



05 DIC. 1979

Chile
matorral
Colliguaya odorifera
fere
acuími ento
fisiología vegetal

Secondary root and stem growth in a Chilean matorral shrub (*Colliguaya odorifera* Mol.)

G. AVILA*, S. ARAYA*, F. RIVEROS* and J. KUMMEROW**

SUMMARY

The annually produced xylem of an individual shrub of *Colliguaya odorifera* Mol. (Euphorbiaceae) was analyzed for four consecutive years (1972-1975). The data indicate that in addition to the primary growth secondary thickening growth in stems and roots contributed to about 20 % of the biomass produced. A survey of the shrub's bark biomass (all tissue peripheral to the vascular cambium) showed that contributions to biomass by bark in smaller branches and roots (diam. < 0.5 cm) were 56 and 90 % respectively, while in larger stems and roots (diam. > 0.5 cm) bark contributions to the dry weight were 22 and 53 % respectively.

RÉSUMÉ

La production annuelle de tissus ligneux par un buisson de *Colliguaya odorifera* Mol. (Euphorbiaceae) a été analysée durant 4 années consécutives (1972-1975). Les données recueillies montrent qu'à la croissance primaire vient s'ajouter une croissance secondaire correspondant à l'accroissement diamétral des tiges et des racines, représentant environ 20 % de la biomasse produite. Un inventaire de la biomasse corticale du buisson (comprenant tous les tissus extérieurs à l'assise cambiale périvascularaire) a montré que sa contribution à la biomasse était, respectivement, de 56 et de 95 % chez les branches et racines de faible diamètre (< 0,5 cm), alors que chez les branches et racines de fort diamètre (> 0,5 cm) cette contribution était, respectivement, de 22 et 53 %.

INTRODUCTION

Intensive biological studies in mediterranean areas of the world, especially in Southern California and Central Chile (MOONEY, 1977; THROWER and BRADBURY, 1977) have advanced understanding of the vegetation of these summer dry areas to the point that an ecosystems model to simulate patterns of resource use and plant response could be developed (MILLER *et al.*, 1978). With the work on the submodel for plant growth it became clear that the available quantitative information on secondary shoot and root growth was insufficient.

The lack of a solid data base regarding the carbon allocation patterns was pointed out by MOONEY (1972). There is ample information available regarding

* Laboratorio de Botánica, Universidad Católica de Chile, Santiago de Chile.

** Botany Department, San Diego State University, San Diego, California, 92182 U.S.A.

the root: shoot biomass ratios in different ecosystems. Recent data from the Chilean matorral and the Californian chaparral show that R: S ratios fluctuate between 0.4 and 0.8 (MILLER and NG, 1977; KUMMEROW *et al.*, 1977; HOFFMANN and KUMMEROW, 1978). But these data do not permit extrapolations of secondary growth increments. In *Heteromeles arbutifolia*, an evergreen shrub species of the Californian chaparral, about 80 % of the terminal branch production is contained in the leaves, 10 % in the stems, and 10 % in reproductive parts (MOONEY and CHU, 1974). Again, there are no comparable data on carbon commitment to older stems and roots.

The mediterranean shrub vegetation is adapted to wide fluctuations of annual precipitations and their correlation with the width of annual growth layers in stems and roots has been shown for two Chilean matorral shrubs by RIVEROS (1973). The purpose of the present study is a detailed analysis of the fluctuations of secondary root and stem growth from 1972-1975 of a single individual of *Colliguaya odorifera*, a common shrub in the central Chilean matorral. The amount of secondary wood produced in stems and roots during these years will be quantified and the possibility of generalizations based on these data will be discussed.

MATERIAL AND METHODS

A 10-year-old shrub of *Colliguaya odorifera* Mol. (Euphorbiaceae), apparently a seedling shrub and not a resprout was carefully excavated towards the end of the growing season in December 1975. The shrub, 1 m tall and 60 cm wide and approximately symmetric in its form, was free standing and fully sun exposed. The specimen grew in the boundaries of the farm "Santa Laura" at 1 000 m elevation about 60 km NNW of Santiago de Chile. A detailed description of climate and biology of this area has been published recently (THROWER and BRADBURY, 1977). Hot and dry summers and cool, wet winters characterize the zone. The mean yearly precipitation from 1971-1977 was 543 mm.

THE MEASUREMENTS

After excavation the shrub was defoliated and divided into branch and root age classes. The number of year rings per branch and root was counted from unstained hand sections. Since stems, and even more so roots, are usually excentric in their cross sections the recorded width of each growth layer was the mean of five measurements.

Stem and root age classes were established and average lengths and dry weights for each size class were recorded.

The yearly length increment of roots and stems was found by means of serial cross sections. Beginning at the distal end of a stem or root, observations on cross sections were made to establish the distance from the shoot (root) tip to the appearance of the next growth layer. This distance is equivalent to the elongation of the shoot (root) during the respective year. The same procedure was then repeated for each new year ring in proximal direction. The obtained results can be validated by observations of the branching patterns in younger stems but not so in roots, since the clustered short internodes at the end of each growing period can be recognized by the leaf scars in the respective stem region. The annual growth layers are considered cylinders superposed over each other. The small error introduced by the fact that these are rather conical figures can be neglected. The length of each hollow

cylinder with the measured wall thickness (= thickness of the annual growth layer) allowed the calculation of the volume of the annual wood production of the respective root or stem. This procedure was repeated with all the roots and shoots of the test shrub. Once a pattern of annual growth layers was established work on stems and roots of similar size progressed quickly. Thus, a reasonable calculation of the volume of annual secondary xylem production in all the roots and stems of this one shrub became possible. The following formula was used:

$$\text{TWP} = \text{WPS} + \text{WPR}, \quad \text{where} \quad \text{WPS} = \sum_{i=1}^4 (ls_i \times As_i \times ns_i)$$

and

$$\text{WPR} = \sum_{i=1}^4 (lr_i \times Ar_i \times nr_i).$$

TWP = total wood production; WPS = wood production of stems and WPR = wood production of roots. ls_i , lengths of year rings in stems for each of the years 1972-1975. As_i , area of year rings in stems for each of the above mentioned years, and ns_i , number of stems in the respective age class. lr_i , Ar_i , nr_i , corresponding categories of the root system.

The weight density of the wood of *C. odorifera* with 0.98 g.cm^{-3} allows a simple translation of the measured cubic centimeters into grams.

RESULTS AND DISCUSSION

The results of age classification of stems and roots of the excavated *Colliguaya* are summarized in table I. The data shows clearly the typical multistemmed character of the shrub species. Seven 8-10-year old branches diverge at ground level. Up to the age of five, the number of branches rises sharply until the maximum of 32 branches of 1-2 years is attained. It can be assumed that a certain number of 1-year-old branches was shed over the past years, probably resulting from the shading of lower branches by the growing crown and severe water stress during the late summers. This phenomenon has been discussed thoroughly by MILLINGTON and CHANEY (1973). It is difficult to correct for this factor. It must be understood that this leads to an underestimation of past secondary wood production. The main root, 10-years old, and probably the original tap root of this shrub, branched 3 cm distal from the root crown and this branching continued more or less regularly year after year. The data in table I shows further that the average length of the 1-4-year branches is about 11 cm while the 5-10-year ones have 17 cm yearly length increments. In roots, the 3-8 year branches were 15 cm long and thus, significantly longer than the 9-year branches which measured only 9 cm of average length. In table I stems and roots were classified by diameter. Analysis shows that diameter and age were, according to expectations, correlated. The average branch length in table I, therefore, should provide the yearly length increment by dividing the mean branch length by the number of growth layers. The direct measurement of annual growth layer lengths (table II) validates this point.

TABLE I

Diameter classes, number of yearly growth layers in each diameter class, and the actual number of branches per diameter class. The average length of branches per size class multiplied by the number of branches indicates the total length of branches in the respective category. The last column shows the dry weight of each branch size class. (S. E.), Standard error.

Years	Stem					
	Diameter (cm)	No. of growth layers	No. of branches	Av. length of branch (cm) (S. E.)	Total length of branches (cm)	Dry weight (g)
1974-1975.....	0 -0.2	1-2	32	11.0 (0.8)	352	20.4
1972-1973.....	0.2-0.5	3-4	28	10.7 (1.1)	300	33.7
1969-1971.....	0.5-0.8	5-7	9	17.0 (1.2)	153	38.5
1966-1968.....	0.8-1.0	8-10	7	17.0 (0.9)	119	111.8
	Root					
	Diameter (cm)	No. of growth layers	No. of branches	Av. length of branch (cm) (S. E.)	Total length of branches (cm)	Dry weight (g)
1974-1975.....	0 -0.2	1-2	19	10.5 (1.7)	200	4.3
1971-1973.....	0.2-0.5	3-5	16	15.5 (0.9)	248	39.8
1968-1970.....	0.5-1.0	6-8	10	15.0 (1.3)	150	42.4
1967.....	1.0-2.0	9	6	8.0 (1.0)	48	117.4
1966.....	2.2	10	1	3.0	3	44.0

TABLE II

Length (cm) of yearly growth layers found by direct measurements. Each value is the mean of eight measurements from different shoots and roots. (S.E.), Standard error.

	Shoot (S. E.)	Root (S. E.)
1975.....	5.60 (1.40)	5.50 (2.23)
1974.....	5.43 (1.03)	4.91 (2.72)
1973.....	4.90 (1.34)	4.91 (2.00)
1972.....	5.17 (1.49)	5.08 (1.63)

Recordings of the width of yearly growth layers over the years from 1972-1975 (table III) demonstrate the decrease of the thickness of each annual growth layer from the base towards the apex. This information and the data in tables I and II allowed the calculation of the volume of secondary xylem produced annually by the entire shrub from 1972-1975. Our data shows that the amount of secondary wood increased steadily in stems and roots from 1972 to 1975 (table IV).

TABLE III

Width of yearly growth layers (mm) measured close to the shoot (root) base and 10-20 cm proximal from the shoot (root) tip. Each value is the mean of 40 measurements on eight different shoots and roots. (S. E.), Standard error.

Year	Close to shoot (root) base		10-20 cm from shoot (root) tip	
	Shoot (S. E.)	Root (S. E.)	Shoot (S. E.)	Root (S. E.)
1975.....	0.51 (0.11)	0.53 (0.02)	0.49 (0.04)	0.43 (0.10)
1974.....	0.35 (0.04)	0.51 (0.15)	0.41 (0.07)	0.43 (0.07)
1973.....	0.48 (0.07)	0.52 (0.11)	0.34 (0.05)	0.38 (0.04)
1972.....	0.53 (0.09)	0.56 (0.08)	0.31 (0.09)	0.36 (0.07)

TABLE IV

Grams of annual xylem production from 1972-1975 in all stems and roots of the analyzed *C. odorifera*

	1972	1973	1974	1975
Stems.....	14.9	20.3	29.9	60.6
Roots.....	19.2	24.9	30.6	40.0

It was considered interesting to establish the ratio of secondary to primary growth. Average yearly production data for *C. odorifera* have been published from the same area. They indicate a total twig and leaf production of 716 g.m⁻² of ground cover yr⁻¹ (438 g twigs and 278 g leaves) for 1973 (MOONEY *et al.*, 1977). The analyzed *C. odorifera* probably had in 1973 a crown projection close to 0.3 m². Thus, for this specific shrub, twig and leaf production must have been about 239 g (twigs + leaves). For the same year (1973) the calculations of the total xylem production indicated 45.2 g (20.3 g stems, 24.9 g roots). With other words, in addition to the leaf and primary twig production about 20% must be added in order to include the secondary growth in thickness.

A complete balance of biomass production requires further consideration of yearly fine root growth (analogous to leaf production) and the growth of the bark (= all tissue outside the vascular cambium). With respect to the fine roots (diam. < 1 mm) only a rough estimate based on results of Californian chaparral shrubs is possible (Kummerow, *unpublished results*). According to the size and leaf biomass of our test shrub the fine root production for 1973 must have been in the order of 50 g.

A survey of the thickness of the bark for two branch size classes is shown in table V. These data permits the conclusion that the dry weight represented by bark tissues is one-third in branches and more than one-half in roots. Unfortunately, there does not seem to exist an easy way to measure the yearly bark production.

TABLE V

Survey of the proportions of the bark and xylem contribution to the total dry weight of shoots and roots of the tested C. odorifera. Analysis according to two arbitrary chosen diameter size classes.

	Bark dr. wt. (g)	Xylem dr. wt. (g)	Bark (%)	Xylem (%)
Stems				
diam. < 0.5 cm..	30.3	23.7	56	44
diam. > 0.5 cm..	33.1	117.2	22	78
TOTAL.....	63.4	140.9	31	69
Roots				
diam. < 0.5 cm..	39.5	4.6	90	10
diam. > 0.5 cm..	108.2	95.7	53	47
TOTAL.....	147.7	100.3	60	40

It is not claimed that the presented values for a single *Colliguaya* are representative for all mediterranean evergreen shrub species. Yet, a survey of year ring widths from seven chaparral and eight matorral shrub species showed that these values were all in the same order of magnitude (Kummerow and Giliberto, *unpublished data*). We feel justified to conclude that the calculated 20 % value is an acceptable mean for the yearly xylem growth of matorral and chaparral shrubs.

The amount used annually for bark growth can only be guessed but may be as high as 5-10 % of the total yearly biomass production.

ACKNOWLEDGEMENTS

The technical help of Mr. Andrés Seguy and Luis Gonzalez is gratefully acknowledged. Dr. Paul Zedler assisted generously with the preparation of the manuscript. The research was supported financially by the National Science Foundation (NSF Grant No. DER-75-19491 and DEB-77-13944) and the Dirección de Investigaciones de la Universidad Católica (DIUC, 20/77).

REFERENCES

- HOFFMAN A. and KUMMEROW J., 1978. — Root studies in the Chilean matorral. *Ecologia*, 32, 57-69.
 KUMMEROW J., KRAUSE D. and JOW W., 1977. — Root systems of chaparral shrubs. *Ecologia*, 29, 163-177.

- MILLER P. C. and NG E., 1977. — Root: shoot biomass ratios in shrubs in Southern California and Central Chile. *Madroño*, 24, 215-223.
- MILLER P. C., STONER W. A. and RICHARDS S. P., 1978. — Medecs, a simulator for mediterranean ecosystems. *Simulation*, 30, 173-190.
- MILLINGTON W. F. and CHANEY W. R., 1973. — Shedding of shoots and branches. In: KOSLOWSKI T. T., Ed., *Shedding of plant parts*. Academic Press, New York and London, 149-196.
- MOONEY H. A., Ed., 1977. — Convergent evolution in Chile and California. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania, 224 pp.
- MOONEY H. A., 1972. — The carbon balance of plants. *Annu. Rev. Ecol. Syst.*, 3, 315-346.
- MOONEY H. A. and CHU C., 1974. — Seasonal carbon allocation in *Heteromeles arbutifolia*, a Californian evergreen shrub. *Ecologia*, 14, 295-306.
- MOONEY H. A., KUMMEROW J., JOHNSON A. W., PARSONS D. J., KEELEY S., HOFFMANN A., HAYS R. I., GILIBERTO J. and CHU C., 1977. — The producers. Their resources and adaptive responses. In: MOONEY H. A., Ed., *Convergent evolution in Chile and California*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania, 85-143.
- RIVEROS DE LA PUENTE F. G., 1973. — Ritmo anual del crecimiento en raíces de *Quillaja saponaria* y *Cryptocarya alba*. Thesis, Universidad Católica de Chile, Instituto de Ciencias Biológicas, Santiago de Chile, 27 pp.
- THROWER N. J. W. and BRADBURY D. E., Eds., 1977. — Chile-California mediterranean scrub atlas. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania, 237 pp.

