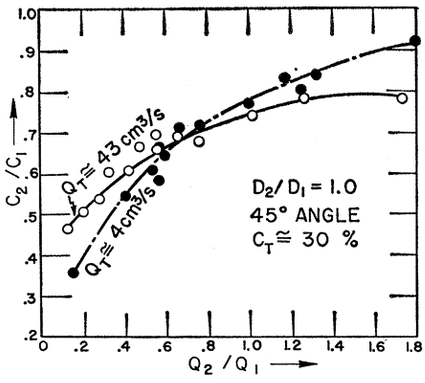

Fig. 2. Effect on C_2/C_1 of a tenfold change in the rate of flow upstream, Q_T.

Finally, the limited influence of the upstream flow rate Q_T on C_2/C_1 can be explained as due to a limited influence of Q_T both on the deflection pattern, a fact observed by Barnett and Cochrane, and on the concentration distribution, a fact as yet hypothetical but consistent with our qualitative observations of the limited variation of the particle distribution with flow rate, and also consistent with quantitative observations of the peripheral layer in the flow of blood in vitro (*6*). At values of Q_T below the range investigated, C_2/C_1 must be expected to be affected by Q_T, because, as shown by Goldsmith and Mason (*7*), a rigid particle would not exhibit a tendency to drift away from the boundary [but a small layer of lower concentration would still be present near the boundary due to purely geometric effects (*8*)].

Application of these findings to the circulatory system requires caution and more understanding of the comparative behavior of suspensions of rigid versus highly deformable particles (such as the erythrocytes) in a shear field.

With deformable particles, drift away from the boundary occurs at very low rates of flow (*7*), whereas, with rigid particles, rates of flow higher by several orders of magnitude are necessary, other factors being equal. Thus, to achieve a system in which the particles behave as in the circulatory system, a model in which rigid particles are used must first be made to operate at sufficiently high Reynolds numbers, as did that in our experiments, so as to insure the occurrence of phase-separation effects. The distribution of the cross-sectional concentrations must also be similar, likewise the variations in concentration with flow rate. Lack of information on both these phenomena, for suspensions of rigid particles as well as for blood, prevents an assessment of the extent to which our model fulfilled these requirements. In first approximation, however, the concentration in the side branch would be governed primarily by the peripheral layer, and the rigid-particle model should, therefore, provide at least a qualitative understanding of the phase-separation phenomena at branchings of similar configuration in the circulatory system. In particular, our experiments concur with the existing observations of the plasma skimming phenomenon, in showing that the hematocrit ratio in the side branches of the smaller vessels should be appreciably lower than in the straight branch downstream of the bifurcation, since, in general, the ratio Q_2/Q_1 will be smaller than unity—that is, in the range where phase separation effects are the most pronounced. With branchings in series, the process could thus lead rapidly to very low hematocrit ratios. Within the range of validity of the results obtained with the model, the phenomenon should be affected only to a minor extent by the angle of the branching and by changes in the circulation rate, but would be sensitive to the relative diameter of the side and straight branches.

In vivo, the pulsating nature of the flow, and the degree of sharpness of the bifurcation edge must also be considered. However, since pulsations are less pronounced in the smaller vessels, where plasma skimming is of importance, and since in our experiments the angle of bifurcation was shown to have limited influence, neither of these factors should alter the basic phenomenon.

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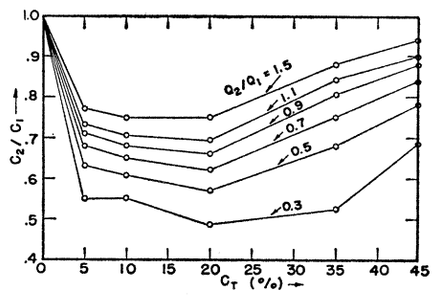

Fig. 3. Variation of C_2/C_1 with upstream concentration C_T, for the narrower side branch ($D_2/D_1 = ½$). The values shown are averages over a range of Q_T values.

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Volatile Growth Inhibitors Produced by Aromatic Shrubs

Abstract. *Root growth of* Cucumis *and* Avena *seedlings is inhibited by volatile materials produced by leaves of* Salvia leucophylla, S. apiana, *and* Artemisia californica. *The toxic substance may be deposited when dew condenses on affected seedlings in the field.*

The role of metabolic products in various forms of growth inhibition has been reviewed extensively since 1950 (*1*). We have in progress an analysis of inhibition of annual herbs by *Salvia leucophylla, S. apiana, S. mellifera, Artemisia californica*, and other aromatic shrubs. The localization of the toxic principles is a first step in their identifications and in the determination of ecological relationships.

The spacing and patterning of annual grassland species in and about colonies of *Salvia leucophylla* and *Artemisia californica* in the Santa Inez Valley, Santa Barbara County, California, suggested this study. Numerous isolated patches of both shrubs occur surrounded by grassland. Annual grasses and forbs are usually absent from the interiors of such patches and there is frequently a zone of bare soil extending 60 to 90 cm beyond the canopy of the shrub branches. Beyond this, a zone of differential inhibition may extend 2 to 6 or even 9 m. In the proximal part of this differential zone an almost pure

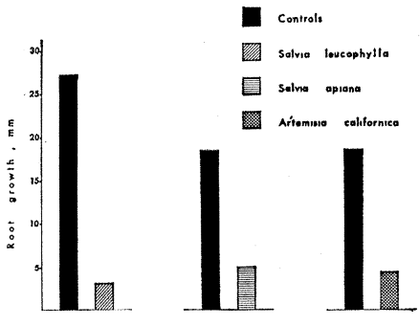

Fig. 1. Growth of *Cucumis* seedling roots suspended above crushed shrub leaves for 48 hours, expressed as average lengths of radicles for 20 seedlings.

stand of stunted *Erodium cicutarium, Festuca megalura,* and *Bromus mollis* may occur from which the annual grasses of adjacent unaffected areas are almost totally excluded. Perennial plants such as *Stipa lepida* and *Poa scabrella* seem not to be affected, but seedlings of these are not observed in the zones of inhibition. The inhibition therefore appears to be effective at the time and place of seedling growth and establishment (*2*).

Preliminary assays showed *Avena fatua* and *Stipa pulchra* seeds and seedlings to be highly susceptible to inhibition by *Salvia leucophylla.* Exploratory assays were performed with *Cucumis sativus* pending the harvest of sufficient native seed supplies.

Whole and macerated young and mature roots of *Salvia leucophylla* failed to inhibit the growth of cucumber seedlings on filter paper in direct contact with the root materials. Similarly, leachate from pots of *Salvia* in native soil failed to inhibit cucumber when used to moisten seeds in germination chambers.

Crushed leaves of *Salvia leucophylla* and leafy twigs of *Artemisia californica* proved strongly inhibitory to both seed germination and seedling growth when assayed in contact. This suggested that toxic materials are localized in the leaves of these plants. Since both shrubs are highly aromatic and inhibition is recognizable 4 to 6 m beyond the reach of their branches, it seemed likely that the toxic principles might be volatile. Several experiments were designed to test this hypothesis and to serve as methods of quick assay for more extensive studies.

Crushed leaves of three shrub species were individually placed in the bottoms of storage dishes. Filter papers bearing cucumber seeds and irrigated with distilled water were supported 4 cm above the leaves on a shelf of wire mesh coated with paraffin so that no aqueous film contact was possible. In the control moist towelling was substituted for crushed leaves. All dishes were then covered and sealed with petrolatum. Results are expressed in terms of average radicle length produced in 48 hours by 20 seedlings (Fig. 1). In every instance volatile materials emanating from the crushed leaves radically inhibited seedling root growth.

Finely sliced leaves of *Salvia leucophylla, S. apiana,* and *Artemisia californica* in varying quantities were placed in 10-ml beakers standing in storage dishes. A uniform pad of cellulose sponge 4 mm thick, soaked in distilled water, was placed beside the beaker on the floor of each dish. Seeds of *Cucumis sativus* and *Avena fatua,* soaked for 2 hours in distilled water, were sown between layers of moist filter paper on the sponge, and the dish was then sealed with petrolatum. *Cucumis* seeds were germinated at a constant temperature of 28°C while *Avena* seeds were subjected to alternating 12-hour periods of 25°C and 17°C, respectively, preliminary tests having proved these thermoperiods effective. Results were recorded as total root length (including branches) produced in 48 hours by *Cucumis* and in 120 hours by *Avena.* The record of the root growth, expressed as averages of those seeds which germinated of the 20 sown in each treatment, appears in Table 1. Germination of *Cucumis* seed approached 100 percent while *Avena* varied from 50 to 75 percent. As the amount of leaf material was increased, there was an increased inhibition of root growth. In the case of *A. californica,* 1.0 g resulted in almost complete inhibition, and additional leaf material proved superfluous.

The lack of any conditions in the field comparable to those in the preceding experiments suggested that the volatile inhibitors must be evaporated from uninjured leaves and deposited, perhaps trapped in dew, upon the inhibited seedlings. In an effort to test this hypothesis, artificial dew condensed on cooling coils was produced from the atmosphere in several places, some where plants of *Salvia leucophylla* were growing and some free of all plants suspected of inhibitory capacity. The dew thus produced was used to soak seeds of *Cucumis* and to irrigate filter paper germination beds sealed in petri dishes.

Several trials proved the "artificial-dew" technique to be very erratic. However, a trial performed on a dry day in early spring when the plants appeared to be at the height of their seasonal growth yielded the results here reported. Tests were made from the atmosphere surrounding (i) ten potted plants of *Salvia leucophylla* grouped on a greenhouse bench in front of the condenser coils, (ii) an empty bench in a neighboring greenhouse containing miscellaneous plants but no *Salvia,* and (iii) distilled water. The results of seedling growth were recorded by measuring the length of the radicle and of each lateral root and then summing these lengths for each seedling. The average lengths for 20 seedlings, respectively, were (i) 57.5 mm, (ii) 176.9 mm, and (iii) 140.6 mm. It is tempting to speculate about the reduction in root growth of more than 50 percent. However, this technique does fail in that a single collection in less than an hour cannot equal nightly depositions over a period of weeks. Although field experimentation is still to be performed, it appears that whole plants of *Salvia leucophylla* release a volatile substance that condenses in

Table 1. Growth of *Cucumis* and *Avena* seedling roots in an atmosphere containing volatile materials derived from various amounts of sliced shrub leaves (*Salvia* and *Artemisia*). Growth is expressed as average total length (in millimeters) of roots produced.

Shrub	Grams of leaf				
	0	0.25	0.5	1.0	2.0
	Cucumis sativus				
S. leucophylla	34.4*	37.0	23.0	17.9	10.2
S. apiana	34.4*	26.9	21.2	16.0	5.3
A. californica	34.4*	18.3	10.5	6.4	3.9
	Avena fatua				
S. leucophylla	57.5*	51.5	21.2	27.3	15.9
S. apiana	57.5*	20.9	38.4	24.5	11.0
A. californica	57.5*	4.9	28.5	1.6	1.6

* Average of 60 seedlings.

dew and that significantly inhibits the growth of cucumber roots.

Although the production of growth inhibitors has been demonstrated for a variety of plants, we believe this to be the first demonstration that a volatile inhibitor may be effective in the field. Its suggested deposition in dew would constitute a novel mechanism of ecological interaction.

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Nucleus of the Trapezoid Body: Dual Afferent Innervation

Abstract. *Lesions of the anterior ventral cochlear nucleus caused degeneration of synaptic endings in the anterior half of the nucleus of the trapezoid body. Lesions of the posterior ventral cochlear nucleus caused similar degeneration in the posterior half of the nucleus of the trapezoid body. Thus, the cochlea projects twice upon the nucleus of the trapezoid body.*

In a series of experiments now being conducted, we wish to determine the projections of the cochlear nuclei upon the components of the superior olivary complex. This work is concerned with two general problem areas. First, we are interested in understanding the ascending connections of the cochlear nucleus, as these shed light upon the way in which the nucleus may be morphologically subdivided. We are also interested in supplying an anatomical basis for the interpretation of physiological studies of the lower auditory system. In this experiment we were concerned with the projection of the cochlear nuclei upon the (medial) nucleus of the trapezoid body.

The nucleus of the trapezoid body is extremely well developed in a number of animals including the bat (*Myotis*), hamster, marmoset, mole (*Scalopus aqueticus*), mouse, rabbit, and the rat. It is clearly present in the cat, dog, giant panda, gorilla, and in man. In the rat, the animal used in this experiment, the nucleus forms the largest component of the superior olivary complex. It has been shown that cells located somewhere in the cochlear nucleus give rise to large fibers which terminate in large synaptic endings (the chalices of Held) upon the cells of the contralateral nucleus of the trapezoid body (*1*). In this experiment, we determined the dual loci of these cells and their mode of termination.

Basically, the method consisted of estimating (by counting) degeneration of the chalices of Held in the nucleus of the trapezoid body of animals in which lesions had been induced in the cochlear nuclei. Lesions were induced in the cochlear nuclei of nine albino rats, and in the cochlea of one rat for control purposes. After 7 to 14 days, the brain of each animal was embedded in paraffin, sectioned at 16 μ, and impregnated according to the protargol method of Bodian (*2*). All chalices of Held were counted in each section, and the results were plotted graphically to show the number of chalices at each level in the nucleus of the trapezoid body from the anterior to the posterior end.

The results of the experiment are summarized in Table 1, from which the following points can be made.

The anterior ventral cochlear nucleus sends fibers to the anterior half of the contralateral nucleus of the trapezoid body (rats P25, P26, and P28). As an example, the graph of the chalice count of rat P25 is shown in Fig. 1. In this animal the anterior ventral cochlear nucleus of the left side was extensively destroyed, especially at its anterior end. Other parts of the

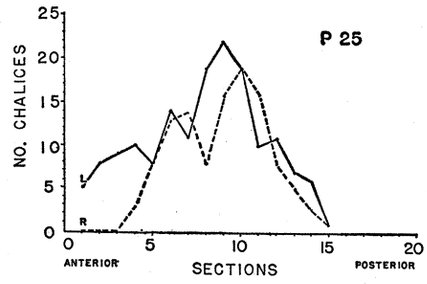

Fig. 1. Rat P25. Count of synaptic endings (chalices of Held) in the nuclei of the trapezoid body (transverse section). The number of chalices is given on the vertical axis and the ordinal position of each section (from the anterior end) on the horizontal axis. The anterior ventral cochlear nucleus of left side was damaged (*L*, left; *R*, right).

cochlear nucleus of the left side were intact, as was the cochlear nucleus on the right side. This damage is reflected in complete degeneration of the chalices of Held in the anterior portion of the right (contralateral) nucleus of the trapezoid body and the normal number of chalices on the left side (Fig. 1). The graph also shows that the number of chalices in the posterior part of the nucleus of the trapezoid body of both sides was approximately the same.

The posterior ventral cochlear nucleus sends fibers to the posterior half of the contralateral nucleus of the trapezoid body (rats P18, P24, and P54). As an example, the graph of the chalice count of rat P54 is given in Fig. 2. In this animal, the posterior ventral cochlear nucleus of the left side was completely destroyed and the anterior ventral cochlear nucleus was virtually intact. On the right side the cochlear nucleus was intact. Figure 2 shows that there was extensive degener-

Table 1. Summary of experimental lesions and synaptic degeneration in the nucleus of the trapezoid body. Abbreviations: Ant., anterior; AVC, anterior part of ventral cochlear nucleus; DCN, dorsal cochlear nucleus; Deg, degeneration of chalices of Held; ICP, inferior cerebellar peduncle; NTB, nucleus of the trapezoid body; Post., posterior; ST, spinal tract of trigeminal nerve. Damage: 0, less than 10 percent of structure damaged; 1, between 10 percent and 50 percent; 2, between 50 percent and 90 percent; and 3, more than 90 percent damage. L, left, R, right side.

Animal	Lesion			Degeneration of Held chalices	
	AVC	PVC	Other	Ant. part NTB	Post. part NTB
P16	0	0	DCN slight	Normal	Normal
P18	0	L, 1; R, 2	—	Normal	L, deg; R, deg.
P23	0	0	ICP slight	Normal	Normal
P24	0	L, 0; R, 2	—	Normal	L, deg.; R, normal
P25	L, 2; R, 0	0	—	L, normal; R, deg.	Normal
P26	L, 1; R, 0	0	—	L, normal; R, deg.	Normal
P27	0	0	ST	Normal	Normal
P28	L, 2; R, 0	0	—	L, normal; R, deg.	Normal
P54	0	L, 3; R, 0	DCN slight	Normal	L, normal; R, deg.
MH12	0	0	Cochlea	Normal	Normal