

# The Relation Between Root and Shoot Systems in Chaparral Shrubs<sup>1</sup>

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The purpose of this paper is to analyse the growth relations between root and shoot systems of chaparral shrubs. Data from the literature and results from our own experiments will be used to demonstrate the plasticity of the root:shoot balance of chaparral shrubs.

Traditionally, the relation between roots and shoots has been described by root/shoot biomass ratios, and values ranging from 0.3-4.9 for non-sprouting and stump sprouting shrubs respectively have been obtained (Miller and Ng 1977, Hoffmann and Kummerow 1977, Kummerow and Mangan 1981). The large ratios, common to stump sprouters, derive primarily from the mass of burls (=lignotubers or root crowns) which are massive woody organs developed from hypocotyl and root crown tissue. It is difficult to demonstrate annual increases in size or biomass of older burls and aging such structures has been possible only by using <sup>14</sup>C methodology with a relatively wide margin of error (Hanes 1965). Thus, in spite of their large biomass, studies of older burls have not contributed much information to our understanding of the seasonal growth dynamics of root systems. A similar argument is valid for larger roots and stems. That is, as important as their functions may be, these organs do not visibly reflect short term changes in the physical environment. A different approach is needed.

The fraction of the root system which is directly responsive to the seasonal changes of the environmental conditions is the "fine root system". This term refers to the population of ephemeral rootlets which do not live for more than one growing season and may be as shortlived as two weeks (Lyr and Hoffmann 1967, Lyford 1975). Data on the seasonal changes in rootlet growth are sketchy. Some information on rootlet phenology from the southern California chaparral has been published (Kummerow and others 1978) but more data are needed.

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Abstract: Purpose of this study was to determine the balance between root and shoot growth in chaparral shrubs. Under controlled conditions with ample water and nutrient supplies, growth of roots and shoots continued exponentially for 5 months. In contrast, in the field shoots had flushing periods in the spring, lasting 31-69 days. Fine root growth however extended over 5-7 months. Fine root surface area and leaf area per shrub were estimated for different environmental conditions. It was found that increasing water stress produced higher fine root surface:leaf area ratios.

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The data base on seasonal shoot growth dynamics is substantially broader. Growth of leaves and branchlets of shrubs has been studied in detail in all the mediterranean areas of the world (Specht 1957, Margaris 1976, Hoffmann and others 1977, Montenegro and others 1979, Kruger 1980). Typically, a growth flush lasting 3-8 weeks occurs between early spring and late summer with some variation depending on local conditions and the species in question.

In the following parts of this paper we will attempt to relate shoot (=leaves + branchlets) and fine root growth. This approach appears useful for several reasons. Leaves and rootlets are analogous with respect to their determinate growth and the distal position in their respective organ systems. Both have as their main function the uptake of basic resources, i.e. light energy and CO<sub>2</sub> by the leaves and water and minerals by the roots. Consequently, both have large surface areas.

## ROOT AND SHOOT PHENOLOGY OF CHAPARRAL SHRUBS

Individual shrubs of Arctostaphylos glauca Lindl., Adenostoma fasciculatum H. & A., Ceanothus greggii var. perplexans (Trel.) Jeps., and Rhus ovata Wats. were selected for a detailed analysis of stem, leaf, and fine root growth. Field research area was confined to our Echo Valley site located at 1000 m elevation about 10 km north of Descanso in San Diego County, California, 55 km east of the Pacific Ocean. Climatic and biological information on this mixed chaparral site has been published previously (Mooney 1977). Individual buds of the above species were tagged and the developing shoots monitored until the end of the growth flush. Total leaf area per shoot was calculated from allometric formulas.

Growth curves of the shoots show the characteristic sigmoid form which has been demonstrated earlier for the California chaparral and Chilean matorral (Kummerow and others 1981). Duration of the flushing period, leaf area per shoot, shoot length, and the rates of leaf area and stem growth, showed significant differences between species (Table 1).

Adenostoma fasciculatum developed a relatively small leaf area (2.5 cm<sup>2</sup> per shoot when com-

Table 1. Leaf area per shoot, growth rates, shoot length, and the length of growth periods of four chaparral shrub species at Echo Valley. Growth rates with the same letters are not statistically different (ANOVA). The rates are calculated on the basis of the entire growth period (Kummerow and others, 1981).

	Leaf area per shoot cm <sup>2</sup>	Rate of leaf area growth cm <sup>2</sup> d <sup>-1</sup>	Mean shoot length in season cm	Rate of shoot elongation cm d <sup>-1</sup>	Date of growth initiation	Duration of growth days
<u>Adenostoma fasciculatum</u> n = 7	2.5 ± 0.45	0.03 ± 0.01a	5.2 ± 1.70	0.09 ± 0.03ab	09 April	69 ± 26
<u>Arctostaphylos glauca</u> n = 17	33.0 ± 6.50	0.82 ± 0.136	6.9 ± 1.24	0.13 ± 0.026	30 April	48 ± 4
<u>Ceanothus greggii</u> n = 20	7.9 ± 1.52	0.12 ± 0.02c	4.2 ± 0.83	0.06 ± 0.01a	12 April	68 ± 4
<u>Rhus ovata</u> n = 6	43.5 ± 24.05	1.19 ± 0.43bc	2.9 ± 1.18	0.08 ± 0.06ab	06 June	31 ± 5

pared with the other 3 species. The shrub with the highest value was Rhus ovata with 43.5 cm<sup>2</sup> leaf area per shoot. This difference is due in large part to differences between species with respect to the number of shoots per m<sup>3</sup> of shrub volume (944 ± 533 in A. fasciculatum, 97 ± 92 in R. ovata). It should be pointed out that leaf area index measurements of the same site gave values of 1.9 for both species (Mooney and others 1977). The situation is further complicated in A. fasciculatum, because of the short shoot organization of this species. New foliage is not limited to current year's growth. Short shoots remain active and produce leaves on 2-8 year-old branches (Jow and others 1980). Of special interest for our comparison of the duration of shoot and root growth is that the growth flush for A. fasciculatum had a duration of 69 ± 26 days vs. 31 ± 5 of R. ovata (Table 1). This then causes the data in Table 1 to be somewhat misleading as the total growth increment of the season was divided by the number of days of the growth flush. Nevertheless, a comparison of the leaf area produced by one shoot during the week of most rapid extension growth does not change the order of the four shrub species. In R. ovata a maximum of 8.4 cm<sup>2</sup> of leaf area per shoot was produced in one week compared to 5.7, 0.9, and 0.3 cm<sup>2</sup> in A. glauca, C. greggii, and A. fasciculatum respectively.

Our knowledge regarding the phenology of root growth is more limited. The seasonality of secondary growth for larger roots has been docu-

mented in central Chile (Riveros de la Puente 1973), and it is assumed that data from other mediterranean type ecosystems would be similar. Year ring widths in stems and large roots were strongly correlated. Fine roots in the chaparral also show clear seasonal trends (fig. 1). These data were obtained from soil core analyses and thus are based on large rootlet populations rather than being derived from non-destructive observations as are possible with individual shoots. Nevertheless, the data demonstrate that in April and May fine root growth increased rapidly; in June and July the values remained on a high plateau and declined in August. The fact that an unusual rainstorm at the end of August, 1976, with 33 mm of precipitation produced a significant increase of rootlet growth, perhaps reflects a soil moisture limitation in the ecosystem. A comparison of the duration of shoot and root growth of our four shrub species demonstrates the main difference between the growth of shoot and root systems. Rootlet growth continued for 5-7 months while shoot growth lasted only 4-9 weeks (fig. 2).

In order to circumvent the destructive nature of root studies in the field and obtain more information on root dynamics, it seemed justified to grow chaparral shrubs hydroponically under near optimum conditions. Such a technique would allow monitoring growth rates of the root system simultaneously with leaf area increases. The results of such an experiment might be expected to demonstrate the equilibrium in the growth of roots and shoots. It is understood of course that the

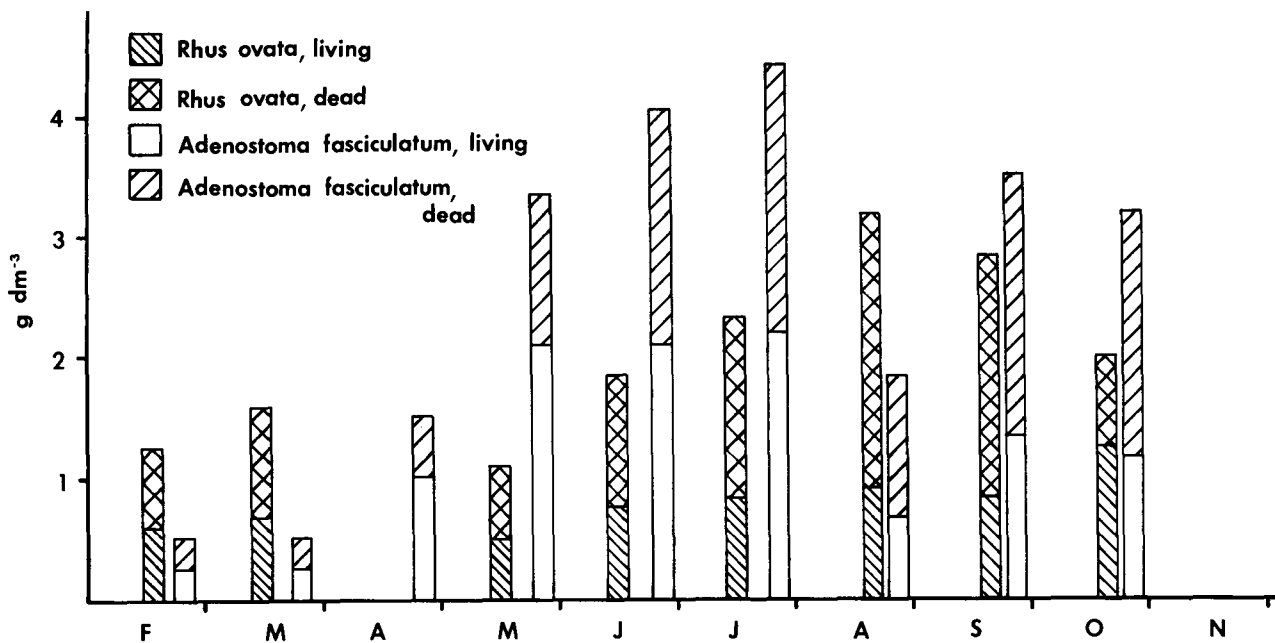


Figure 1--Seasonal changes in fine root biomass of 2 chaparral shrub species. Note the increasing amount of dead fine roots in summer and autumn. Each column represents a mean value of 12 soil cores of 125 cm<sup>3</sup> each (after Kummerow and others 1978).

appropriate intervals to avoid water and nutrient stress. Over the 5 months experimental period all plants were maintained under controlled environmental conditions at 16 h light 25°C and 8 h dark, 20°C. Light intensity was  $800 \pm 60 \mu\text{E m}^{-2} \text{sec}^{-1}$ .

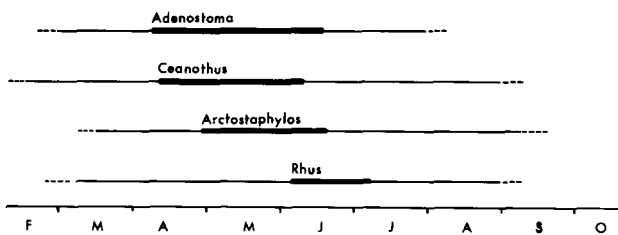


Figure 2--Timing and duration of shoot growth (thick line) and fine root growth (fine line) of 4 chaparral shrubs. Initiation and end of fine root growth not as well defined as shoot growth (dashed line).

Root volumes and leaf areas were determined for each plant at two week intervals. The root volumes were obtained by water displacement using adequately sized glass cylinders. The leaf areas were determined by measuring shoot lengths and using an allometric formula for shoot length conversion into leaf area.

results from such an experiment cannot be applied directly without further work under field conditions.

The two computer fitted regression lines (fig. 3) represent the leaf area and root volume increases. They document the continuous exponential growth of the two plant compartments. The fact that the regression line for root growth shows a greater slope than the one for leaf area increase is irrelevant in this context, because area is not quantitatively compared with a volume. In the framework of our theme it is significant that root and shoot system grew continuously in a balanced way over the five month experimental period. The root/shoot biomass ratios at the end of the experiment for the solution grown plants reached a value of  $0.52 \pm 0.3$  (n=12) and  $0.53 \pm 0.5$  (n=3) for the sand-peat moss grown plants. This means that the ratio of root/shoot biomass had not been altered by the growth substrates.

Fifteen 2-months old seedlings of *A. fasciculatum* were selected from healthy nursery stock. Twelve were cultivated individually in 14 1 plastic buckets with aerated standard Hoagland solution. The remaining 3 plants were potted and grown in a sand-peat moss mixture. The nutrient solutions were changed every 2 weeks and the potted plants were irrigated and fertilized at

#### THE INFLUENCE OF SOIL MOISTURE ON FINE ROOT SURFACE AREAS

The role of root/shoot biomass ratios and their limitations regarding interpretation of growth dynamics in arid areas have been discussed (Barbour 1973). It has also been shown that under controlled conditions the physical character of

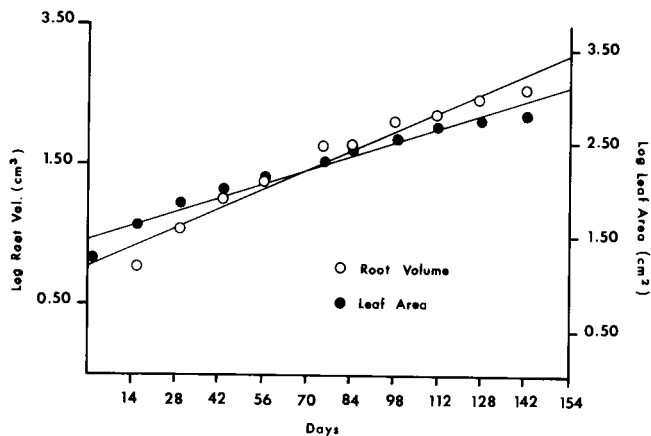


Figure 3--Root volume and leaf area growth in 2-month old *Adenostoma fasciculatum*, cultivated in aerated nutrient solution. Each data point represents the mean of roots and leaves from 12 plants.

the root environment did not influence root/shoot ratios as long as nutrients and water were not limiting. Since chaparral shrub growth has frequently been considered as water and nutrient limited (Hellmers and others 1955, Vlamis and others 1954, Vlamis and Gowans 1961), it appeared to be of interest to test the hypothesis that the root systems of chaparral shrubs, exposed to variable degrees of water stress, should be more extensive than those from an environment without water stress. However, it would be difficult to test such an hypothesis when one considers the level of accuracy which can be obtained from field observations. Further, root systems of young seedlings may have growth patterns different from those of older plants and larger roots with secondary growth and their large biomass may well camouflage changes in the biomass of fine roots. To overcome these difficulties at least in part it was decided to assess fine root densities and the fine root surface area of container grown chaparral shrubs and relate the estimated absorbing root surfaces with the leaf area of the respective shrub. This ratio would allow for a comparison of shrubs of heterogeneous sizes and relate the CO<sub>2</sub>-fixing leaf area with the nutrients and water absorbing root surface.

Redwood boxes, 75 cm high, 60 cm wide, and 20 cm deep, filled with a fertilized sand-peat moss mixture, were planted in March 1976, with 1.5 year old *Adenostoma fasciculatum*, *Arctostaphylos glauca* and *Yucca whipplei*. Six of these redwood boxes were placed in a relatively shaded area and watered frequently, thus simulating a moist ravine. Three boxes were fully sunexposed and watered only when wilting symptoms became visible. The last four boxes were transported to the Echo Valley research area and placed into a ditch excavated

for this purpose. After sinking these boxes into the ditch the plants were level with the original soil surface; empty spaces between the boxes and the ditch were filled with the excavated soil. No rain fell between March and October but these boxes were watered three times. Presumably these plants experienced severe water stress as only two survived.

Between October 25 and November 10, 1976, all the plants were harvested. The leaf area (LA), as well as leaf and stem biomass were recorded for each shrub<sup>3</sup>. The total root mass was extracted from the redwood boxes and separated into fine roots (diam. <1.0mm) and larger roots. A representative sample of the fine roots was separated visually into suberized and non-suberized surface. For the estimate of "absorbing" fine root surface (FRSA) only whitish and light brown fine roots were considered. This distinction is somewhat arbitrary since suberized roots can absorb water (Kramer and Bullock, 1966). The mean diameter of the unsuberized fine roots was measured and the length of 1 g fresh weight of these rootlets was estimated by the line intersect method of Newman (1966) as modified by Tennant (1975). This estimate was used to calculate the unsuberized fine root surface area. Although the number of analyzed shrubs was too small for far reaching conclusions a trend was evident: With increasing aridity of the rooting medium the FRSA:LA ratio increased (fig. 4). These results could be interpreted to mean that under water stress relatively more carbohydrate is allocated to the fine root system.

#### THE EFFECT OF PERTURBATIONS ON SHOOT AND ROOT GROWTH OF CHAPARRAL SHRUBS

Abundant information regarding the effect of major perturbations such as burning, browsing, or fertilizer application has been accumulated (Mooney and Conrad 1977). However, this information refers to the above ground plant parts and the effect of these disturbances on the root systems remains unstudied.

In spite of this lack of information we can draw some tentative conclusions based on field observations and some smaller experiments under controlled environmental conditions. The interpretation of the effect of burning of obligate seeder shrubs is relatively straightforward. The destruction of the shoot system causes the consequent decay of the roots. Shrub reestablishment is possible only by seedlings. The aboveground structures of resprouting shrubs are likewise destroyed by fire. However, new shoots emerging

<sup>3</sup>Data on file, Botany Department, San Diego State University

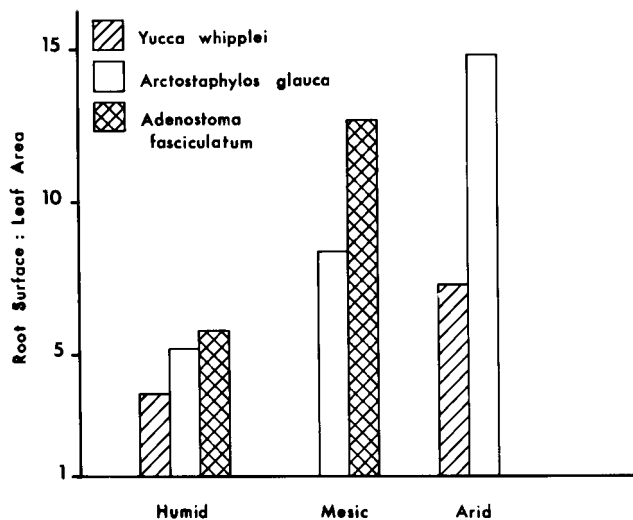


Figure 4--Root surface/leaf area ratio in 3 chaparral shrubs cultivated under 3 different watering regimes. The column of *Arctostaphylos* at the humid site represents the mean from 3 plants (range of the ratio 4.7-5.9) and 1 plant from the mesic and the arid site. *Yucca*: 2 plants at the humid site (range 3.3-4.2) and 1 plant at the arid site. *Adenostoma*: 1 plant each at the humid and the mesic site.

from burls insure permanence of the shrub on its site. These burls can reach considerable size and substantial amounts of non-structural carbohydrates (TNC) have been found. Values ranging from 2 percent to 9 percent TNC for *Adenostoma fasciculatum* and *Rhus ovata* respectively were found<sup>4</sup>. *Quercus dumosa* burls with 15 kg dry weight, 3 to 4 times the biomass of the aboveground plant structures, are by no means exceptional (Kummerow and Mangan, 1981). Thus, adequate amounts of TNC for re-sprouting shoots after fire would seem to be available. However, the question remains, how much of the original root system survives fire. We can only assume that the surface-close fine roots will be killed by fire while deeper located roots, protected from excessive heat, can survive. Stored carbohydrate has been shown to be important in shrub survival after shoot destruction (Jones and Laude, 1960). Thus, fire at a time of minimum TNC stored will be more destructive than at a time with high amounts of TNC in burl and large root tissue.

Partial destruction of shoot systems by browsing deer or cattle or by insect predation should be considered in the same line of thought. If the severed shrub has enough TNC accumulated, reduction of the leaf area can be buffered by TNC reserves. If these reserves are low and damage to the shrub is extensive, reduction of the absorbing

root surface may result. Experiments with hydroponically grown *Ceanothus tomentosus* seedling plants showed that pruning of 1/2 and 3/4 of the shoot system resulted in a significant decrease of root system development<sup>4</sup>. These observations are supported indirectly by results from root pruning experiments which established in all cases the close interdependence of root and shoot systems (Buttrose and Mullins 1968, Raper and others 1978).

A special case of disturbance is chaparral fertilization. The growing influx of permanent residents and visitors into the seasonally dry mountain areas of southern California has created deficiencies in waste disposal systems and the potential of waste water use for chaparral fertilization for biomass harvesting has been tested (Youngner and others 1976). A fertilizer experiment with conservative doses of nitrogen and phosphorus, 80 kg and 40 kg ha<sup>-1</sup> respectively, produced significant aboveground shrub biomass increase. Unfortunately, corresponding values of the belowground vegetation could not be analyzed. However, it follows from the data shown by Turner (1926) and Shank (1945) that increasing amounts of nitrogen and phosphorus reduced significantly the root/shoot ratios of various crop plants. The complex effect of fertilizer addition to chaparral becomes especially evident when observations include the herbaceous vegetation. Annuals absorbed a substantial fraction of the applied fertilizer, thus competing successfully with the woody vegetation<sup>4</sup>. Thus we can but speculate that fertilizer addition to chaparral may reduce the fine root:leaf area ratios in shrubs. Experimental work has to be done to test the hypothesis that fertilized shrubs would be exposed earlier to water stress with increasing summer drought than unfertilized plants.

#### CONCLUSIONS

Interpretation of chaparral growth dynamics requires consideration of both shoot and root growth. Growth occurs in seasonal flushes with shoot growth lasting only a fraction of the time of seasonal root growth. Growth in chaparral is limited by water and nutrients. With increasing water and nutrient stress the relative allocation of carbohydrates to the fine root system probably increases. Fertilizer application to the chaparral produces increased aboveground biomass but may decrease the relative carbohydrate allocation to the root system. Thus, biomass increase with fertilizer may result in shrubs with high water loss through transpiration and a relatively small fine root system. Such an imbalance of leaf area and fine root surface area may result in less drought resistant chaparral shrubs. Experimental work is needed to test this hypothesis.

<sup>4</sup>Data on file, Botany Department, San Diego State University

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