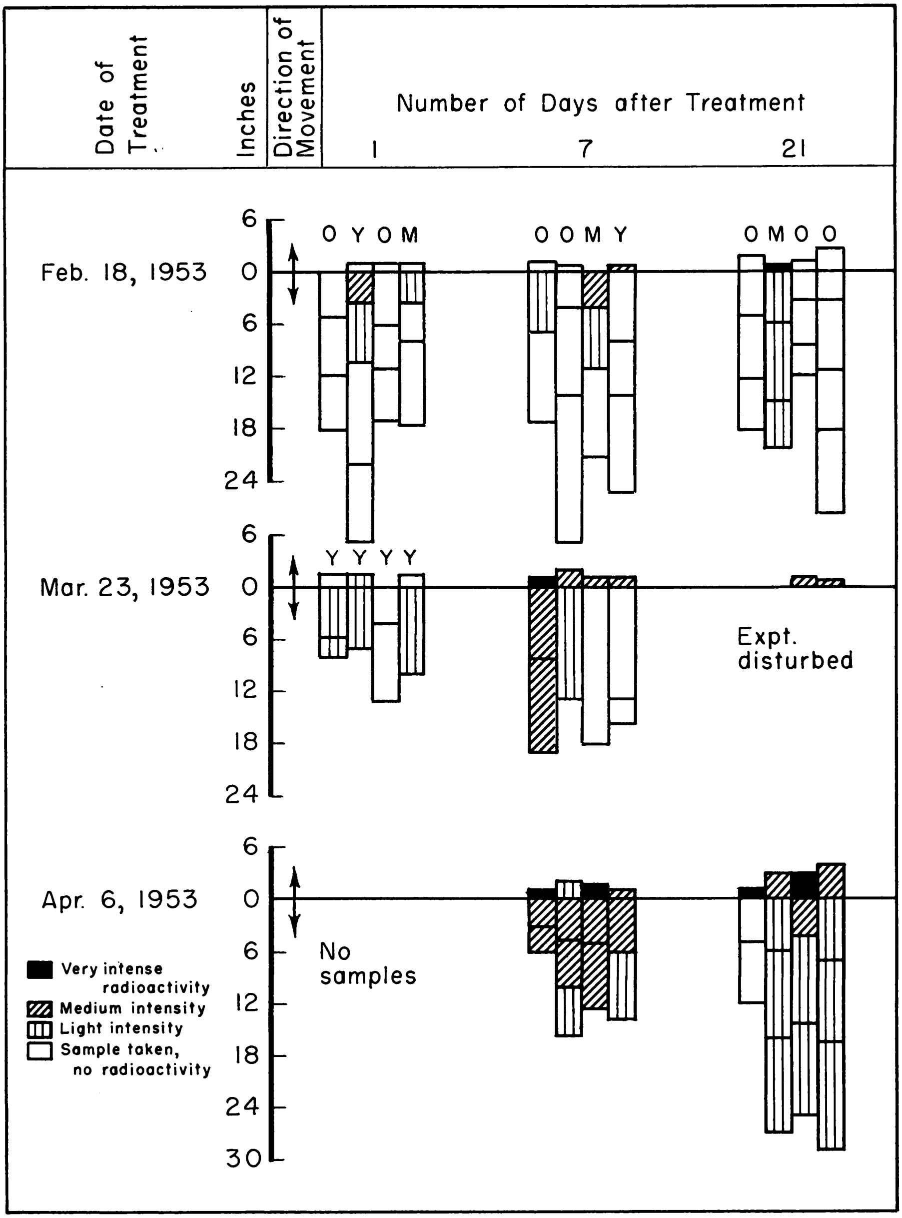

Fig. 15A. Charts showing distribution of radioactivity in shoots of coyote brush after leaves were treated with 2,4-D*. Bars above zero lines represent upward movement of the tracer; below zero, downward movement. O = old leaves; M = mature; Y = young.

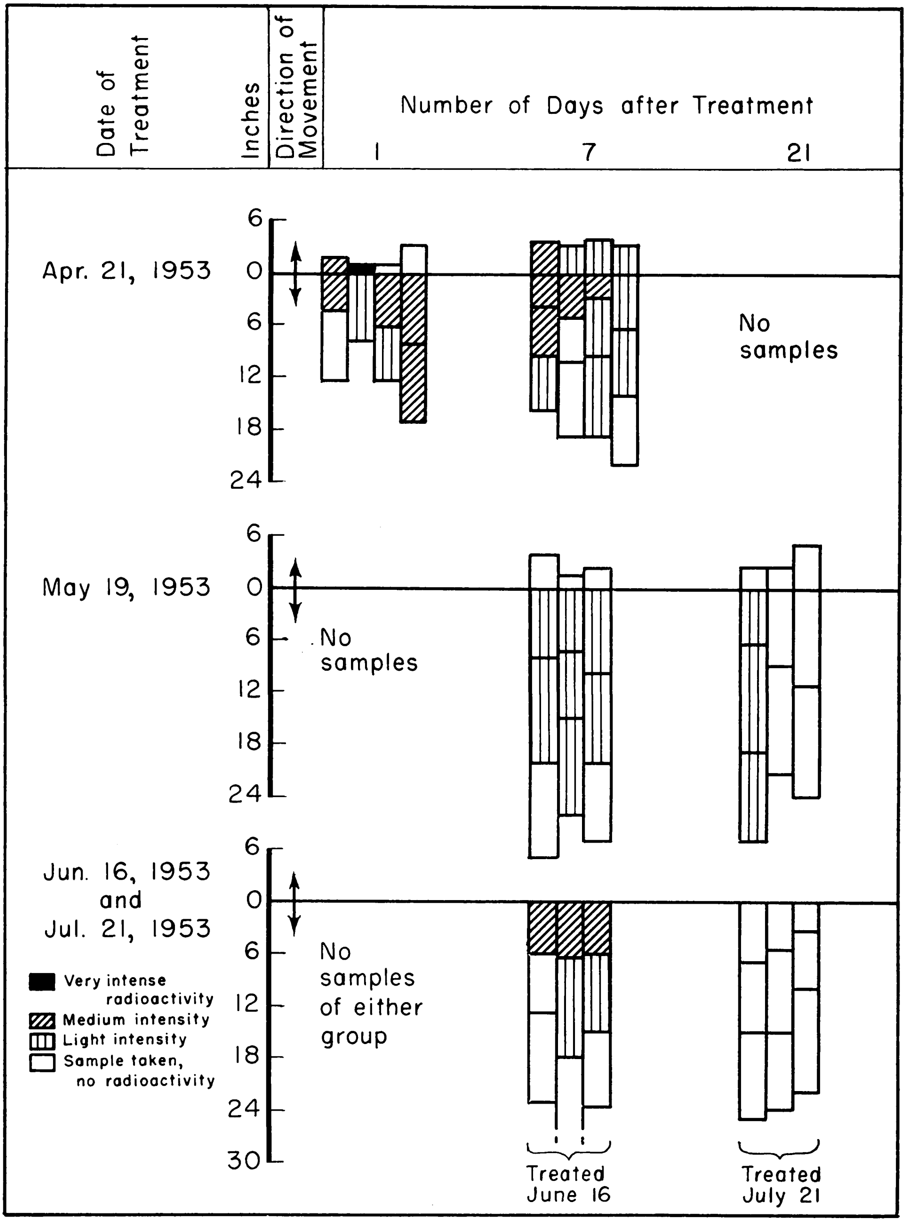

Fig. 15B. Coyote brush: same as 15A except that all treated leaves were mature.

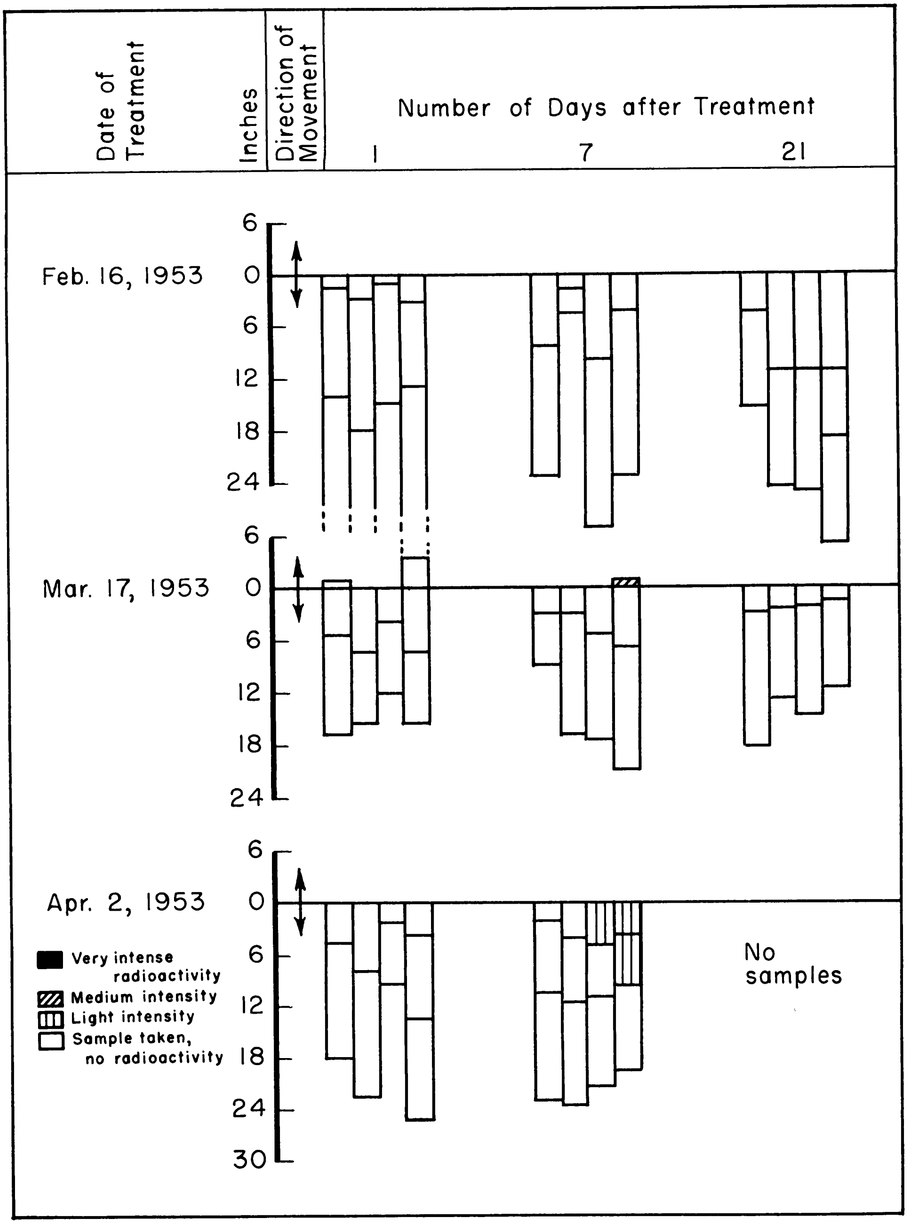

Fig. 16A. Charts showing distribution of radioactivity in shoots of willow after leaves were treated with 2,4-D*. Bars above zero lines represent upward movement of the tracer; below zero, downward movement. All treated leaves were young.

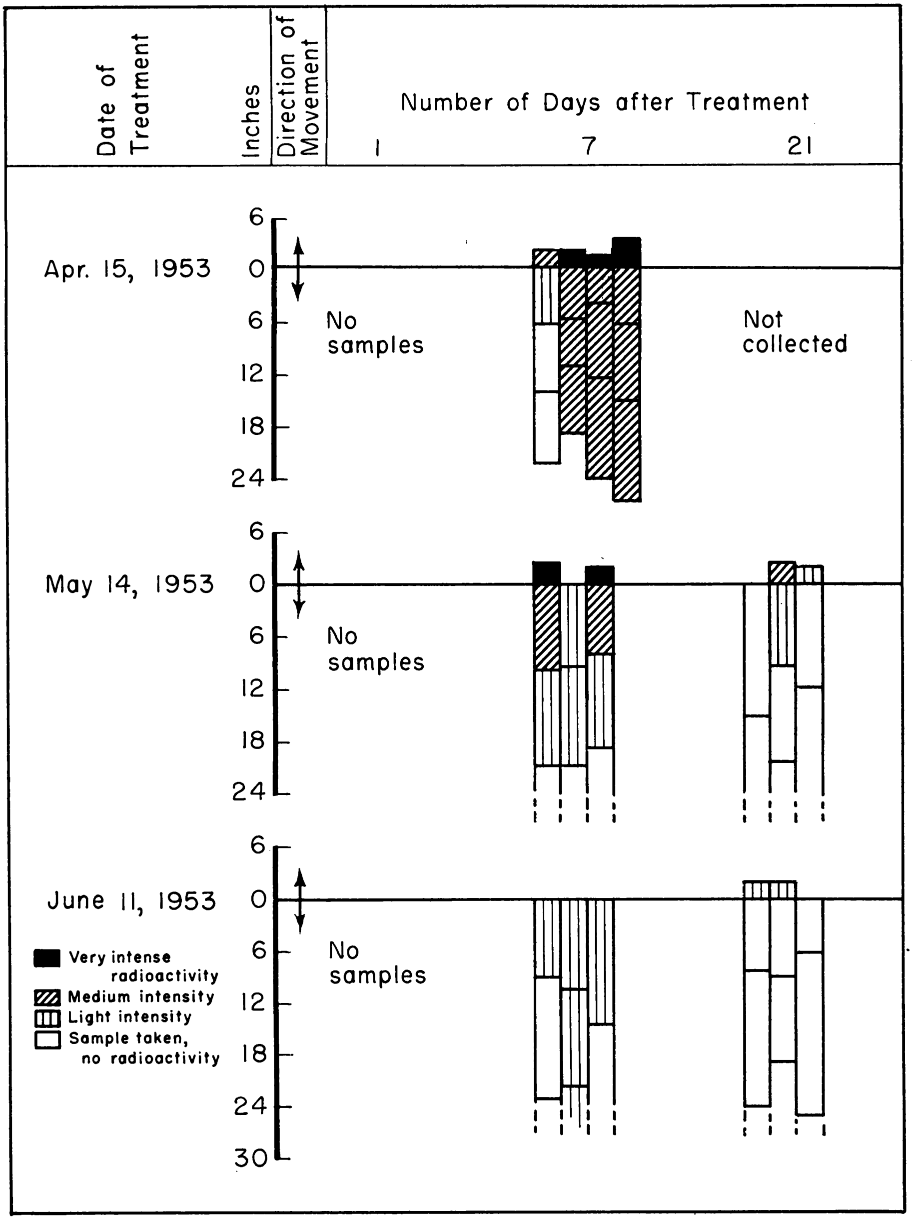

Fig. 16B. Willow: same as 16A except that treatments were later as indicated. All treated leaves were mature.

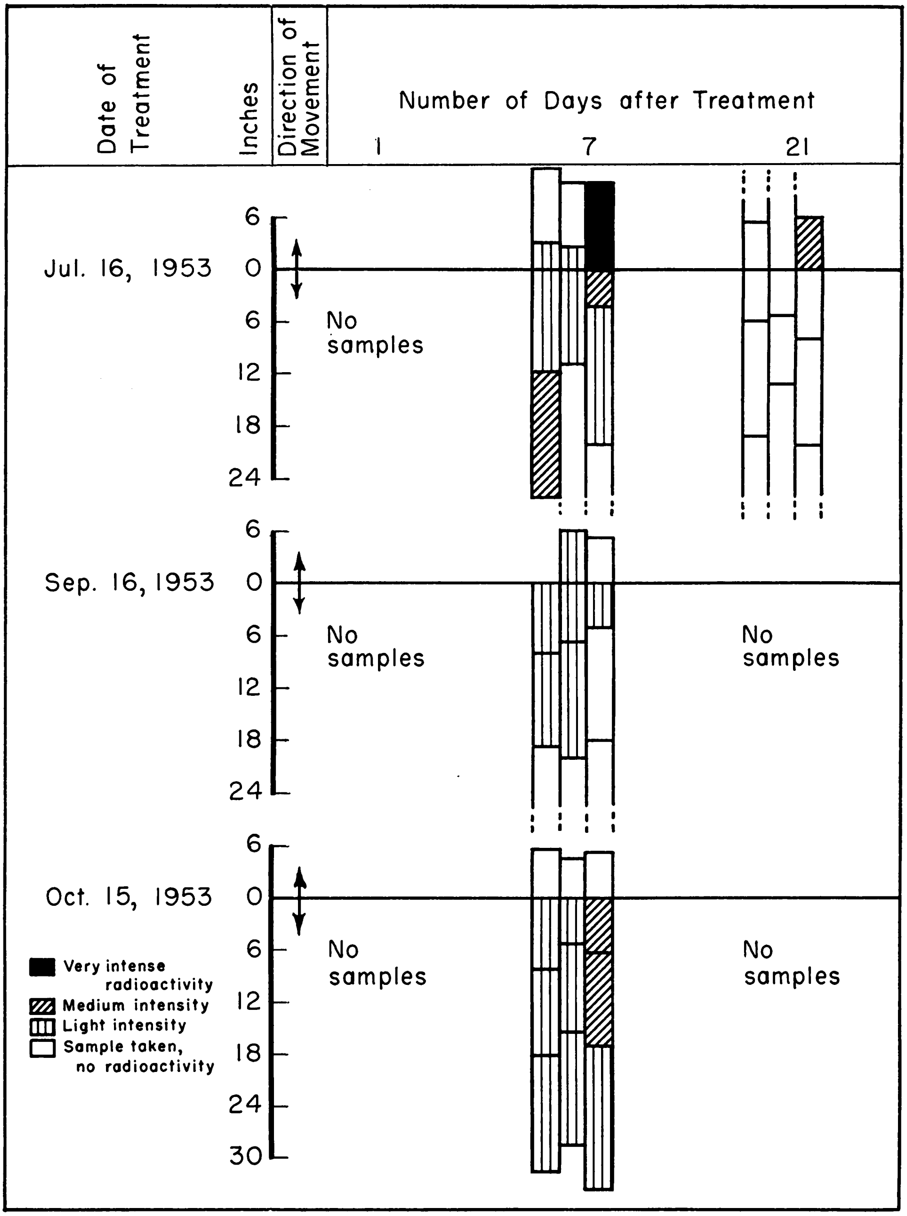

Fig. 16C. Willow: same as 16A except that treatments were later.

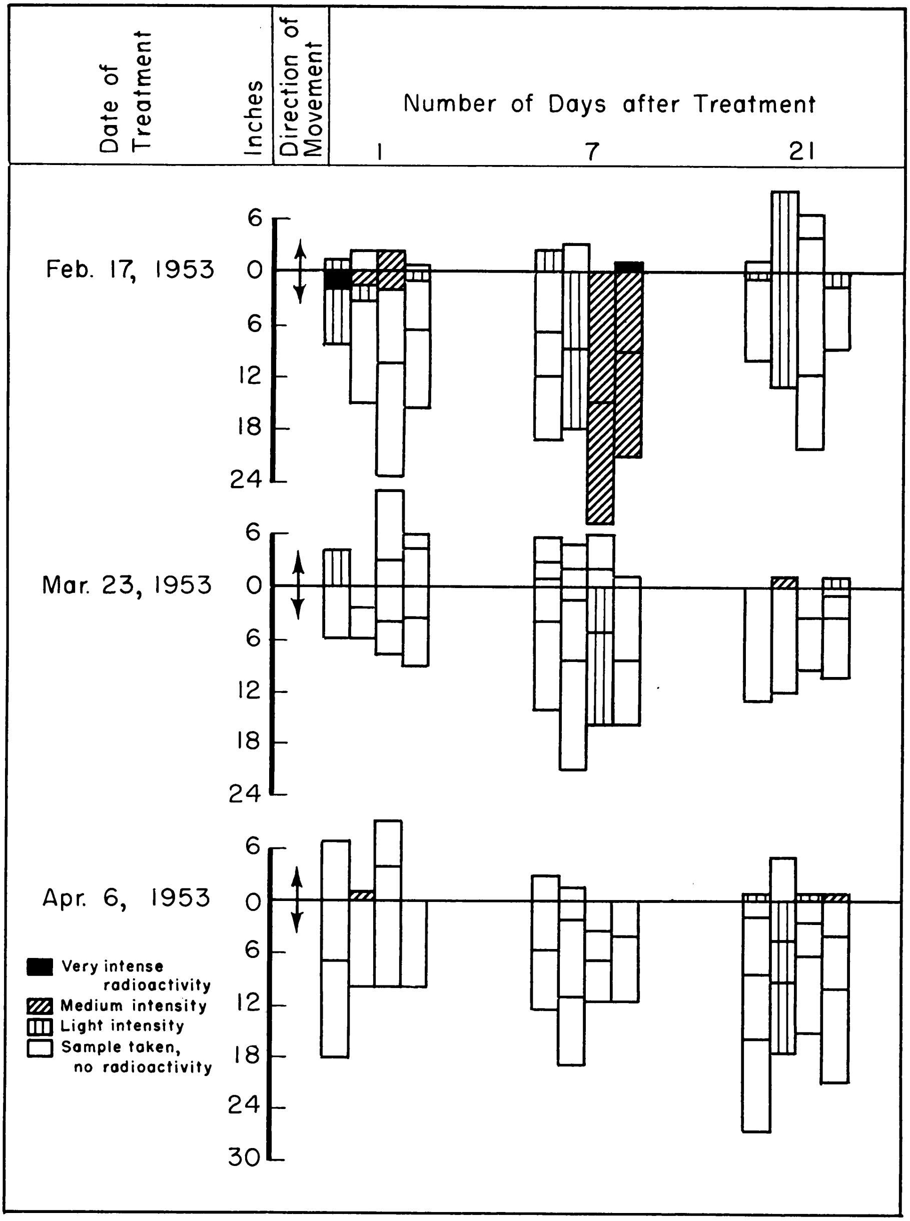

Fig. 17A. Charts showing distribution of radioactivity in shoots of *Ceanothus cuneatus* after leaves were treated with 2,4-D*. Bars above zero lines represent upward movement of the tracer; below zero, downward movement. All treated leaves were mature.

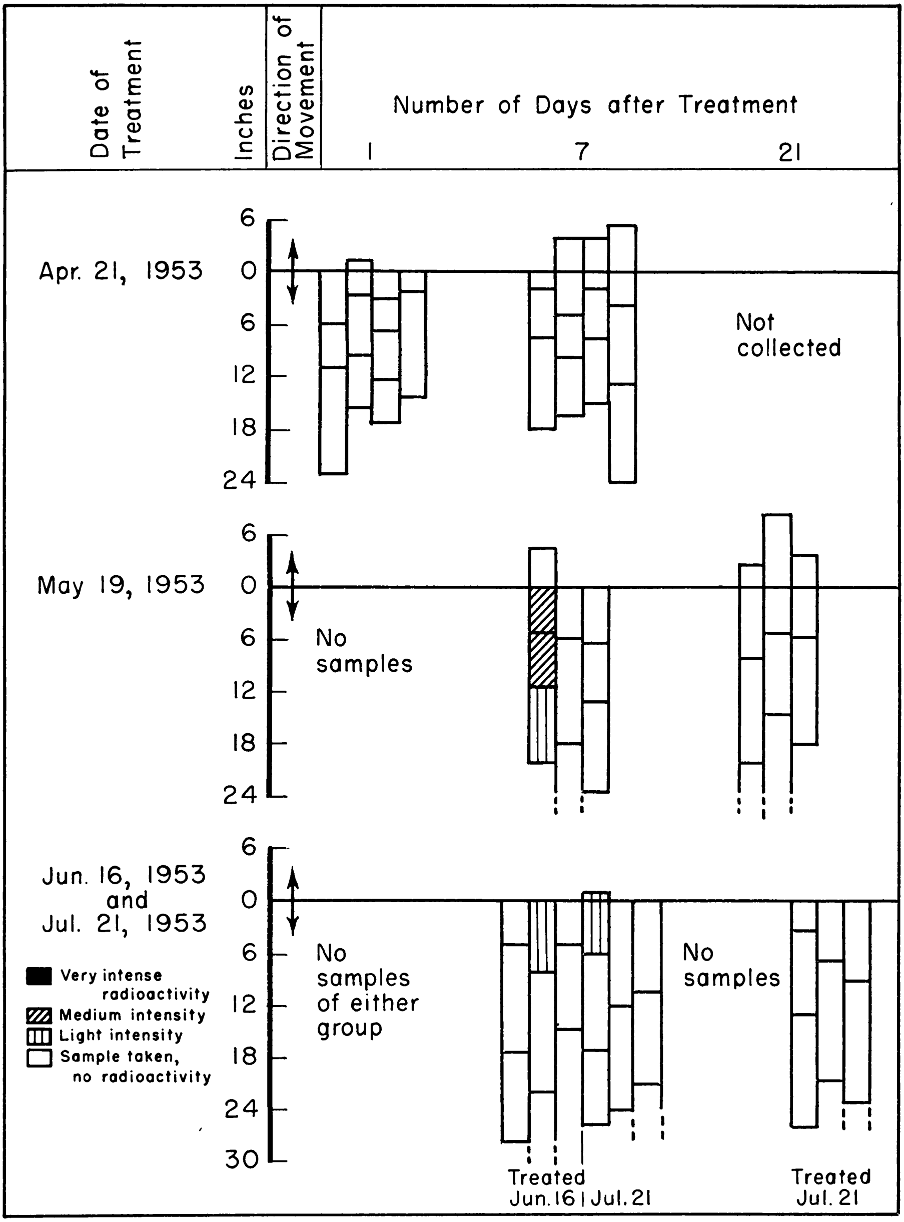

Fig. 17B. *C. cuneatus:* same as 17A except that treatments were later. All treated leaves were mature.

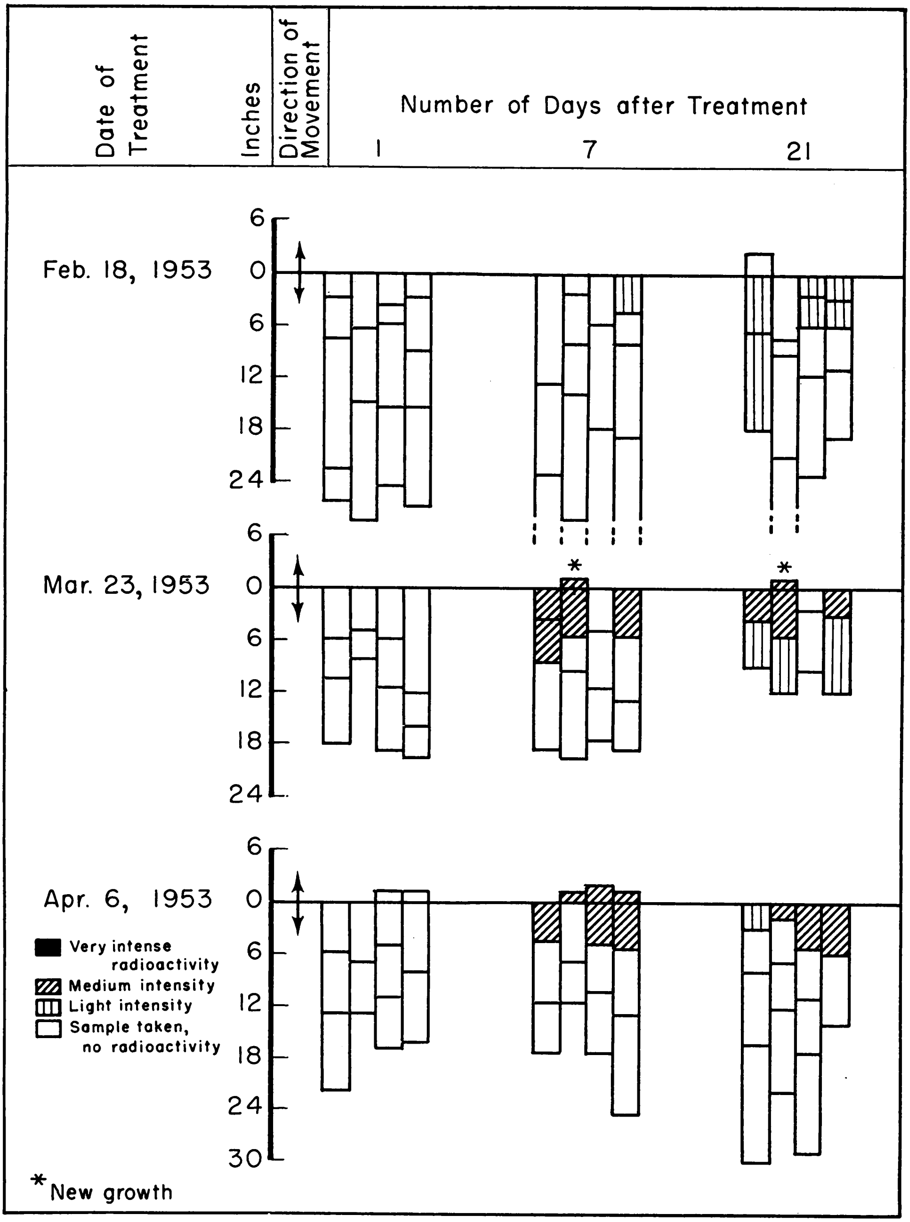

Fig. 18A. Charts showing distribution of radioactivity in shoots of *Arctostaphylos manzanita*. All treated leaves were mature.

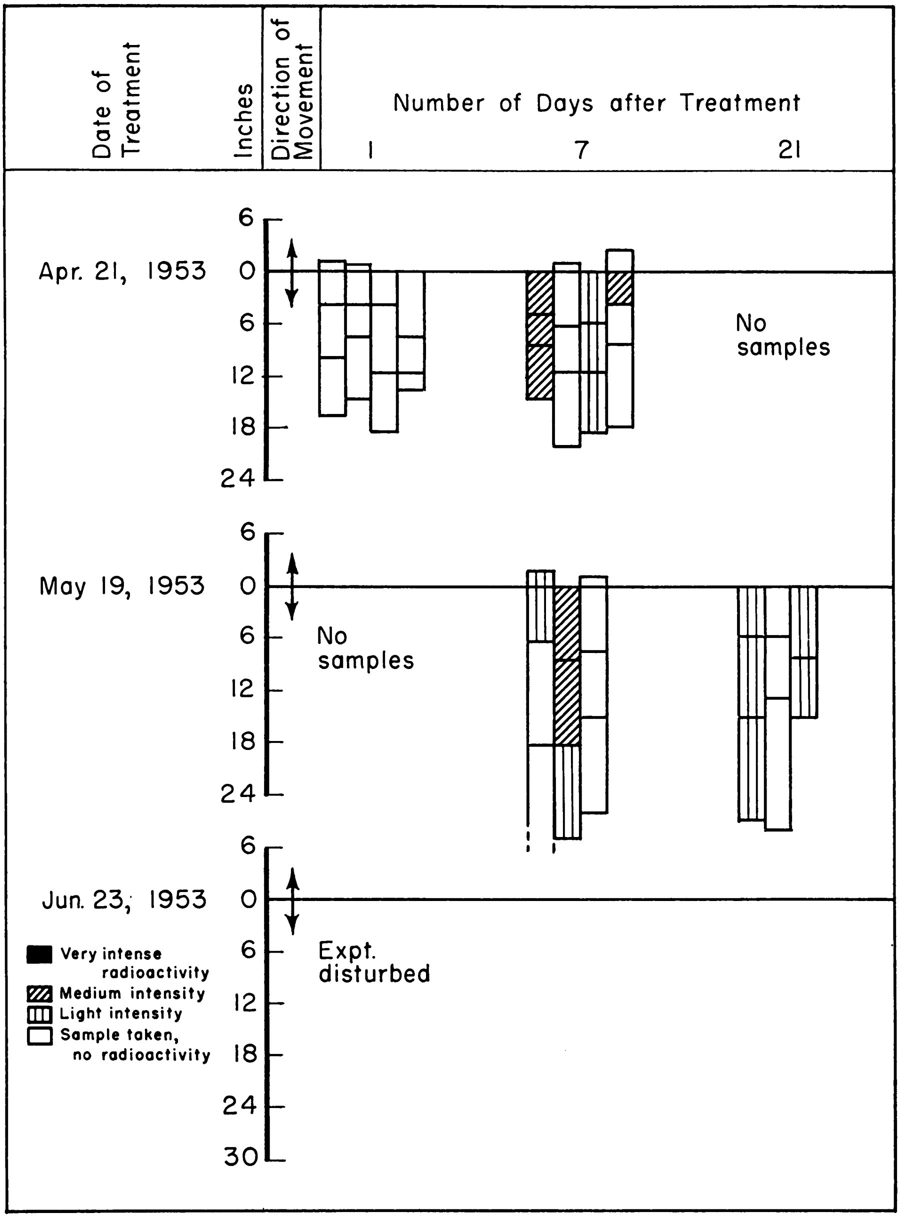

Fig. 18B. *A. manzanita:* same as 18A except that treatments were later. All treated leaves were mature.

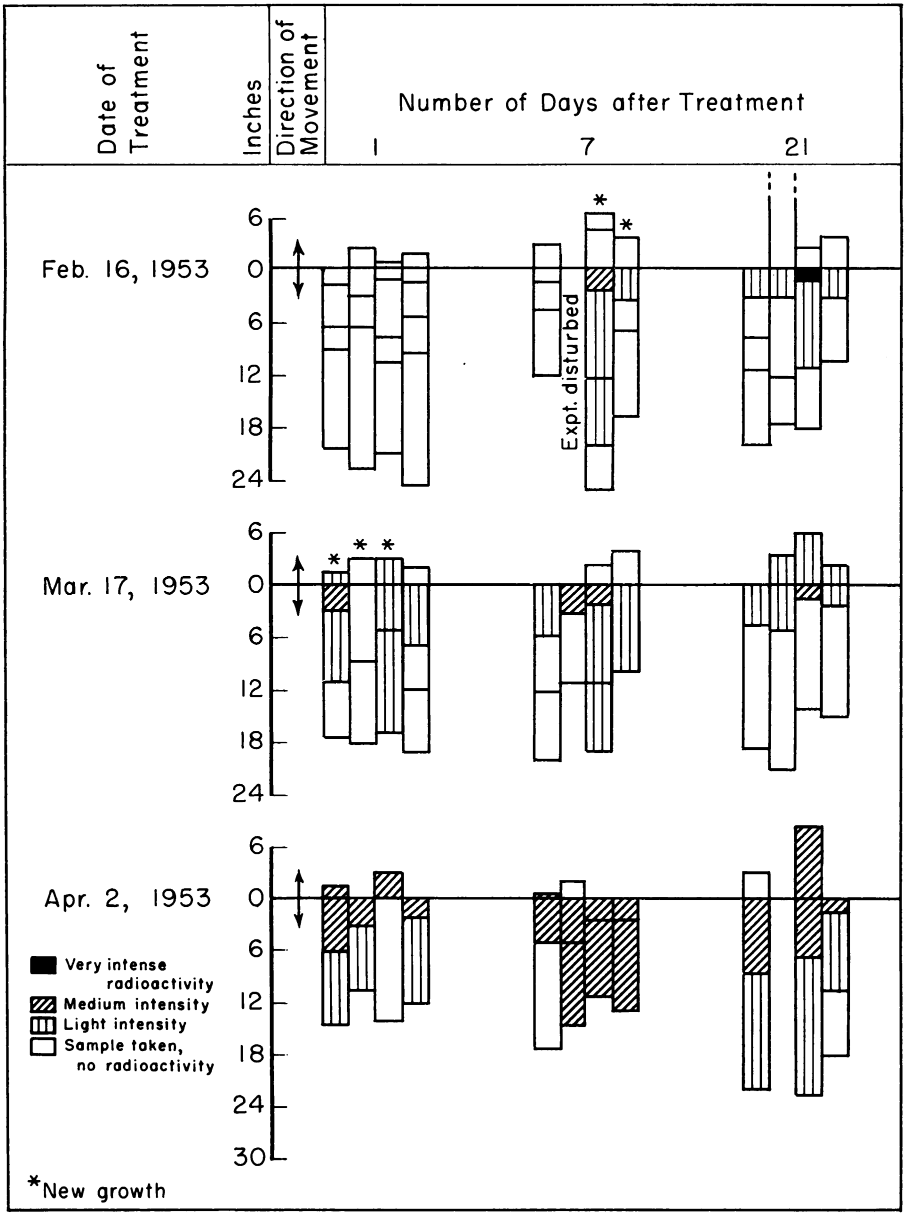

Fig. 19A. Charts showing distribution of radioactivity in shoots of toyon after leaves were treated with 2,4-D*. Bars above zero lines represent upward movement of the tracer; below zero, downward movement. All treated leaves were mature.

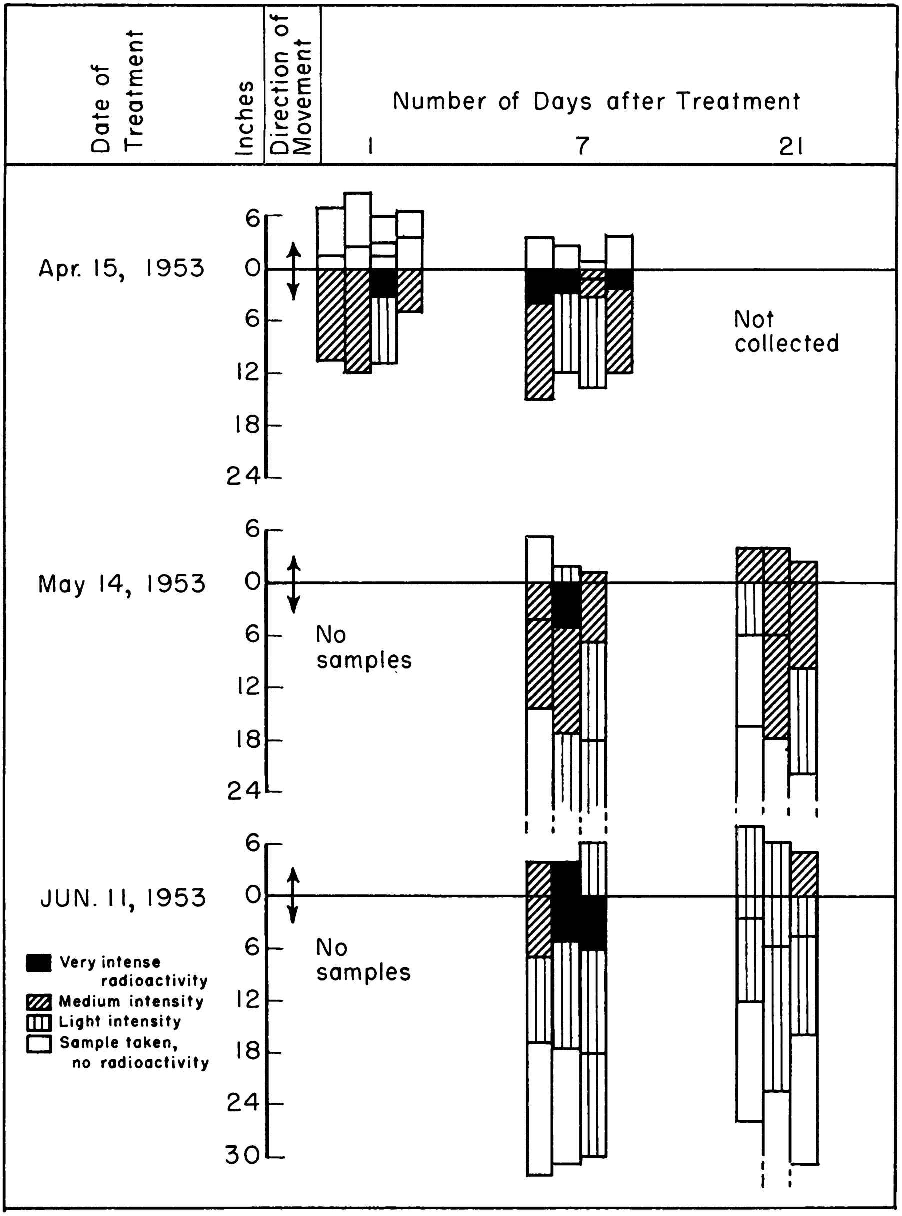

Fig. 19B. Toyon: same as 19A except that treatments were later.
All treated leaves were mature.

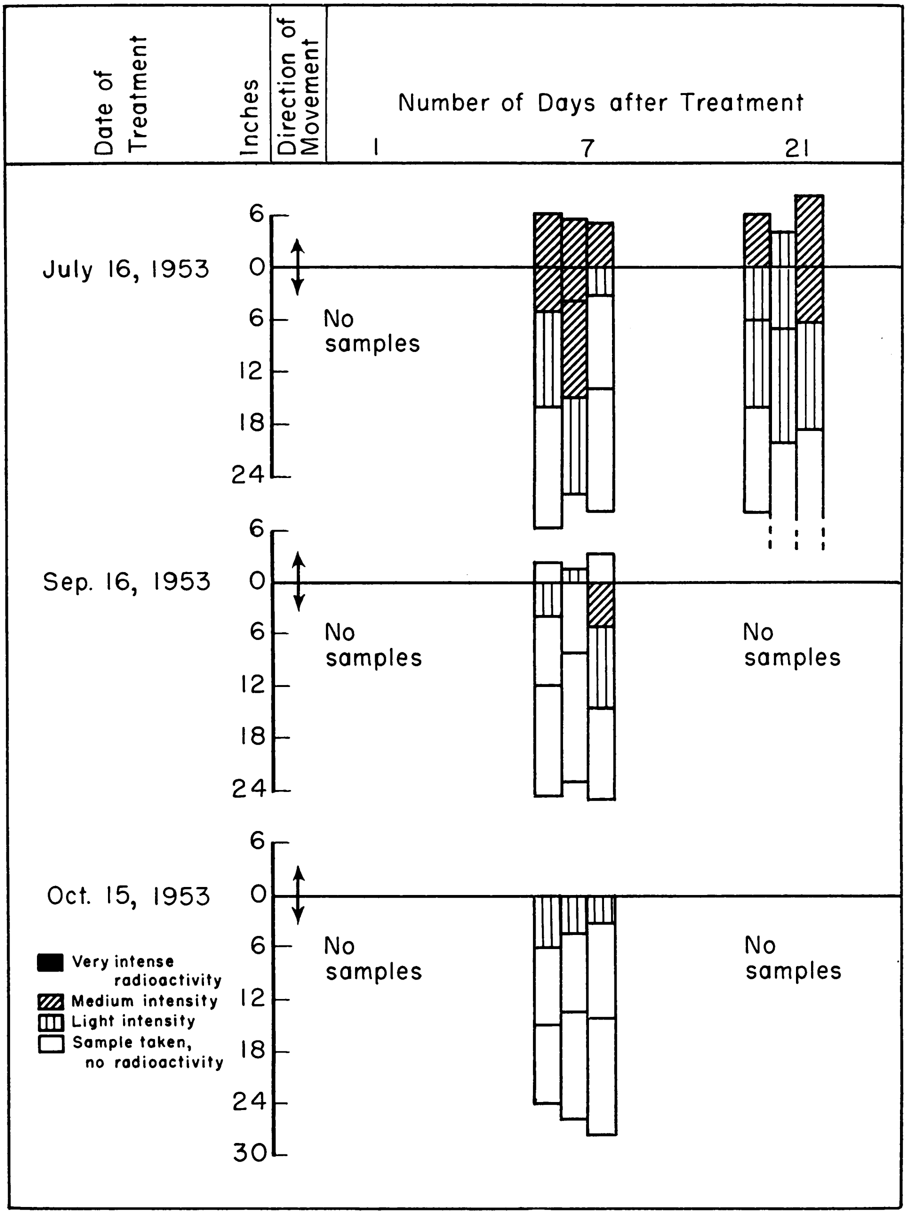

Fig. 19C. Toyon: same as 19A except that treatments were later.
All treated leaves were mature.

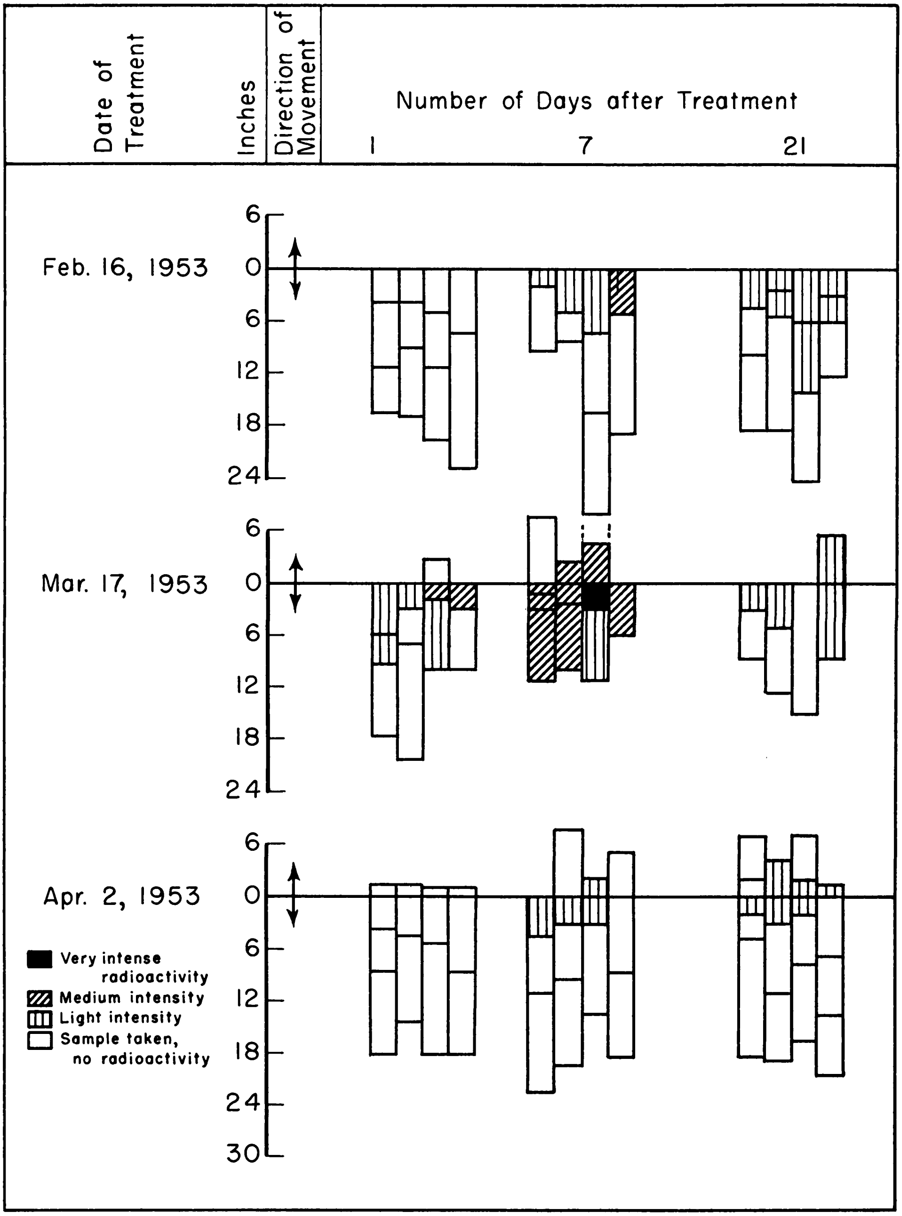

Fig. 20A. Charts showing distribution of radioactivity in shoots of live oak after leaves were treated with 2,4-D*. Bars above zero lines represent upward movement of the tracer; below zero, downward movement. All treated leaves were mature.

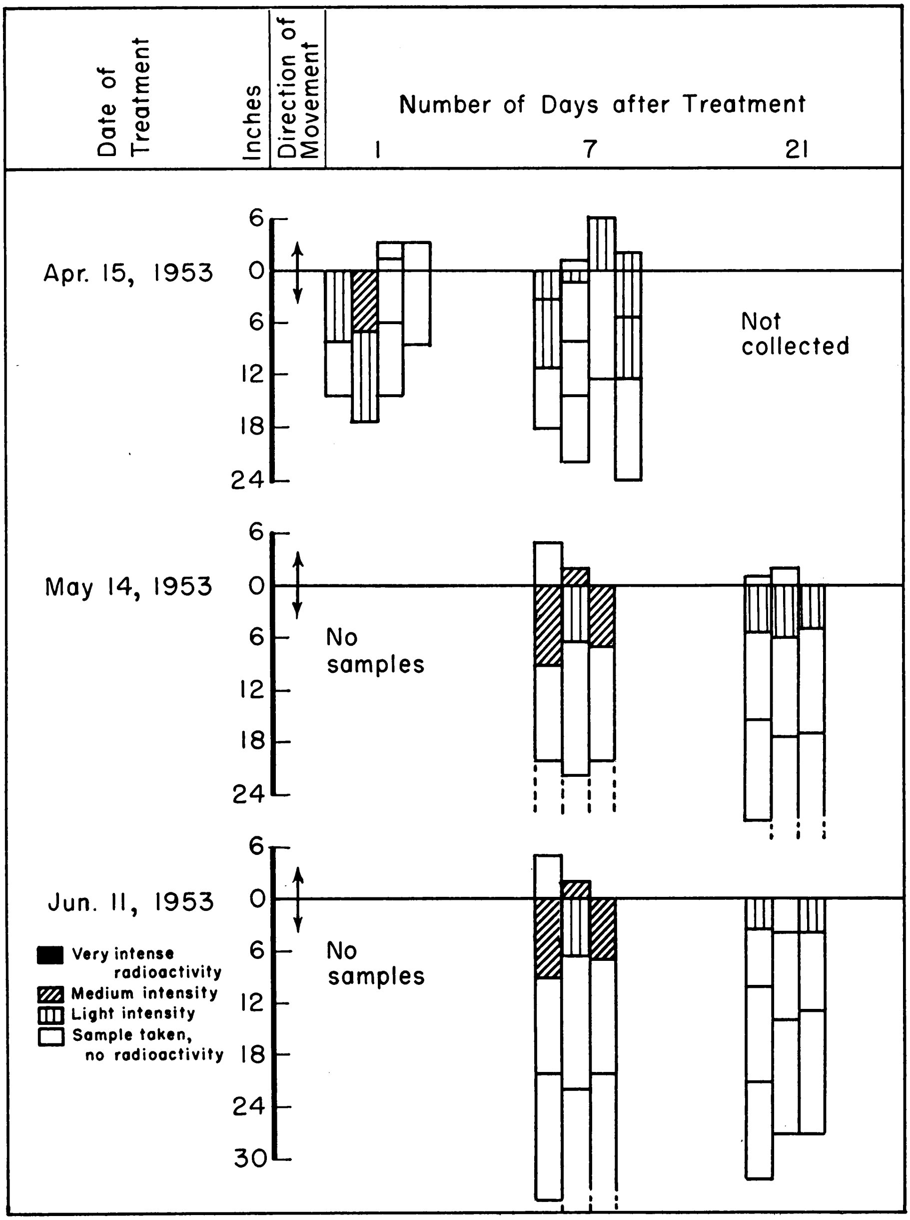

Fig. 20B. Live oak: later treatments. All treated leaves were mature.

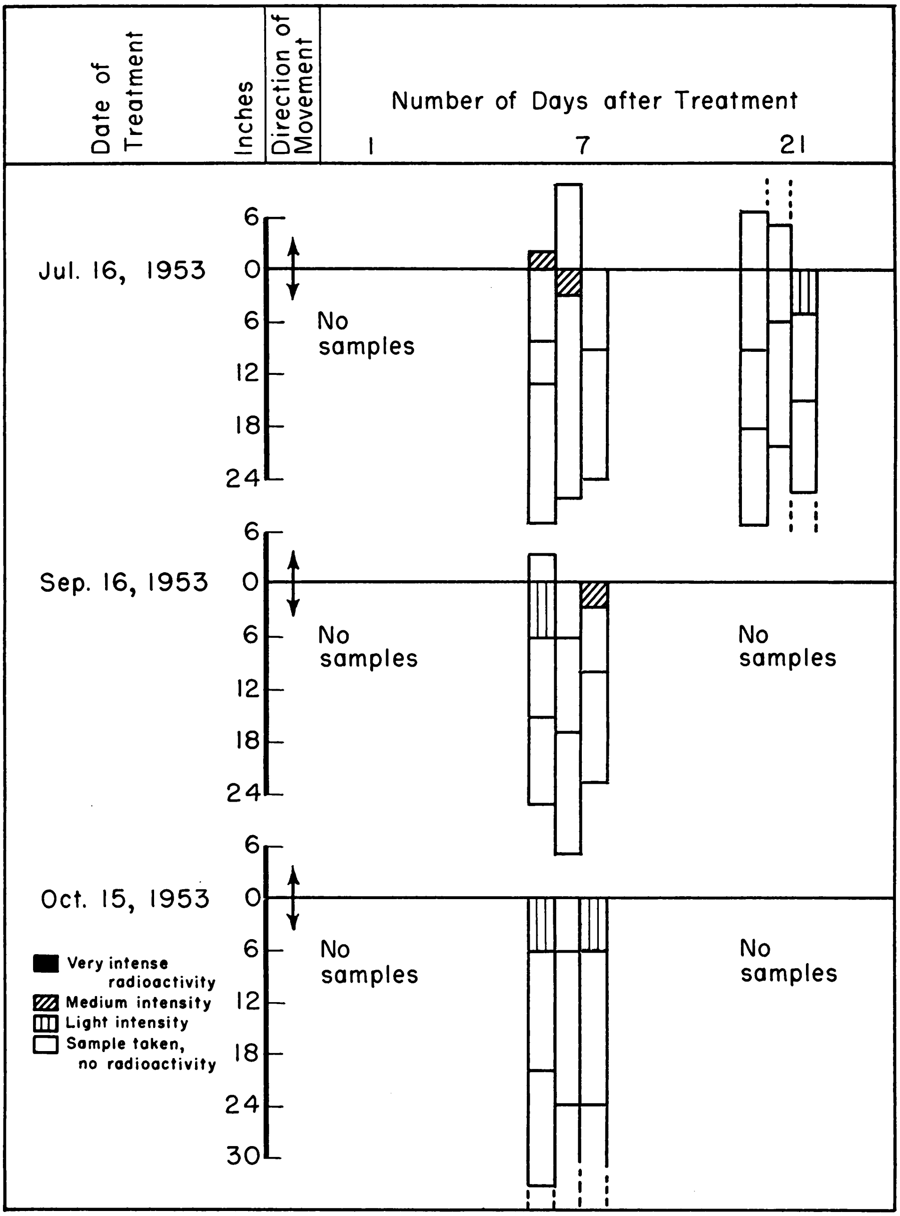

Fig. 20C. Live oak: later treatments. All treated leaves were mature.

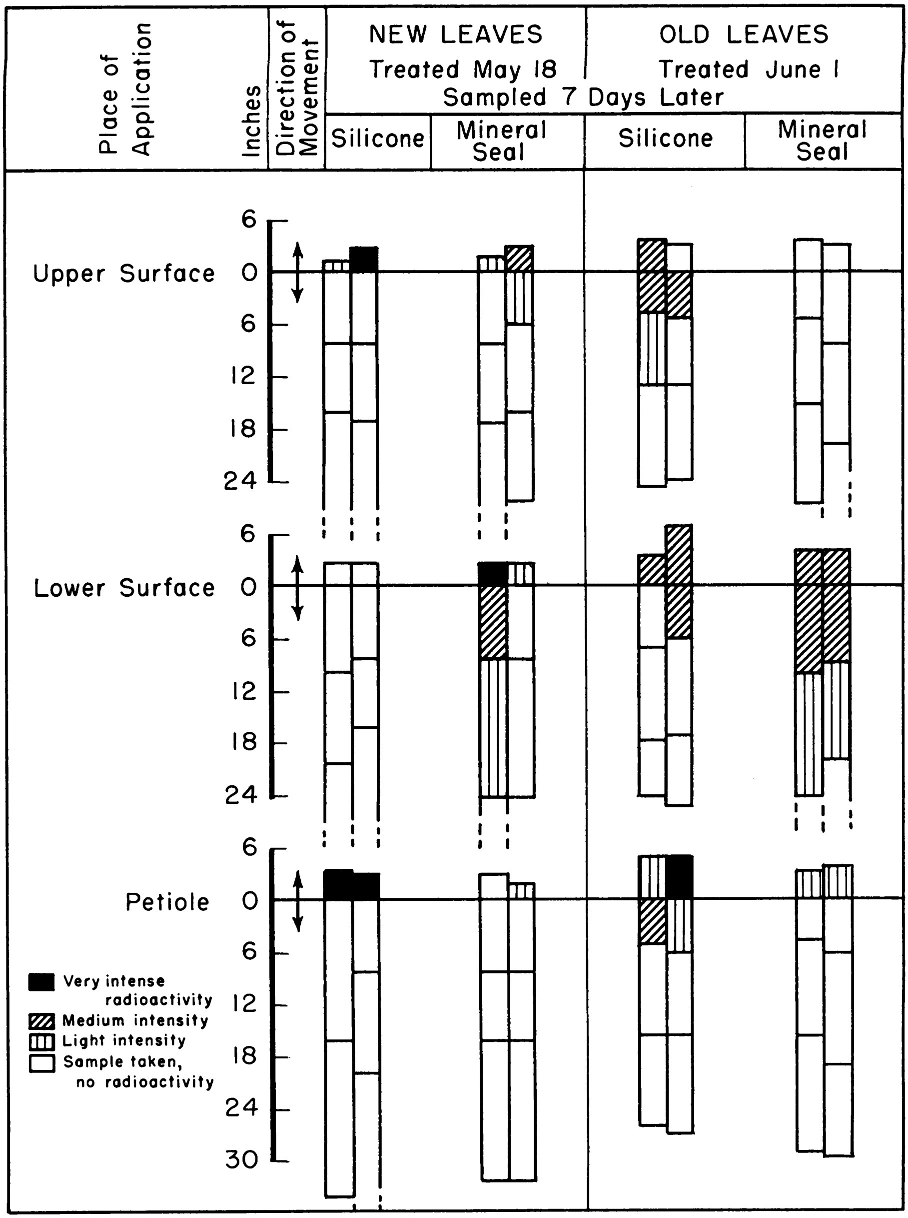

Fig. 21A. Charts showing distribution of radioactivity in shoots of toyon treated with two formulations designed to show differences in penetration. Bars above zero lines represent upward movement of the tracer; below zero, downward movement.

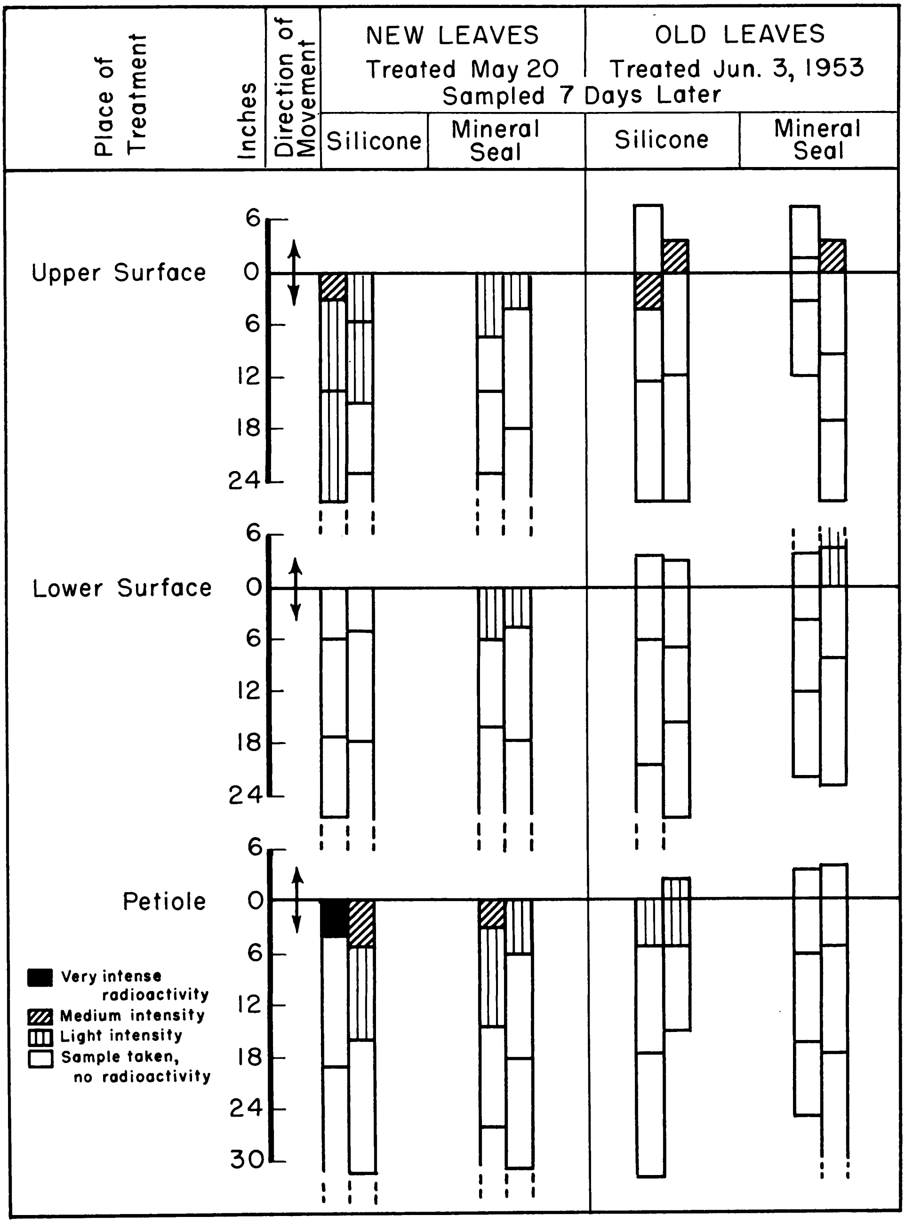

Fig. 21B. Same as 21A, but on shoots of live oak.

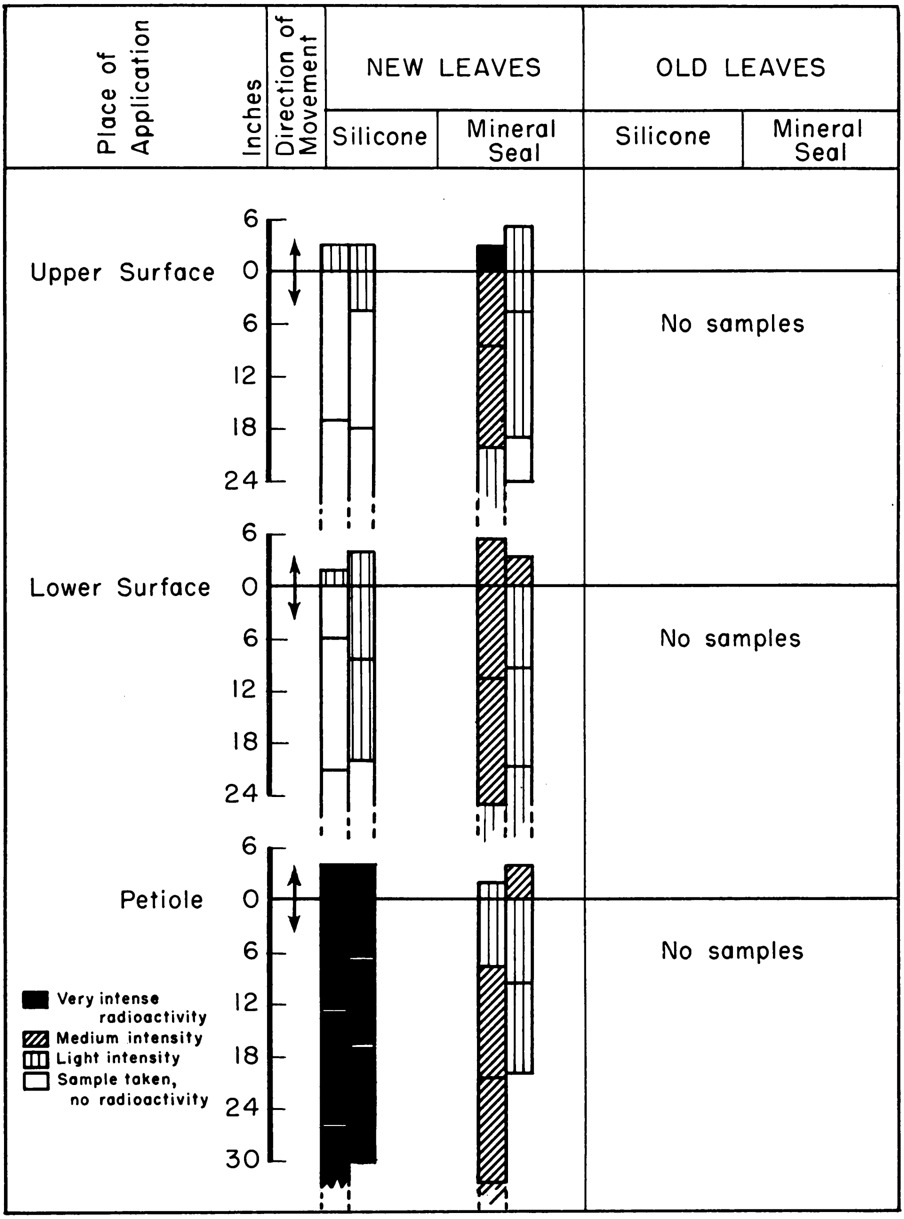

Fig. 21C. Same as 21A, but on shoots of coyote brush.

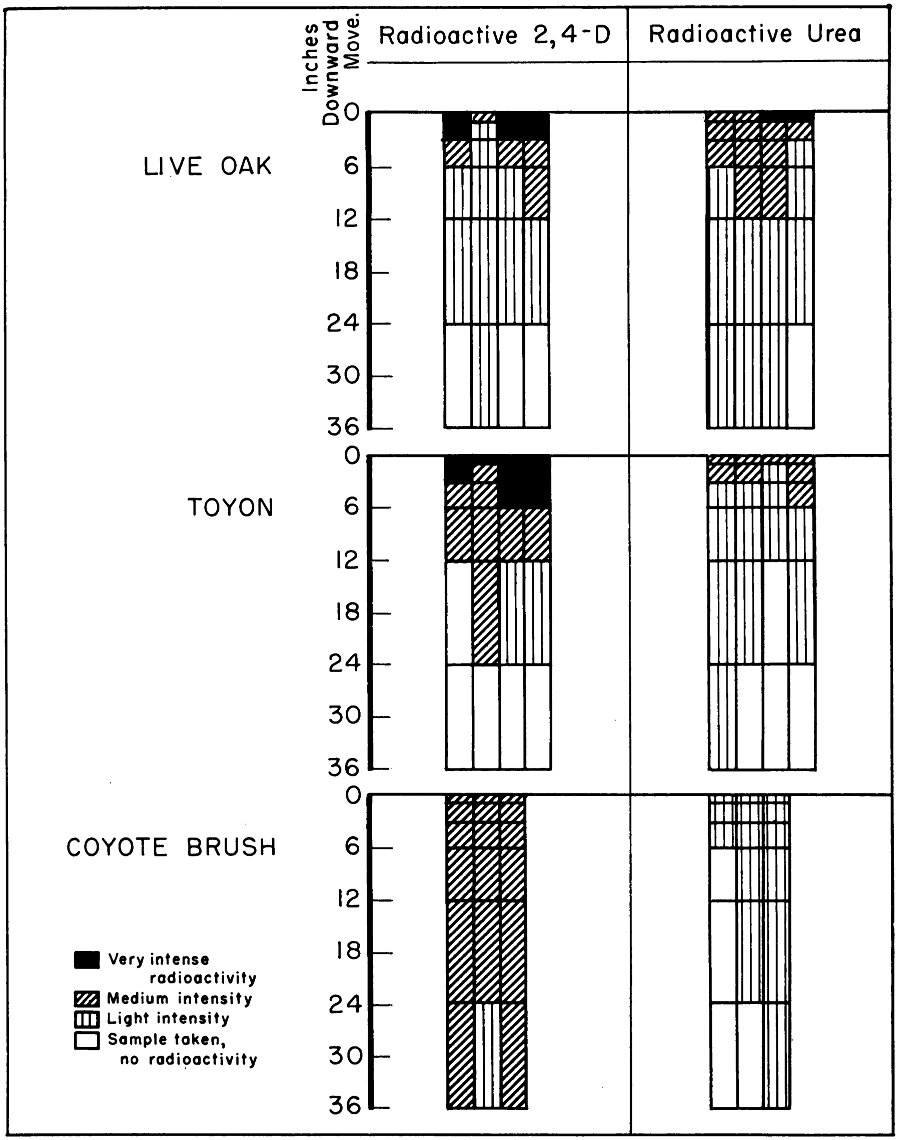

Fig. 22. Movement of radioactive 2,4-D and radioactive urea in live oak, toyon, and coyote brush. Applications were made on April 5, 1954, and samples were collected eight days later. Ten leaves were treated per branch.

4m-12,'56(B3170)BEB-LL

141

The journal *Hilgardia* is published at irregular intervals, in volumes of about 600 pages. The number of issues per volume varies.

Subscriptions are not sold. The periodical is sent as published only to libraries, or to institutions in foreign countries having publications to offer in exchange.

You may obtain a single copy of any issue free, as long as the supply lasts; please request by volume and issue number from:

Agricultural Publications
Room 22, Giannini Hall
University of California
Berkeley 4, California

The limit to nonresidents of California is 10 separate issues on a single order. A list of the issues still available will be sent on request.

In our publications it is sometimes convenient to use trade names of products or equipment rather than scientific identifications. In so doing it is unavoidable in some cases that similar products which are on the market under other trade names may not be cited. No endorsement of named products is intended nor is criticism implied of similar products which are not mentioned.