

Carbon Balance Studies in Chaparral Shrubs: Implications for Biomass Production¹

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There is considerable energy available for harvesting in chaparral biomass. Each year, on the average, about 3 percent of California's 3.3 million hectares of chaparral burns. Using values from Riggan and Dunn (*In press*), at an average biomass of 50 m tons per hectare this 100,000 hectares burned represents the gross energy equivalent of 18.2×10^6 barrels of oil or 546 million dollars at current oil prices. This is roughly the energy equivalent of 2 Hoover Dams or 1/2 of the on shore oil production of the central California coast (2×10^{13} kcal of renewable energy, McCartor 1976).

The magnitude of the energy available means that it is possible that chaparral will be utilized as an energy source at some point in the near future.

If chaparral is to be used as an energy source, there are several major management problems to consider including the environmental effects of harvesting and how to mitigate them and the best way to maximize yield on a sustained basis. Mooney (*In press*) noted the major biological factors which must be considered in making management decisions. These included life history attributes, fluxes of minerals and environmental responses of species. This paper will consider the contribution that carbon balance research can make to the last two of these areas as input to management considerations.

The controls on net carbon uptake is of obvious importance in evaluating the potential for biomass harvesting in chaparral and in evaluating optimal harvesting patterns to maximize long term production while minimizing flammability. This paper will consider the intrinsic and extrinsic controls on photosynthesis and respiration in chaparral plants and the implication of carbon allocation patterns, nutrients, moisture, temperature and stand age on net production of chaparral stands in southern California.

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Abstract: Photosynthesis and respiration rates were determined for chaparral shrubs as a function of temperature and/or light intensity. In mature stands at Echo Valley, Calif., net seasonal carbon assimilation by leaves ranges from a dry weight equivalent of $673 \text{ g m}^{-2} \text{ y}^{-1}$ in pure stands of *Rhus ovata* to $1439 \text{ g m}^{-2} \text{ y}^{-1}$ in *Arctostaphylos glauca*. Net accumulation of dry matter ranges from $261 \text{ g m}^{-2} \text{ y}^{-1}$ for *R. ovata* to $525 \text{ g m}^{-2} \text{ y}^{-1}$ for *A. glauca*. Stem respiration utilizes about 30 percent of the assimilated carbon; total respiration accounts for about 60 percent of the carbon assimilated. This data and growth models are used to calculate optimal harvest intervals and productivity of shrubs.

This paper will not make major management recommendations, but will present information upon which management decisions can be based and which will suggest areas for further research.

Controls on Net Photosynthesis

Potential net photosynthesis

Maximum photosynthetic rates in evergreen chaparral shrubs vary by species. This means that stand productivity may vary with species composition according to the realized patterns of net photosynthesis. In one study, measured maximum photosynthetic rates varied from $7.6 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ for *Ceanothus leucodermis* to $1.1 \text{ mg CO}_2 \text{ g}^{-1} \text{ dry wt h}^{-1}$ for *Rhus ovata* (table 1). Photosynthesis decreased in the order: *C. leucodermis* > *Cercocarpus betuloides* > *Arctostaphylos glauca* > *Quercus dumosa* > *Adenostoma fasciculatum* > *Ceanothus verrucosus* > *Rhus integrifolia* > *R. ovata*. Because of differences in leaf density thickness, the pattern on a surface area basis may be quite different. These maximum observed rates are further modified by site and environmental factors to yield an observed annual value.

Photosynthesis varies seasonally, by elevation, and by slope. The seasonal total photosynthetic uptake correlates strongly with the cover produced by various evergreen shrub species in the chaparral. Species with higher seasonal photosynthetic uptake rates tend to have higher observed cover in the chaparral. Competitive advantage is therefore correlated to photosynthetic ability (Oechel and Mustafa 1979).

Temperature

Temperature appears to exert little limitation on net photosynthesis over normally experienced ranges of temperature (Figs. 1 and 2). The average Californian shrub or the average Chilean shrub shows relatively high photosynthesis rates at 5°C and at 40°C. For Californian species the average photosynthetic rate at 40°C is greater

Table 1--Maximum photosynthesis rates in May and June determined by $^{14}\text{CO}_2$ and infrared gas analysis (IRGA) techniques and leaf density-thickness for chaparral species in San Diego County (modified from Oechel et al. In press).

Growth form and species	Elevation (m)	Sampling date (Day/Mo/Yr)	Leaf density-thickness (g dry wt dm ⁻²)	Maximum photosynthesis rates		
				(mg CO ₂ g ⁻¹ dry wt h ⁻¹)		(mg CO ₂ dm ⁻² h ⁻¹)
				$^{14}\text{CO}_2$		IRGA
Evergreen sclerophyllous shrubs						
<u>Adenostoma fasciculatum</u>						
Equator-facing slope	1000	03/06/76	1.17	3.6		4.3
Equator-facing slope	1000	17/05-01/06/76				6.6
Pole-facing slope	1000	05/06/76	1.17	3.0		3.5
<u>Arctostaphylos glauca</u>						
Equator-facing slope	1000	03/06/76	2.08	4.1		9.0
Equator-facing slope	1000	03-14/06/76				10.5
Pole-facing slope	1000	05/06/76	2.18	3.5		7.6
<u>Ceanothus greggii</u>						
Equator-facing slope	1000	03/06/76	3.13	3.3		10.4
Equator-facing slope	1000	16-20/06/76				7.6
<u>Ceanothus leucodermis</u>						
	1000	05/06/76	0.94	7.6		7.2
<u>Ceanothus verrucosus</u>						
	120	12/06/76	3.13	2.6		8.3
<u>Cercocarpus betuloides</u>						
	1150	10/06/76	1.56	4.3		6.8
<u>Quercus dumosa</u>						
	1000	05/06/76	1.56	4.0		6.2
<u>Rhus integrifolia</u>						
	85	12/06/76	3.13	1.4		4.3
<u>Rhus ovata</u>						
Equator-facing slope	1000	03/06/76	3.13	1.1		3.5
Equator-facing slope	1000	22-27/06/76				4.7
Mean				3.5		6.5
						7.4

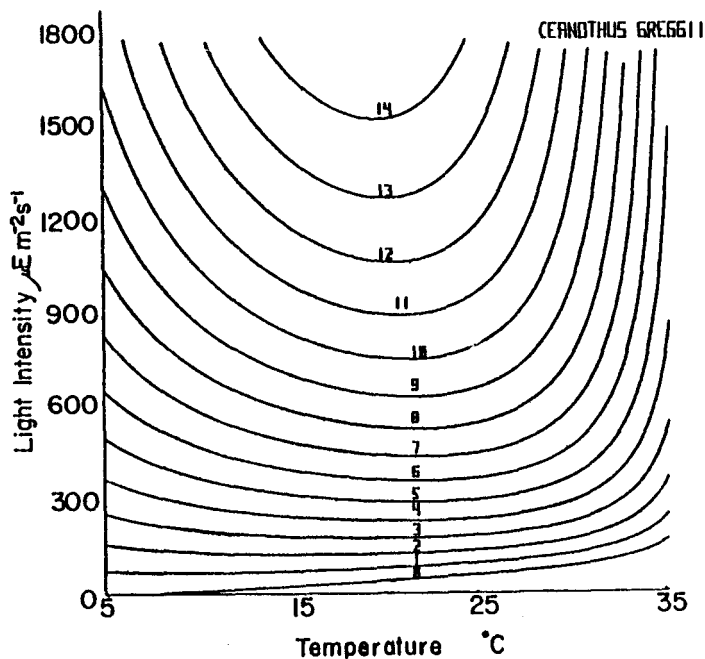


Figure 1--Isopleths of photosynthetic rates with respect to temperature and light intensity for Ceanothus greggii growing at Echo Valley, California in May 1976. Rates predicted with nonlinear regression analysis using a Michaelis-Menton form for the light response. From Oechel, Lowell, and Jarrell (In press).

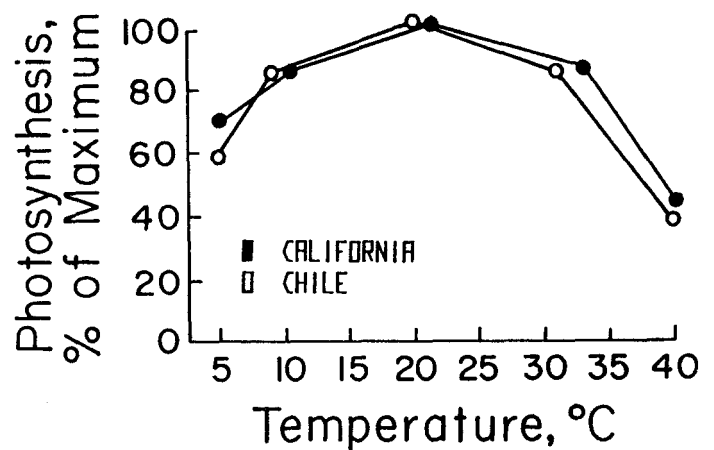


Figure 2--Average photosynthetic response of four chaparral species (●): Ceanothus greggii, Arctostaphylos glauca, Adenostoma fasciculatum, and Rhus ovata; and four matorral species (○): Trevoa trinervis, Colliguaya odorifera, Satureja gilliesii, and Lithraea caustica to temperature at saturating light (1,401-1,800 $\mu\text{E m}^{-2} \text{s}^{-1}$). From Oechel et al. (In press).

than 45 percent of the maximum rate (fig. 2). Low winter temperatures would seldom suppress photosynthesis. At 5°C the photosynthetic rate is still about 70 percent of the maximum rate. This implies that substantial increases or decreases in annual mean temperature which could be caused by differences in elevation or latitude would have little effect on net photosynthesis. Simulations confirmed this showing that an increase or decrease in mean annual temperature would have less than a 10 percent effect on photosynthetic uptake over the course of the season (fig. 3). Temperature is therefore unlikely to limit production in chaparral over much of range of chaparral in southern California.

Light

Light levels may have a major influence on photosynthesis rates and productivity. At optimal temperature, light levels below full sunlight may limit photosynthesis of intact branches with naturally oriented leaves (e.g. see fig. 1). Therefore, even at full solar radiation levels, light may limit photosynthetic rate within the canopy, especially at higher leaf area indices.

Periods of reduced radiation, whether due to time of day and/or cloud cover, will reduce productivity. The short photoperiods in winter, which often occur when ample moisture is available for photosynthesis and when temperature allows appreciable photosynthetic rates, may result in marked limitation in photosynthesis below that potentially possible.

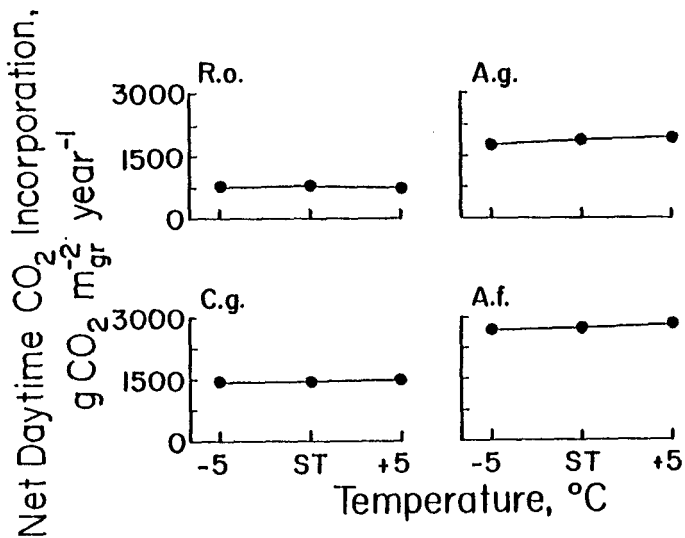


Figure 3--The effects on simulated seasonal (daytime) photosynthesis incorporated in grams CO₂ per square meter of ground per year of an increase or decrease in temperature of 5°C from observed standard temperatures (ST) in 1973-1974 in *Rhus ovata* (R.o.), *Arctostaphylos glauca* (A.g.), *Ceanothus greggii* (C.g.), and *Adenostoma fasciculatum* (A.f.) with a leaf area index of 1 and a stem area index of 0.9. From Oechel et al. (In press).

Moisture

As water potential decreases, plant moisture stress has a major effect on photosynthetic rate through its effect on stomatal conductance. *Arctostaphylos glauca*, decreases from a maximum daily uptake rate of 33 mg CO₂ g⁻¹ dry wt d⁻¹ at -0.5 MPa bars dawn water potential to 7 mg CO₂ g⁻¹ dry wt d⁻¹ at -3.5 MPa bars dawn water potential (fig. 4). *Adenostoma fasciculatum* shows a somewhat less rapid decline in daily photosynthetic rate with decreasing maximum water potential. In both cases, zero daily carbon uptake is projected to occur at about -4 to -4.5 MPa.

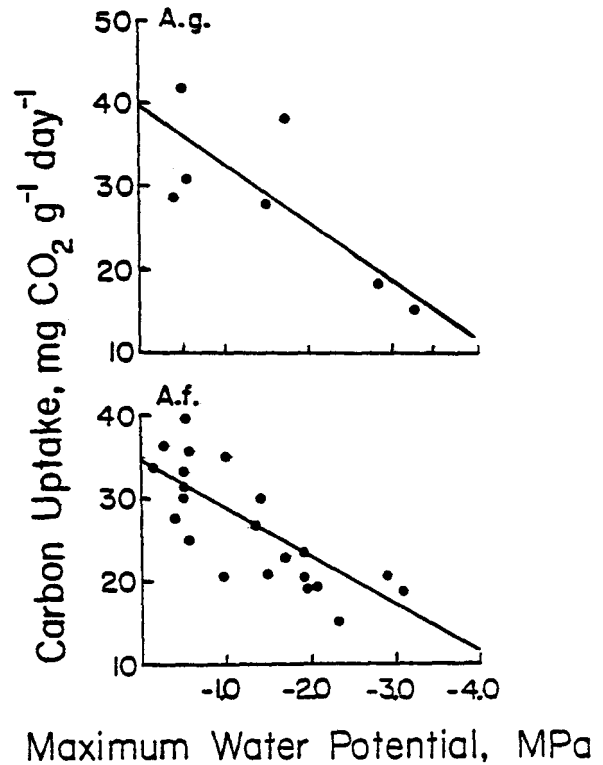


Figure 4--Relationship between maximum (dawn) water potential and seasonal daily carbon uptake of *Arctostaphylos glauca* (A.g.) and *Adenostoma fasciculatum* (A.f.) in San Diego County, California. From Oechel et al. (In press).

Species vary with respect to the limitation of carbon uptake by summer drought. For example, compared to spring (May) values, *Adenostoma fasciculatum*, *Quercus dumosa*, and *Cercocarpus betuloides* may show less than 40 percent depression in carbon uptake by late summer (August) (fig. 5). Other evergreen species including *Rhus ovata*, *Rhus integrifolia*, *Ceanothus greggii*, and *Ceanothus verrucosus* may show greater than 60 percent depression in photosynthesis during the summer. Species which show the greatest suppression in photosynthesis may not necessarily be those experiencing the greatest water stress. This is especially true in the case of *Rhus ovata* and *Rhus integrifolia* which reduce stomatal conductances at relatively high water potentials (Poole and Miller 1975),

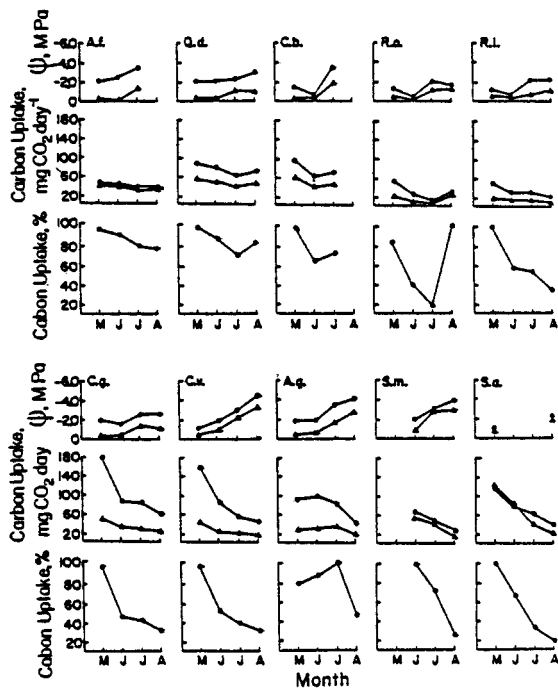


Figure 5--Seasonal patterns of dawn (▲) and midday (●) water potentials in MPa, carbon uptake in milligrams of CO₂ per day per gram dry weight of leaf (▲) and per square decimeter of leaf (●), and the relative carbon uptake as a percent of the maximum monthly rate for *Adenostoma fasciculatum* (A.f.), *Quercus dumosa* (Q.d.), *Cercocarpus betuloides* (C.b.), *Rhus ovata* (R.o.), *Rhus integrifolia* (R.i.), *Ceanothus greggii* (C.g.), *Ceanothus verrucosus* (C.v.), *Arctostaphylos glauca* (A.g.), *Salvia mellifera* (S.m.), and *Salvia apiana* (S.a.).

and which experience marked depression in photosynthesis at midday water potentials of -2.0 MPa. *Adenostoma fasciculatum* and *Quercus dumosa* on the other hand, maintain substantial photosynthetic rates at midday water potentials of -3.5 to -4.0 MPa. As a result, both the site moisture status and the species specific photosynthesis vs. plant water potential relationships must be considered when predicting site carbon balance.

Nutrients

Nutrient responses of photosynthesis yield conflicting results. While production of chaparral species is stimulated by nitrogen fertilization (Kummerow pers. cow.), laboratory studies may indicate an inverse relationship between treatment nitrogen levels and photosynthetic rate (Oechel, Lowell, and Jarrel *In press*). Despite this reduction in photosynthetic rate with increasing nitrogen, whole plant carbon balance and growth increase with increasing nitrogen treatment. This indicates a negative correlation between photosynthetic rate and growth rate in this situation.

However, marked increases in photosynthetic rates following fire indicate a nutrient limitation of photosynthesis in the field (Oechel and Hastings *In press*). Following a fire, young plants tend to have higher photosynthetic rates than do mature species. These rates may be up to 500 percent higher in *Adenostoma fasciculatum* burn resprouts than in the mature vegetation (Oechel and Hastings *In press*). Interestingly this elevation of photosynthetic rate does not appear to be primarily due to an increase in available moisture (fig. 6). Resprouts of *A. fasciculatum* following hand-clearing showed little increase in photosynthetic rate. The conclusion is that the nutrients released following fire produce the elevated photosynthetic rates.

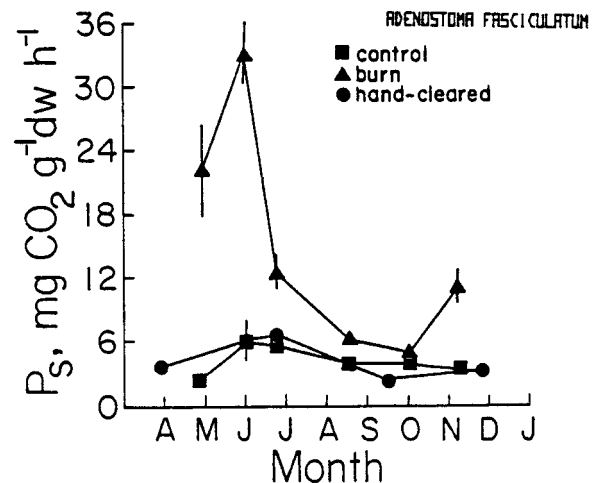
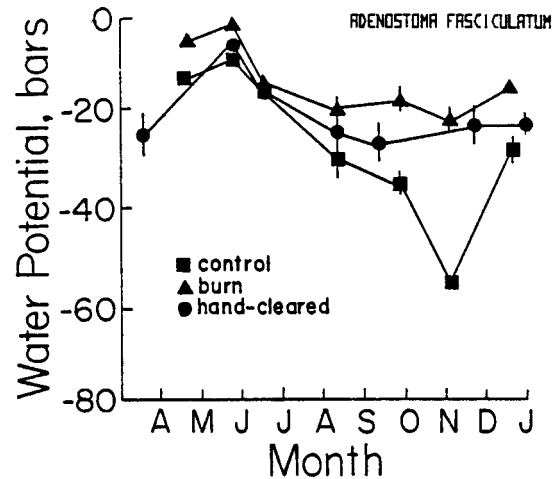


Figure 6--Photosynthesis rates and tissue water potential in 1980 in mature (34 year old) *Adenostoma fasciculatum* control plants and in resprouts following hand-clearing in June 1979 and burning in November 1979.

Water relations and photosynthetic rates following biomass harvesting

Harvesting immediately reduces leaf area index which generally takes several years to restore its original area. As a result, water potentials in plants are elevated in resprouts for at least 20 months following harvesting. For example, plants were harvested from plots between 30 May and 13 June 1979. Near the end of the drought in October 1980, midday, water potentials for *Adenostoma fasciculatum* averaged -5.7 MPa in mature vegetation versus -2.9 MPa in resprouts (fig. 6). *Arctostaphylos glandulosa* resprouts and *Quercus dumosa* resprouts showed similarly elevated water potentials in the resprouts (Hastings and Oechel *In press*, Oechel and Hastings *In press*) (fig. 7). This elevated water potential allows increased leaf conductances and, for some species, increased photosynthetic rates. Leaf conductances are systematically elevated in the resprouts compared to the mature vegetation. In October, mature vegetation and resprouts showed conductances in *A. fasciculatum* of .12 and .26 cm s^{-1} , the rates were .22 and 0.38 cm s^{-1} for *A. glandulosa* and in *Q. dumosa* conductances were 0.51 and 1.37 for mature vegetation and resprouts respectively. At almost all measurement periods, resprouts of *Quercus dumosa* had equivalent or higher conductances than mature vegetation (fig. 7). For *Quercus dumosa*, this elevated water status apparently resulted in an increase in the photosynthetic rate of resprouts compared to mature vegetation. The elevation in photosynthetic rate on resprouts of *Quercus dumosa* is appreciable, with the photosynthetic rates in June in mature plants being 4.3 $\text{mg CO}_2 \text{ g}^{-1} \text{ dry wt. h}^{-1}$ versus 6.6 for the resprouts. In October, the photosynthetic rate of mature vegetation is 2.8 while the resprout are 230 percent higher at 6.5 $\text{mg. CO}_2 \text{ g}^{-1} \text{ dry wt. h}^{-1}$. As discussed earlier, *A. fasciculatum* shows only a marginal increase in photosynthetic rates, in hand-cleared resprouts compared to burn resprouts. *Arctostaphylos glandulosa* resprouts following hand clearing initially show a higher photosynthetic rate but by August, 9 months after harvesting the rates are only marginally higher (Oechel and Hastings, unpublished data). Since resprouts following hand-clearing do not show the marked increases in photosynthetic rate generally shown by post-fire resprouts it appears that nutrient release associates with fire is more important than improved moisture status following fire in elevating resprout photosynthetic rates. This difference between photosynthesis rates in resprouts following burning and hand-clearing makes it difficult to predict regrowth rates following biomass harvesting from regrowth rates following fire. While data for growth rates following fire is limited, regrowth rates following harvesting is more limited and extrapolations from fire resprouts is tenuous.

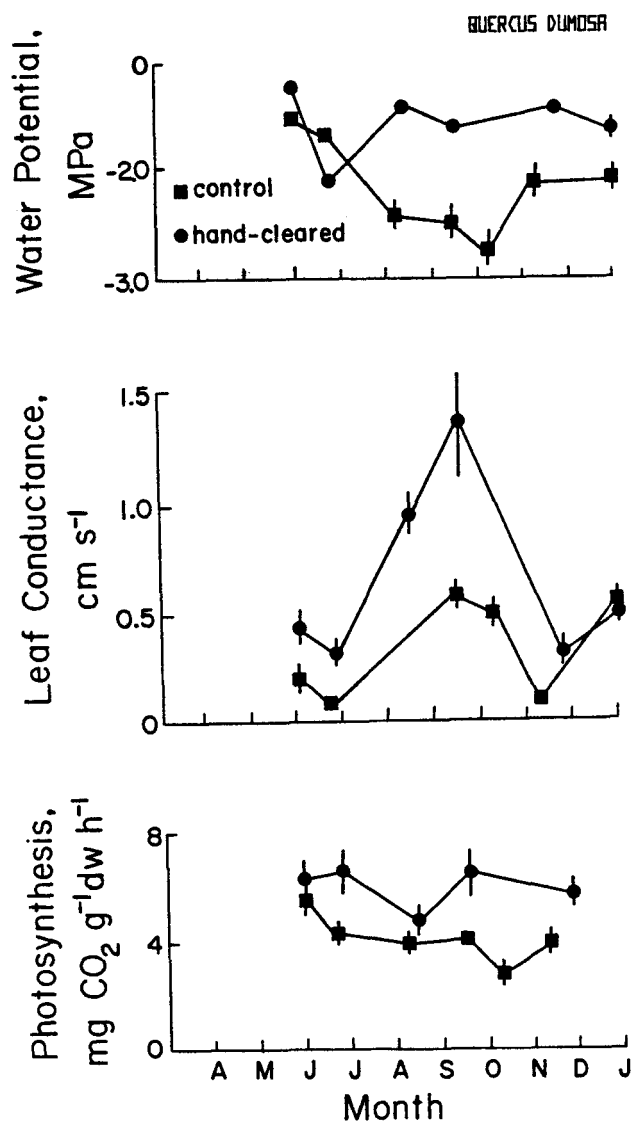


Figure 7--Photosynthesis rates, leaf conductance, and tissue water potential in 1980 in mature (34 year old) *Quercus dumosa* and in *Q. dumosa* resprouts following harvesting in June 1979.

Controls on Net Carbon balance and Biomass Accumulation

Net productivity depends on net photosynthesis, respiration and carbon allocation patterns. Respiration rates for stems is fairly low on a dry weight basis, the rates being less than 0.8 $\text{mg g}^{-1} \text{ dry wt. h}^{-1}$ in stems larger than 6 mm in diameter. However stem diameter effects respiration rate on a dry weight basis with decreasing diameter below 6 mm, respiration rapidly increases on a dry weight basis (fig. 8).

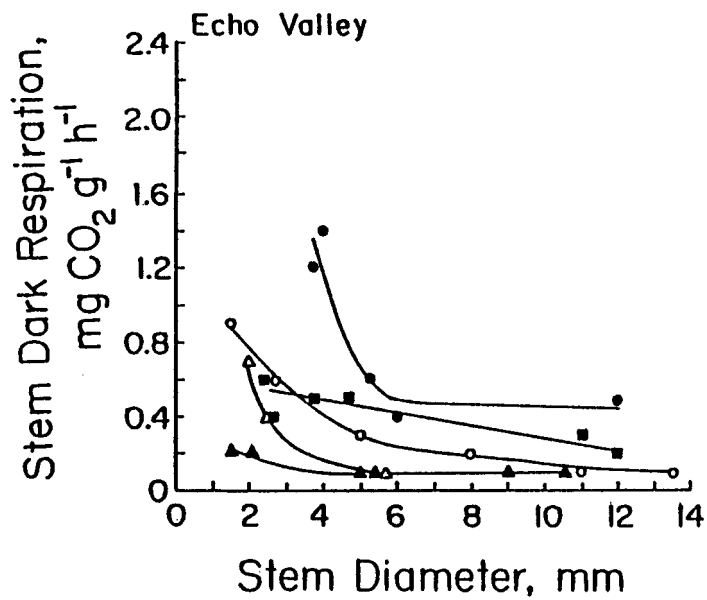


Figure 8--Relationship between stem diameter and stem dark respiration rate at 25°C for: *Arctostaphylos glauca* (●), *Quercus dumosa* (■) *Rhus ovata* (Δ), *Ceanothus greggii* (○), and *Adenostoma fasciculatum* (▲) measured in May-June at Echo Valley. From Oechel and Lawrence (In press).

In mature shrubs about 2/3 of the net photosynthesis goes to maintenance and growth respiration leaving about 1/3 of the net photosynthesis for growth (fig. 9). Carbon allocation is about equally distributed between leaves, stems and roots, each receiving about a third of the fixed carbon. The harvested material, however, well may be comprised of leaf material which will turn over at a high rate (72-235 g m⁻² y⁻¹) (Oechel et al. In press) but which will not accumulate on an annual basis once the maximum leaf area index is reached following harvesting. This means that the only accumulation accessible for harvesting comes from

Table 2--Simulated annual allocation (g dry wt m⁻² y⁻¹) to leaves, stems, main roots and absorbing roots in four shrubs from pure stands of 22-year-old Californian chaparral (modified from Oechel and Lawrence In press).

Species	Leaves	Stems	Main roots	Absorbing roots	Total
	g dry wt m ⁻² y ⁻¹ (pct. of total)				
<i>Arctostaphylos glauca</i>	235 (48)	74 (14)	22 (4)	194 (37)	525
<i>Adenostoma fasciculatum</i>	72 (17)	190 (22)	94 (22)	67 (16)	423
<i>Ceanothus greggii</i>	181 (49)	58 (16)	25 (6)	108 (29)	372
<i>Rhus ovata</i>	109 (42)	64 (25)	31 (12)	57 (22)	261

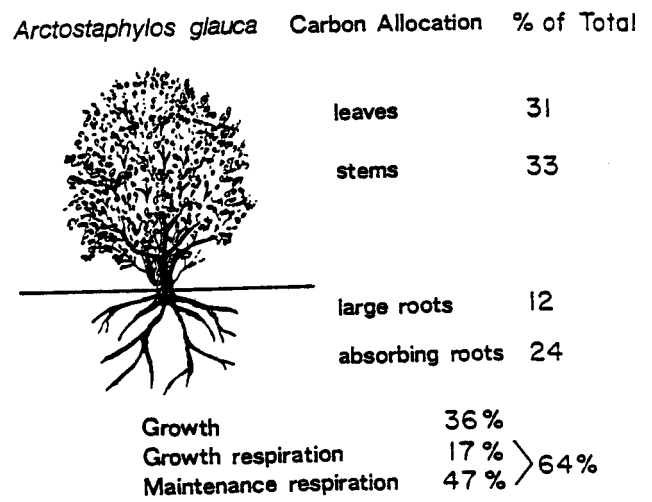


Figure 9--Estimated carbon allocation to growth and respiration of various structures in *Arctostaphylos glauca*. Values were calculated from field and laboratory experiments, field observations, and calculations and extrapolations using simulation models. From Oechel and Lawrence (In press).

stem growth, which is only 14 to 45 percent of the total plant biomass production and only 5 to 16 percent of the net photosynthesis (table 2) (Oechel and Lawrence In press).

Allocation patterns of shrubs in the chaparral are of prime importance in attempting to model biomass accumulation following harvesting. However, relatively little is known of the pattern of carbon accumulation following fire or harvesting.

In young seedlings of *Ceanothus crassifolius* fertilized with 1/4 strength Hoagland's solution and 1 mM NO₃, only about 50 percent of the carbon taken up in photosynthesis is respired by the plant. The remaining 50 percent goes to growth (table 3). Stem respiration, which is a major

Table 3--Calculated annual budget for *Ceanothus crassifolius* seedlings receiving one-quarter strength Hoagland's solution containing 1mM NO₃. Respiration calculated for 24 h/d at 15°C except for leaves (11 h/d). Photosynthesis is calculated at the maximum photosynthesis rate for 12 h/d (modified from Oechel, Lowell, and Jarrell In press).

Leaf photosynthesis	Leaf respiration	Stem respiration	Root respiration	Net plant CO ₂ flux
g CO ₂ y ⁻¹ plant ⁻¹				
512	179 (35)	57 (11)	31 (6)	243 (48)

source of carbon loss in mature stands, accounts for only an 11 percent loss of the carbon assimilated in photosynthesis by the seedling. Similarly, root respiration is much lower in seedlings than in mature plants being 6 percent of the net CO₂ uptake in Ceanothus crassifolius seedlings (table 2) compared to a calculated 26 percent in mature Ceanothus greggii individuals (table 4). Therefore, seedlings would be expected to accumulate carbon more rapidly than mature individuals of the same leaf area index, due to the lower loss of carbon to respiration in the seedlings.

Table 4-- Simulated carbon budget (g CO₂ m⁻² y⁻¹)

for four shrubs from Californian chaparral (modified from Oechel and Lawrence In press).

Species	Net CO ₂ uptake	Leaf respiration	Stem respiration	Root respiration	NA plant CO ₂ uptake
<u>Arctostaphylos</u> <u>slimes</u>	2116	300 (14)	615 (29)	429 (20)	772 (36)
<u>Adenostoma</u> <u>fasciculatum</u>	1784	638 (30)	291 (14)	232 (11)	622 (29)
<u>Ceanothus</u> <u>greggii</u>	1556	222 (14)	390 (25)	397 (26)	547 (35)
<u>Rhus ovate</u>	978	130 (15)	176 (18)	267 (27)	384 (39)

Interestingly, 11 month old seedlings of Ceanothus crassifolius accumulate carbon at the annual rate of 248 g CO₂ per plant. At a density of 1 plant per meter square, this translates to a dry weight accumulation of 165 g dry wt m⁻² y⁻¹. For plants of only 22 g m⁻² the rate of biomass increased is 165 g m⁻² y⁻¹. This is 44 percent of the value achieved by mature Ceanothus greggii with a standing crop of 5085 g dry wt m⁻² (Oechel and Lawrence In press)

Lower accumulation rates of biomass with increased age are well known for chaparral (Sampson 1944, Mooney 1977). Two factors may account for this. Firstly, resprouters possess a well formed root system following fire which facilitates water and nutrient uptake. The extent of the root die back following fire is not known, but the major roots and many of the fine roots may persist to maintain favorable moisture and nutrient balances following fire or harvesting. Secondly, immediately after fire or harvesting, stored reserves in the burl may augment initial shoot growth, resulting in rapid initial rates of growth. Thirdly, younger plants have a lower "overhead" of respiring stem mass. Young plants from seed also lack a massive burl and root system to maintain.

Short rotation intervals have been suggested for shrub harvesting. However, on a short rotation basis, respiration rates of the burl and secondary roots may begin to consume large proportions of the available carbohydrate, and may result in lower production than predicted from data acquired from regrowth rates following

longer rotation intervals where reserves have had an adequate period to accumulate.

The rate of shoot-growth may be very great the first year after fire. This rapid growth rate is presumably largely dependent on reserves stored since the last fire and may be enhanced by the increased moisture and nutrient availability following fire. This spurt of growth may be important when competing for light and other resources after harvesting or fire. Rapid exposure of leaf area may be very important in the long term net carbon uptake by an individual. Therefore, it would be dangerous to extrapolate from regrowth following fire to regrowth following harvesting, especially under altered periods between regrowth.

As the interval between harvesting decreases, the time to restore reserves used in the regrowth process also decreases. The net result may be decreasing reserves in the burl and hence regrowth rates less than those predicted from resprouts following fire.

Also, photosynthetic rates will be lower in resprouts following biomass harvesting due to the lack of stimulation of growth and photosynthesis from the increased nutrient availability which follows fire.

There is little evidence of stem or leaf carbohydrate levels being lower in resprouts following harvesting (Oechel and Hastings In press). However, the abundant carbohydrate levels found in resprout stem and leaf material may represent movement of carbohydrate from the burl and root system to growing points in the shoots.

CONCLUSIONS AND FUTURE RESEARCH NEEDS

Possible management techniques include managing for fewer, larger diameter stems rather than smaller diameter stems which have higher respiration rates. Stands with younger, higher density seedlings and sprouts should be much more productive than mature stands with the same leaf area index. To predict the long term potential of harvesting chaparral, and the optimal intervals for harvesting, studies of the entire carbon balance of resprouts are necessary. Such a study should include photosynthetic rates, respiration rates, nutrient levels and the carbohydrate content of leaves, stems, burls and root systems following harvesting. These results should be compared to those from fire resprouts.

Further research needs include:

- 1) Study of the fate of the fine root systems of resprouters following fire and harvesting;
- 2) Determination of the carbohydrate content of burls and secondary roots of resprouts following fire and harvesting;
- 3) Determination of the changes in stem size classes and distribution through time;
- 4) Determination of the causes of elevated photosynthetic rates of resprouts

harvesting with rotation intervals.

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