

# Nutrients and Water Relations in Mediterranean-Type Ecosystems<sup>1</sup>

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The broad correspondence between the sclerophyllous shrub form and the climate in mediterranean-type ecosystems indicates a climatic control over the vegetation particularly with respect to the summer drought, but all five regions are noted for nutrient deficiencies, especially Australia and South Africa. As studies of these ecosystems are completed, divergences related to the control of community structure, function, and form are becoming apparent. Differences in species composition and growth form are apparent on nutrient poor and base rich sites (Specht and Moll 1981). The mediterranean type ecosystems in South Africa and Australia are generally considered nutrient poor relative to the mediterranean-type ecosystems in Chile, the United States, and the Mediterranean Area. In Australia phosphorus limitation is assumed to have selected for sclerophylly, which preadapted the flora to the more recent summer drought climate (Beadle 1954, Specht 1979 Moll and others 1981). In South Australia the overstory vegetation is believed to be evergreen because of climate, while the understory is evergreen because of nutrient impoverishment (Specht 1972). In California the overstory is believed to be evergreen because of climate, and the understory is deciduous because of microclimate near the soil surface (Miller 1981). Nutrient deficiencies have been suggested to explain other aspects of the community structure in the mediterranean-type ecosystems; such as succession following fire (Specht 1972), species richness in South Africa and Australia (Kruger 1979), the distribution of fynbos and heathlands in South Africa and Australia over a wide range of annual precipitation (300-3000 mm/yr) (Specht 1979), and specialized morphological structures (Lamont 1972, 1973, 1980, 1981).

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Abstract: Mediterranean regions of the world are characterized by winter rain, summer drought precipitation cycles and by their generally low nutrient status. This paper reviews concepts relating to water and nutrient use by vegetation in these regions.

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In contrast, in California and Chile the length of the summer drought is thought to control sclerophylly (Miller 1981). Evergreen sclerophyllous shrubs are believed to occur in California where the length of the soil drought is about 100 days or less (Miller and Mooney 1974). In California the leaf area index develops until water use by the chaparral creates a drought lasting about 100 days (Miller and Poole 1981). In Australia evergreen shrubs moderate water use so that the period of summer soil drought is minimized (Specht 1972); water is then available throughout the summer to support photosynthesis and growth in summer. In some regions of high annual precipitation in South Africa and Australia, the soils are either rocky and sandy or are underlain by a hardpan, so periodic drought is possible in spite of high rainfall.

The objective of this paper is to review concepts of nutrient and water relations in mediterranean-type ecosystems, indicate interactions between the two, and suggest possible needs for future research.

## SOIL-PLANT NUTRIENT RELATIONS IN MEDITERRANEAN-TYPE ECOSYSTEMS

The role of nutrients, especially phosphorus, in determining the vegetation in mediterranean-type ecosystems has been emphasized in Australia and South Africa (Kruger 1979, Specht 1979). Specht (1979) argues that nutrients, rather than light or soil moisture, cause succession in mediterranean-type ecosystems. In South Australia, the herbaceous component in heath increased after fertilizing with phosphorus (Specht 1963). In California, fertilizing with nitrogen and with nitrogen plus phosphorus increased shrub and herb growth. Fertilizing with phosphorus alone had no effect (Hellmers and others 1955, Kummerow unpublished data, Miller unpublished data). Nitrogen fixation by *Ceanothus* species may be important in northern California (Delwiche and others 1965, Gray and Schlesinger 1981) and may increase *Ceanothus* abundance on nitrogen poor sites. But in mature chaparral in southern California

nitrogen fixation by C. greggii is negligible (Kummerow and others 19786). Christensen and Muller (1975a) concluded that nutrients enhanced seedling survival but not seed germination. They also showed that nitrate was washed from the canopy with the first rain in the fall and that, following fire, nutrients were most available near the soil surface. The nitrate washed into the soil in the fall is subject to leaching by the winter rains before root growth and nitrogen uptake begin. In the chaparral root growth occurs after February and nitrogen uptake occurs in March and April (Kummerow and others 1978b, Mooney and Rundel 1979, Shaver 1981). The soil chemistry affecting leaching is unknown in chaparral. Nitrification occurs in chaparral soils (Marion and others 1981).

The few experiments that exist on species interactions in chaparral indicate competition for nutrients. In a stand composed mainly of C. greggii and A. fasciculatum, eliminating all A. fasciculatum increased herb production, but eliminating C. greggii and leaving A. fasciculatum gave no change in herb production. Eliminating C. greggii increased A. fasciculatum production slightly but decreased the growth of individual shoots (Kummerow unpublished data). In fertilizer experiments, nitrogen addition also increased shrub production but decreased the individual shoot growth (Kummerow et al. unpublished data). These experiments taken together indicate that higher available nitrogen, either from fertilization or from eliminating competitors, increases production not by increased shoot growth but by increased numbers of individual shoots per square meter. Additionally, it appears that C. greggii may suppress the growth of A. fasciculatum by more effective nitrogen capture, while the opposite does not appear to occur. The latter conclusion is consistent with a higher nitrogen capture ability of C. greggii relative to A. fasciculatum (Zinke 1977, Miller 1981) but was unexpected because Ceanothus species can fix nitrogen under some conditions (Delwiche and others 1965, Cray and Schlesinger in press). Because of their capacity to fix nitrogen, Ceanothus species could be poor at taking up mineralized nitrogen. Adenostoma fasciculatum tends to occur on low nitrogen sites (Zinke 1977, Marion and others 1981).

#### SOIL-PLANT WATER RELATIONS IN MEDITERRANEAN TYPE ECOSYSTEMS

The annual pattern of soil drought and air temperature along an elevational transect from 0 to 2 000 m in southern California was calculated from the annual courses of precipitation and potential evapotranspiration (Miller 1979). Such a pattern was postulated by Mooney and others (1972) and Mooney and Dunn (1970a, b). Xylem pressure potentials, which were measured to check the calculations (Poole and Miller 1981), decreased earlier in the summer at the coastal

and desert edges of the chaparral and later toward the center of the chaparral. Poole and Miller (1975) showed that xylem pressure potentials of Rhus spp. and Heteromeles arbutifolia decreased earlier at the coast than in the center of chaparral. The pattern of drying was affected by the vegetation cover (Miller and Poole 1980). At the edges of the distribution, water use was about 200 mm/yr per unit leaf area index ( $A_1$ ) which occurred with precipitation of about 400 mm/yr. Soil evaporation and interception losses account for the remainder of the precipitation. With higher precipitation the leaf area index increases until the resulting transpiration rate decreases to about 200 mm/yr/ $A_1$ . Without disturbance, chaparral vegetation should develop until the water use per unit leaf area and the duration of the summer soil drought are similar throughout the distribution of the chaparral. The resulting period of summer drought should be about 3 months long. This hypothesis is consistent with the patterns of water and soil drought measured under the vegetation of pole- and equator-facing slopes at Echo Valley (Miller and Poole 1979; Ng and Miller 1980) and with the pattern of several leaf properties (Poole and Miller 1981).

A pattern of moderate water use would allow sufficient water throughout the drought period for photosynthesis to offset maintenance respiration and allow for growth (Specht 1972a,b). Walter (1973) pointed out the evenness of water potentials in deep rooted evergreen shrubs in mediterranean type regions. These findings are consistent with the pattern of water use on the equator-facing slope at Echo Valley (Ng and Miller 1980) which was dominated by a single species, A. fasciculatum, with the pattern of water use in Q. dumosa and R. ovata, and with the pattern of water use in the Chilean shrubs. Rhus ovata also has a high temperature requirement for growth, similar to Australian shrubs (Specht 1969a, b). The Chilean shrubs appear to have low temperature requirements for growth (Jacobson and others 1981). Specht's suggestion is not consistent with the pattern of soil moisture on the pole-facing slope which is dominated by several evergreen species including A. glauca and C. greggii. Thus, the patterns of water use must be viewed in the context of various physiological characteristics and the floral history of the area. The Australian mediterranean vegetation has no cool temperate species, but such species are present in the chaparral and matorral because of the migrations of the flora during the Pleistocene (Axelrod and Raven 1978; Solbrig and others 1977). The need for conserving water is more important for species with high temperature requirements for growth.

In Californian chaparral, transpiration in the evergreen shrubs varied seasonally (Miller and Poole 1979). Although leaf conductances were high in winter, transpiration was low because net radiation was low and vapor density deficits were

small. In the spring, transpiration increased because of increased daylength, since leaf conductances and vapor density deficits were nearly constant. In June and July, transpiration decreased because leaf conductances decreased, even though vapor density deficits increased. Arctostaphylos glauca showed a complete cessation of transpiration for almost 2.5 months. Rhus ovata, H. arbutifolia, and C. greggii showed no transpiration for about 1 month. Similar annual patterns were shown for heath in South Australia (Specht 1957a). In mature shrubs transpiration during spring was  $0.7\text{--}2.0\text{ mm day}^{-1}\text{ m}^{-2}$  of leaf area. Annual water use on a square meter of leaf basis was 150-190 mm/yr from A. fasciculatum, 145-195 from C. greggii, 280-290 from A. glauca, and 127 from R. ovata (Miller and Poole 1979).

Several sets of measurements and calculations indicate that chamise chaparral, grasslands, and bare soil lose water similarly while mixed chaparral loses more water (Shachori and Michaeli 1965, Miller and Poole 1979, Miller and Stoner 1979, Ng and Miller 1980, Patric unpublished data). In simulations transpirational water loss increased with foliage area. Soil evaporation decreased with foliage area and was 200-300 mm/yr in southern California and about 200 mm/yr in central Chile. Total evapotranspiration from the vegetation and soil increased with foliage area index in species which had high transpiration rates but remained constant in species which had moderate or low transpiration rates. In these latter species increased transpirational losses were compensated by decreased soil evaporation. Nitrogen release decreased as foliage area increased, because the additional foliage area increased transpiration which decreased the available soil moisture and therefore the length of the decomposition season.

With relatively low precipitation (<400 mm/yr) only low foliage areas can be maintained (<  $2.0\text{ m}^2/\text{m}^2$ ), soil evaporation is high, and the transpiration:precipitation ratio is low. In simulations as the foliage area index increased from 0 to  $2\text{ m}^2/\text{m}^2$ , soil evaporation decreased to two-thirds. A similar relation between transpiration and annual precipitation has been noted for grasslands and other semiarid lands (Fischer and Turner 1978; Sims and Singh 1978). Based on field observation in southern California and theory, an annual precipitation of 400-450 mm/yr is required to maintain a foliage area index of about 2 in the chaparral (Miller and Poole 1981). Thus, with precipitation below about 400 mm/yr transpiration can be expected to decrease rapidly with decreasing precipitation. Above 450 mm/yr precipitation the foliage area which can be maintained is limited by the photosynthesis-light responses of the species and leaf turnover during the drought. Transpiration is limited by foliage area, and the transpiration:precipitation ratio decreases while drainage increases as precipitation increases above 450 mm/yr.

The low transpiration:precipitation ratio (transpiration efficiency) of chamise chaparral at low elevations and an drier sites and the higher ratio of mixed chaparral at mid-elevations and on more mesic sites are consistent with the theoretical trends. The matorral stands at Fundo Santa Laura have relatively low transpiration efficiencies because of relatively high precipitation and low net radiation in winter. Because of its shade intolerance, chamise chaparral has a relatively low foliage area index, high soil evaporation, and relatively low transpiration efficiency. The low transpiration efficiency of matorral is caused by the low foliage area. Similar constraints are expected to reduce transpiration efficiencies in other Southern Hemisphere mediterranean climate regions compared to Northern Hemisphere regions. In contrast to the evergreen shrubs, the transpiration efficiency of the drought semideciduous shrubs decreases with increasing precipitation. With respect to elevation, the maximum transpiration efficiency of a species occurs at elevations below those at which the maximum abundance of the species occurred, supporting the generality for mediterranean-type ecosystem that water is the limiting factor at the lower elevational limit of a species.

Year-to-year variations in precipitation affect transpiration efficiencies because leaf growth occurs after the period of receipt of the precipitation and varies less than does precipitation. The simulated response of production to precipitation was flatter than the usual production-precipitation relations in arid regions (Chang 1968, Whittaker 1975) and was flatter at Fundo Santa Laura than at Echo Valley. The flatness of the response was partly due to the low fraction of annual precipitation received during the growing season.

Other plant characteristics should correlate with the precipitation gradient. Transpiration and the transpiration:precipitation ratio increase with high leaf conductances, steeply inclined leaves, narrow leaves, high leaf reflectances, and high leaf area to dry weight ratios, which increase soil shading. With low precipitation (< 400 mm/yr) and low foliage area index, rapid use of water by plants is advantageous because otherwise the water is evaporated. Because the soil drought is lengthened by the soil evaporation and high transpiration rate, drought deciduous species are favored. The advantage of steep leaf inclination is balanced against the advantage of shading the soil surface and reducing soil evaporation. At higher precipitation levels (> 550 mm/yr) water is lost by drainage; transpiration is increased with higher leaf conductances; the length of the drought is short. Leaf width, inclination, and color can be more variable without affecting water loss. At intermediate precipitation levels (400-550 mm/yr) the composition of the vegetation changes the length of the soil drought by changes in the abundance of species with different leaf

conductances and different leaf area indices. The transpiration:precipitation ratio is controlled by the vegetation composition and can be relatively high.

The expected trends in water relations occur in chaparral and matorral species (table 1). Maximum leaf conductances of Californian species arranged from highest to lowest were: A. californica, Salvia apiana, A. glauca, C. greggii, A. fasciculatum, Q. dumosa, and R. ovata. The sequence of species was similar for the minimum xylem pressure potentials, for the duration of low pressure potentials, and the variability of pressure potentials through the year. Osmotic concentrations at turgidity were similar and moderate, ranging from -2.0 to -3.0 MPa. The depth of rooting probably also increases in the same sequence. Artemisia californica, S. apiana, C. greggii, and A. glauca are recognized as shallow rooted, while Q. dumosa and R. ovata are thought to be deep rooted (Hellmers and others 1955; Kummerow and others in press). The sequence of species also segregate obligate seeders and sprouting shrubs. The sequence occurs along a gradient of increasing annual precipitation. Different patterns of reproduction may reinforce the patterns of water-use characteristics. Seedlings and resprouts have different water environments when young. Schlesinger and Gill (1980) showed lower water potentials during the summer in seedlings than in mature individuals of Ceanothus megacarpus. Radosevich and others (1977) indicated that resprouts of A. fasciculatum generally had higher water potentials than the unburned control vegetation. The higher soil moisture under Banksia ornata (Specht 19576) and decreased water use with reduced stem densities of Acacia aneura (Pressland 1976) appear to be consistent with the expected interaction between leaf area, leaf conductance, and water loss.

The Chilean species, arranged by maximum leaf conductance from highest (about 0.5 cm/s) to lowest (about 0.15 cm/s), are S. gilliesii, T. trinervis, C. odorifera, Q. saponaria, C. alba, and L. caustica. The sequence was similar for the lowest xylem pressure potentials measured but was not as consistent as with the Californian species. Rooting depth may be similarly arrayed in the Chilean species (Avila and others 1975, Giliberto and Estay 1978). The sequence is not as clearly related to reproductive patterns as with the Californian shrubs.

The maximum leaf area index which could be maintained with different annual precipitation amounts was estimated by simulations (Miller 1981). These leaf area indices increased as precipitation increased to about 400 mm/yr with the Californian shrubs and to 350 mm/yr with the Chilean shrubs. The calculated steady state leaf area indices were similar to those measured in the field (Miller and Poole 1980).

## INTERACTIONS BETWEEN NUTRIENTS AND WATER

The available nutrients and water and the rate of turnover of leaves and stems affects the biomass that can be supported. The steady state biomass (B) can be expressed in terms of the precipitation (Ppt), transpiration efficiency (Tr/Ppt), water-use efficiency ( $P_S/Tr$ ), maintenance and growth respiratory costs ( $r_m$ ,  $r_g$ ) and leaf longevity ( ) by

$$B = (Ppt) (Tr/Ppt) (P_S/Tr)/(r_m + r_g) \quad \text{Eq. 1}$$

Annual precipitation and nitrogen taken up by the vegetation should be interrelated. In the steady state nitrogen taken up must equal that lost as plant parts are shed. Thus,

$$B = (N_{up}) / [(N_d)] \quad \text{Eq. 2}$$

where  $N_{up}$  is the nitrogen taken up, and  $N_d$  is the nitrogen content of plant parts at death. Equations 1 and 2 indicate that the steady state biomass should increase by 400-500 g/m<sup>2</sup> for every 100 mm/yr increase in annual precipitation and by about 400 g/m<sup>2</sup> for every additional g N m<sup>-2</sup> yr<sup>-1</sup> taken up. Increasing leaf longevities more than 2 years have smaller effects on the steady state biomass than increasing leaf longevities from 1 to 2 years. Within a precipitation regime leaf longevity should increase in accordance with nitrogen limitation because turnover rate is more closely related to nitrogen uptake than to precipitation.

Interactions between water and nitrogen availability can be calculated. A gram of nitrogen taken up and incorporated into aboveground tissue yields an increment of about 166 g dry weight/g N of new biomass. Leaf area is increased by about 0.004 m<sup>2</sup>/g dry weight although some of the new biomass is in stems. This increment of leaf area increases transpiration by about 0.67 kg day<sup>-1</sup> g<sup>-1</sup> N. Allowing for the dry weight and water costs involved in the growth of the leaf area, the net increase in transpiration is about 0.33 kg day<sup>-1</sup> g<sup>-1</sup> N. The increased transpiration decreases the length of the season in which soil moisture is available. The length of the growing season changes with transpiration according to the amount of water available divided by the square of the daily evapotranspiration rate. Thus, the reduction in the growing season because of added nitrogen would be about 0.33 x 38 or 12 days per gram nitrogen taken up by the chaparral in southern California and by about 10 days per gram nitrogen taken up by the matorral in central Chile. This shortening of the growing season should reduce growth by about 48 g dry weight m<sup>-2</sup> yr<sup>-1</sup> in southern California and by 20 g dry weight m<sup>-2</sup> yr<sup>-1</sup> in central Chile, while the increased nitrogen should increase growth by about 166 g dry weight. Thus, net growth should increase about 118 g dry weight/g N taken up in California and 146 g dry weight/g N taken up in

Chile, even though the growth period is limited by temperature and water.

Long leaf duration, from whatever cause, affects the availability of nitrogen. The presence of ligneous and herbivore defense compounds can reduce the quality of the substrate for decomposition and mineralization. The selection of evergreen leaves by the seasonal patterns of temperature and water availability favors leaves of about 1-year duration but does not necessarily favor leaves with more than 1-year duration. The evergreen leaves should have structural modifications to maintain rigidity under water stress and to reduce the intensity of water stress (Beadle 1966; Cutler and others 1977). According to heat transfer theory, such leaves should be rigid, narrow, steeply inclined, and light colored to reduce cellular distortion, plant temperatures, and transpiration rates. Small cell size is advantageous (Cutler and others 1977). Leaf longevities may increase with nitrogen limitation (Monk 1966). Although evergreenness caused by nitrogen limitation does not require the adaptations to survive drought (Beadle 1966), the general biochemical composition of nitrogen-limited leaves may be similar to that of water-limited leaves, resulting in similar sclerophyll indices, which are, based on lignin, cellulose, and nitrogen content (Loveless 1961). Water limitation creates a direct need for sclerophyllous tissue, while the nitrogen or phosphorus limitation may reduce protein formation due to low nutrient availability, which may increase cellulose and lignin formation because of excess carbohydrate (Loveless 1961, Beadle 1966, Steubing and Alberdi 1973).

Specht and others (1981) discuss the seasonality of leaf growth and leaf drop in Australia and South Africa. Their opinions are similar to opinions developed in studies of chaparral and matorral in California and Chile. The indications are that if water limits biomass, leaf drop will follow leaf growth, which occurs in most evergreen shrubs in California and Chile (Mooney 1977). But if nutrients limit biomass and growth, leaf drop will be synchronous with leaf growth, as occurs in *Quercus* sp. and in Australia and South Africa (Specht and Moll 1981).

Of the five mediterranean regions of the world, the mediterranean region of central Chile is relatively nutrient rich. Vegetation is climatically selected, and leaf turnover rates are relatively high. In southern California and southern Europe, soils are less nutrient rich, but climate is still a strong selective agent; leaf turnover is slower than in central Chile. In the mediterranean regions of Australia and South Africa where old, nutrient poor soils occur, leaf turnover is lower than in California (Kruger 1979, Specht 1979, Miller and others unpublished data), and the climatic effect is reinforced by nutrient limitations.

In South Africa, pines are rapidly invading undisturbed fynbos, and pine plantations on unfertilized fynbos soils have higher productivity than the native fynbos or than the pines in their native Northern Hemispheric habitats (Van der Zel and Kruger 1975, Hall and Boucher 1977). Rough estimates indicate that annually the pines take up three times the nitrogen as does the fynbos on the same soil (Miller and others unpublished data). The Proteaceae and Restionaceae lack mycorrhizal associates (Lamont 1981). Experiments with tree seedlings show a nearly 50-fold increase in growth when the seedlings are inoculated by mycorrhizae. Proteoid roots may merely compensate for the reduced nutrient and water uptake caused by the lack of mycorrhizae. The introduced pines have mycorrhizae. In South Africa at least, the apparent nutrient impoverishment may not be due to the soil supplying ability but to the plant uptake ability.

The low production in South African fynbos and Australian heath may also be due to high temperature requirements for growth (Specht 1972). Because these temperatures occur during the summer drought, the growing season is severely truncated. In both countries the flora in the mediterranean regions has evolved from a tropical flora, which has not been invaded by more polar elements. In Chile, California, and the Mediterranean Sea regions, a more polar floral element with cooler temperature requirements for growth has mixed into the vegetation (Raven 1973, Axelrod and Raven 1978). Temperature limitations on growth in South Africa and Australia could have allowed excessive leaching of nutrients resulting in the current nutrient impoverishment of mediterranean-type ecosystems in these countries. The Southern Hemisphere mediterranean regions receive less spring precipitation than the Northern Hemisphere mediterranean regions, which speeds the onset of summer drought in the Southern Hemisphere (Miller 1981). The low production in South African and Australian mediterranean regions may also be due to high cloudiness and low solar irradiance during the winter which reduce photosynthetic rates. A limitation on photosynthesis by solar irradiance was indicated for central Chile (Miller 1981). Thus, the plants in the Southern Hemisphere may enter the spring with lower carbohydrate reserves and lower growth potential.

#### RESEARCH NEEDS

In spite of the recognition of divergent causes of vegetation form in mediterranean-type ecosystems, functional measurements of nutrient and water availability have not been carried out with identical techniques. A direct functional comparison is needed. Static comparative soil statistics, which are now becoming available, do not show great differences in soil organic matter content, total nitrogen, available nitrogen,

total phosphorus, available phosphorus, percent base saturation, and pH between South Africa, Australia, California, and Chile (Thrower and Bradbury 1977, Miller et al. 1977, Kruger 1979, Boone unpublished data). Earlier measurements of available nitrogen and phosphorus in California and Chile, which are often cited in comparing mediterranean-type regions, are rejected because of the length of time between collection and processing of the samples.

Direct comparable measurements on soil nutrient supplying power and plant uptake ability are needed to define the controls on the composition and form of mediterranean-type ecosystems in the five mediterranean regions of the world. In addition, a synthesis of these measurements and existing data is needed and should lead to a quantification of nutrient cycling, its control, and an explanation of how nutrient cycling processes deviate in mediterranean-type ecosystems. Such a synthesis is timely. Much descriptive information has been collected and is being published (Specht 1979, Kruger 1981, Miller 1981). Some functional relations have been established for some mediterranean-type ecosystems and collated in original and review papers (Kruger and Siegfried 1981, Miller 1981). The communication and cooperation among investigators in the mediterranean-type ecosystems is good. The synthesis should clarify whether the similarity in vegetation form is only coincidentally associated with the mediterranean-type climate but is caused by differences in soil and climate in the five mediterranean regions.

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