Net Primary Productivity of Some California Soils Compared to Those of the Santa Catalina Mountains, Arizona[1]

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Abstract: Soil properties and climatic parameters were used to develop above-ground net primary productivity equations from published data for the Santa Catalina Mountains, Arizona, and for annual grassland and chamise-chaparral sites in California. An equation with soil properties only had nearly as low a standard error of estimate (SE) as the best equation (i.e. lowest SE) with estimated actual evapotranspiration included, and is more widely applicable.

Net primary productivity (NPP) is the rate of biomass (or energy) accumulation by autotrophic plants (Whitaker, 1975). In green plants, which are the major sources of primary productivity in terrestrial ecosystems, NPP is the difference between organic matter produced by photosynthesis and that consumed by respiration. NPP of natural unmanaged vegetation is the most suitable index for comparing the inherent productivity of all land. Yields of cultivated crops are not such universally suitable indices, because no single plant species grows on all soils. Although the natural vegetation varies in species composition from one soil to another, it is not arbitrary. Each soil, under natural conditions, supports the particular vegetation that is characteristic for it and its environment. Natural conditions include disturbances responsible for cyclical changes in the vegetation (White, 1979).

Little data on NPP are available, because they are difficult to obtain. Even in annual plant communities, where the data are relatively easy to obtain, the productivity is so variable from year to year that it must be averaged over a number of years in order to derive reasonable estimates. Lieth (1973) has reviewed historical developments in the field of predicting the NPP of terrestrial ecosystems. He has settled on actual evapotranspiration (AET) and mean annual air temperature (MAT) for predicting world-wide NPP. Most attempts to predict NPP rely solely on climatic data. Even when utilizing AET, a single value is usually assumed for the plant available water capacities of all soils.

Soils are important not only for their physical properties, which affect root distribution and water supply, but also for their fertility, which is the effect of plant nutrient supply on productivity. Since soils are so important to plant growth, it should be possible to improve the predictions of NPP by adding soil properties, as well as climatic factors, in predictive equations. However, there is little soils data from sites where NPP has been determined. Therefore, in testing the applicability of soil parameters, only the most basic properties (for example, particle-size distribution or clay content, pH, plant available water-holding capacity, and C/N ratio) which have either been measured at sites of NPP determinations or can be inferred from data for similar soils near the sites are utilizable. Data from California (Fig. 1) and the Santa Catalina Mountains of southern Arizona were used to develop equations for predicting NPP from both soil properties and climatic parameters.

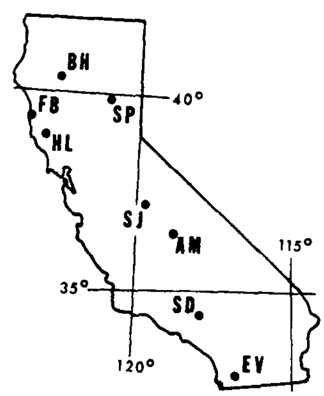

Figure 1—A map of California with the locations of the sites with NPPa data. The site names (Table 1) are Hopland (HL), San Joaquin (SJ) Bald Hills (BH), San Dimas (SD), Ash Mountain (AM), Echo Valley (EV), Spanish Peak (SP), and Fort Bragg (FB, 15 sites).

MODEL

NPP is estimated by measuring the rate of carbon or organic matter accumulation in living autotrophic plants. When plants die, most of their organic matter remains in the same ecosystem for some time, generally until the organic matter decomposes to inorganic compounds. During this process some organic matter is stored above ground and some is stored in the soil. A model for predicting NPP from soil properties and climatic factors can be developed if the amount of organic matter stored in the soil can be related to the amount produced by autotrophic plants in the ecosystem.

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In early stages of stand development (secondary succession), a large proportion of the production accumulates in living plants. As succession progresses, increasingly larger proportions of the production are returned by way of fallen leaves, dead stems, and discarded root tissues to the pool of non-living organic matter subject to decomposition. Finally, in mature stands, the recharge to this pool is equal to the NPP and the temporal change in non-living organic matter (OM) which is subject to decay is equal to the gains from primary production (NPP) minus the losses due to decomposition. Thus

$$d(OM)/dt = NPP - k\,(OM) \qquad (1)$$

where k is a general decay constant which integrates the effects of different decay rates resulting from different kinds of organic matter in different ecosystem microenvironments. This equation follows a more general formulation of Olsen (1953). Sometime after a stand reaches maturity, organic matter contents reach steady state values throughout the ecosystem and the overall change in organic matter content ceases, or at least becomes so negligible that essentially d(OM)/dt = O. Hence, equation 1 becomes

$$NPP = k\,(OM) \qquad (2)$$

in mature ecosystems.

Since the decay constant (k) has different values in different ecosystems with different environments, it must be related to soil properties and environmental parameters before the steady state equation can be used for predicting NPP. According to Meentemeyer (1977), the logarithm of the decay constant for leaf litter is proportional to AET; that is, Ln(k) = a + b AET, when a and b are constants. Without contrary information for the decay constants of other ecosystem organic matter components, assume that they too are related to AET by an equation of the same form. Then, taking logarithms of equation 2, Ln(NPP) = Ln(k) + Ln(OM), and substituting Meentemeyer's relationship for Ln(k),

$$Ln(NPP) = a + b\,AET + Ln(OM). \qquad (3)$$

Equation 3 might be used for predicting NPP if data were available for determining the constants. They will be different from the constants determined by Meentemeyer who dealt with leaf litter only rather than all ecosystem organic matter not in living plants. Since much of the data for NPP does not include below ground productivity, above ground net primary productivity (NPPa) is substituted for total NPP. Also, it is convenient to substitute soil organic carbon (OC) for all ecosystem organic matter not in living plants, because more data are available for soil organic carbon, it is easier to obtain, and it is affected less by short-term ecosystem disturbances or human manipulations. The justification for this substitution is that there must be a close relationship between soil organic carbon and ecosystem organic matter production, because large proportions of the organic matter in stems, branches, roots, and leaves which accumulate on the ground are incorporated into the soil before they are completely decomposed to inorganic carbon. With substitutions of NPPa for NPP and a constant (c) times Ln(OC) for Ln(OM) into equation 3,

$$Ln(NPPa) = a + b\,AET + c\,Ln(OC). \qquad (4)$$

Although these substitutions are based more on analogies than on precise relationships, it is the utility of equation 4 and its derivatives for predicting NPPa that is the primary concern rather than rigid derivations. This was tested by least squares regression analyses. Other soil parameters were added to equation 4 as linear variables, assuming that the decay constant is related to them much as it is related to AET, unless the regression analyses indicated that other forms are obviously better.

MODEL DEVELOPMENT AND EVALUATION PROCEDURE

NPPa data were obtained from published sources (Table 1). Most of these sources have data on surface soils but lack subsoil data, which generally had to be derived from other sources. Soil bulk densities were calculated from organic carbon contents (Alexander, 1980). Available water capacities were estimated from soil textures and depths. Climatic data for the Santa Catalina Mountains were extrapolated from the data of Sellers and Hill (1974) and data for California sites were extrapolated from various sources.

A large part of the data are from 13 sites in the Santa Catalina Mountains, Arizona. Chow's test (Chow, 1950) was used to determine the suitability of combining data for the 13 Arizona and 7 California sites (Fig. 1) and treating them as one data set. Westman and Whittaker (1975) have published net primary productivity data for 15 sites near Fort Bragg, California, which are not listed separately in Table 1.

The independent variables used in various combinations to predict NPPa (t/ha) were (1) the logarithm of organic carbon content in mineral soil to one meter depth (kg/m^2m); (2) mean annual air temperature (MAAT, °C); (3) actual evapotranspiration (AET, cm/yr) calculated by the Thornthwaite procedure; (4) a function of evapotranspiration (FET) equal to $AET/(1-Ln(AW/AWC))$, ($AW/AWC \geq 0.01$), where AW is the mean monthly plant available water and AWC is the available water capacity of a soil; (5) mean carbon to nitrogen ratio (C/N) in the upper 10 cm of soil; (6) mean clay content (percent) in the upper 25 cm of soil; and (7) mean pH in the upper 10 cm of soil. Coastal California soils of the Fort Bragg area are in four soil drainage classes, which were considered as discrete independent variables. The best equations for predicting Ln(NPPa), the dependent variable, were considered

Table 1--Site information, above ground net primary productivity, soil properties, and sources of data.[4]

Site[1]	Lat.	Alt.	Vegetation	Soil Series	NPPa	Stand[2] Age Span	MAAT	AFT	Soil Organic Carbon	Surface Soil		
										Clay	C/N	pH
	N	meters			t/ha	yr	°C	cm/yr	kg/m²m	pct		
44, SCM	32.5°	2720	Subalpine Fir Forest	-	8.7	mature, last 5	7.6	53.9	19.0	21	36	6.0
46, SCM	32.5°	2640	Douglas-fir Fir Forest	-	11.2	"	8.1	51.5	14.5	9	23	5.2
47, SCM	32.5°	2650	Douglas-fir Forest	-	8.4	"	8.1	51.3	17.1	9	23	5.2
48, SCM	32.5°	2470	Mixed Pine Forest	-	6.2	"	7.5	46.9	4.9	3	12	4.5
49, SCM	32.5°	247	Ponderosa Pine Forest	-	5.8	"	9.3	51.7	9.3	9	22	4.8
50, SCM	32.5°	2180	Pine-Oak Forest	-	5.0	"	11.2	51.7	10.9	10	25	5.5
51, SCM	32.5°	2040	Pine-Oak Woodland	-	4.5	"	12.2	50.3	9.4	10	19	6.8
52, SCM	32.5°	2040	Pygmy Conifer-Oak Scrub	-	1.9	"	12.2	49.6	2.1	6	16	6.2
53, SCM	32.5°	1310	Open Oak Forest	-	1.5	"	17.1	40.4	4.2	12	16	6.8
54, SCM	32.5°	1220	Desert Grassland	-	1.4	"	17.1	41.6	3.5	6	12	7.5
55, SCM	32.5°	1020	Spinose-Suffrut. Shrub	-	1.3	"	19.0	34.3	3.2	12	12	7.0
56, SCM	32.5°	870	Paloverde-Busage Shrub	-	1.0	"	20.0	31.1	2.8	12	11	7.0
57, SCM	32.5°	760	Creosotebush Des. Shrub	-	0.9	"	20.8	27.8	3.2	18	6	7.0
Hopland	38°59′	300	Annual Grassland	Laughlin-Sutherlin	2.3	mean, 16 ann.	14.4	39.3	7.5	22	12	5.4
S. Joaquin	37°01′	335	Annual Grassland	Ahwahnee	2.4	mean, 35 ann.	15.3	20.3	3.8	8.5	11	6.4
Bald Hills	40°25′	335	Annual Grassland	Sehorn	2.6	mean, 4 ann.[3]	15.3	34.5	6.9	48	10	6.2
San Dimas	34°10′	900	Chamise Chaparral	Cieneba	1.5	0-18	14.3	27.4	2.1	4.5	14	5.6
Ash Mtn.	36°30′	800	Chamise Chaparral	Sierra	2.0	0-20	13.8	35.6	7.4	13	14	5.8
Echo V.	32°54′	1000	Chamise Chaparral	Vista	3.6	current, 22-24	13.5	29.5	5.5	15	13	6.5
Spanish Pk.	39°55′	2070	Red Fir Forest	Waca	8.4	0-120	4.8	29.8	14.7	5	28	5.8
Ft. Bragg	39.5°			-		mature, last 5						

[1]Numbers 44 through 57 are Whittaker's, SCM = Santa Catalina Mountains.

[2]Stand age for NPPa determinations.

[3]Two sites with two years of data from each.

[4]Data sources by site for NPPa, surface soil and subsoil properties, respectively: Santa Catalina Mountain sites - Whittaker and Nierinq (1975), Whittaker et al. (1968) and Martin and Fletcher (1943): Hopland - Murphy (1970), Zinke and Stanqenberqer (1975); San Joaquin - Duncan and Woodmansee (1974), Duncan (1975) with soil descriptions by K. Chang; Bald Hills - Powell (1965), Zinke and Stanqenberqer (1975); San Dimas - Specht (1969) plus litter production from Kittredge (1955), Mooney and Parsons (1973) plus SCS (1973); Ash Mountain - Rundel and Parsons (1979), Parsons (1976) and SCS (1973); Echo Valley - Mooney and Rundel (1979), Bradbury (1977); Spanish Peak - Stanqenberqer (1978), Stanqenberqer (1978) and SCS (1973); Fort Bragg - Westman and Whittaker (1975), Westman (1971) and Gardner and Bradshaw (1954) plus Zinke and Stangenberger (1975).

to be those with the lowest standard errors of estimate (SE).

RESULTS AND DISCUSSION

Ln(OC) was included in every equation considered, because it is essential to the model. Although NPPa is highly correlated with MAAT, the temperature coefficients in predictive equations are negative, which is opposed to the expected temperature effect on the decay constant. This anomaly is due to increasing precipitation and its greater effectiveness with increasing altitude and decreasing temperature in Arizona and California. AET incorporates air temperature and is a more satisfactory independent variable because it does not increase indefinitely with increasing altitude. Equations with MAAT greatly over estimate the NPPa at the Spanish Peaks site, which is the only one at relatively high altitude in California. Therefore, AET was used as an independent variable, instead of MAAT, because the predictive equations using it are more likely applicable to a wider range of environments.

The results of regression analyses are presented in Table 2. Adding more than three independent variables for the Arizona set and more than four for the combined set of Arizona and inland California site data increases the standard errors of estimate. Chow's test indicates that the best equation for the 13 Arizona sites, $Ln(NPPa) = 0.0260 + 0.5330\ Ln(OC) + 0.0376\ AET - 0.2548\ pH$, is not appropriate for the combined set of Arizona and seven inland California soils ($F = 8.35$, $p<0.01$). However, none of the best equations, with up to five independent variables (Table 3), for the combined set of Arizona and inland California soils are statistically differentiable from equations for the Arizona soils only. The NPPa and soil organic matter decay rates of the soils in the Fort Bragg area are so dependent on soil drainage, which cannot be confidently determined from information in the published sources, that no equations were developed for the coastal California soils. All the 13 Arizona and the seven inland California soils are well drained.

Table 2-Degrees.,of freedom (DP), coefficients of determination (R^2), and standard errors of estimate (SE) for equations to predict NPPa. All variable combinations were tested, but the Napierian logarithm of soil organic carbon content (OC) was retained in all equations. Following Ln(OC), variables are listed in the orders that they contribute to reductions of the standard errors of estimate.

	Arizona Sites			Arizona and Inland California		
Variable	DF	R^2	SE	DF	R^2	SF
Ln(OC)	11	.790	.4352	18	.739	.4139
AET	10	.939	.2454			
pH	9	.975	.1655	17	.831	.3425
Clay				16	.952	.3197
C/N				15	.872	.3177

Table 3--Constant and coefficients of variables in equations for predicting NPPa from the 13 Arizona and 7 inland California soils. Each column represents the best equation for the specified number of independent variables, including the constant. The dependent variable is Ln(NPPa).

	Number of Independent Variables			
Variable	5	4	3	2
Constant	1.4846	1.4824	1.6971	-0.6515
Ln(OC)	0.6731	0.8481	0.7899	0.9799
pH	-0.2952	-0.2941	-0.3329	
Clay	-0.0103	-0.0147		
C/N	0.0194			
OF	15	16	17	18
R^2	0.872	0.962	0.831	0.739
SE	0.3177	0.3197	0.3426	0.4139
[1]F	3.06	2.70	2.55	0.75

[1]Values of F for Chow's test are nonsignificant (p = 0.05), indicating that equations developed for the 13 Arizona sites are statistically undifferentiable from these equations.

The Arizona sites can be divided into two groups, each with linear but distinctly different AET-NPPa relationships: (1) a group of seven sites with forest cover (NPPa = -51.74 + 1.123 AET, r^2=0.952) and (2) a group of six sites with open woodland, scrub, or desert vegetation (NPPa = -.33 + .044 AET, r^2=0.954). The discrepancy between these two groups was eliminated by substituting for AET a function of evapotranspiration (FET) equal to the sum of twelve monthly values of AET/(1-Ln(AW/AWC)). This function implies that the ratio of NPPa to evapotranspiration decreases as soil water is depleted and becomes less readily available to plants. It is analogous to the expression AET/(1-H), when 4 is relative humidity, used by Arkley and Ulrich (1953) for predicting crop yield. With FET as an independent variable, Ln (NPPa) = -.6574 + 0.0761 FET (r^2=0.913, SE = 0.2794) for the 13 Arizona sites. Although FET is better than AET alone for predicting NPPa, its advantage is greatly diminished when more independent variables are utilized.

With the set of 13 Arizona soils and 7 inland California soils, the equation for predicting NPPa from Ln(OC), pH, clay content, and C/N ratio is best (Table 2). AET is not one of the most useful independent variables for this set of data. The regression coefficients for pH and clay are negative and the coefficient for C/N is positive (Table 3).

The negative coefficient for pH implies that the rate of organic matter decay increases as the soil pH decreases. However, the negative coefficient reflects the very high negative correlation between NPPa and soil pH (Table 4), thus invalidating the implied effect of soil pH on the decomposition of soil organic matter. The correlation of increasing NPPa with decreasing soil pH is probably related to the contributions of precipitation to both NPPa and leaching of bases. The trend to greater NPPa with lower pH is reversed on the extremely acid, poorly drained soils of the pygmy forests of coastal California, where the NPPa averages only 2.6 t/ha. The highest productivity is on the slightly to moderately acid (about pH 6) soils of the coastal redwood forests, where the NPPa averages 14 t/ha.

The negative coefficient for clay (Table 3) implies that soil organic matter disappears less rapidly as the clay content increases. This might be expected from the fact that clay mineral-organic matter complexes increase the stability of the organic matter. It is in accord with the findings of Harradine and Jenny (1958) that soils from mafic volcanic rocks have both more clay and more organic matter than soils from granitic rocks. The quantity of clay to one meter, or some other depth, may be the best soil textural parameter to use for predicting NPPa, but the percentage of clay in the <2 mm fraction of surface soil was utilized due to lack of more appropriate data.

The positive coefficient for C/N (Table 3) is contrary to the negative effect that a high C/N ratio might be expected to have on the decay constant (Witkamp, 1971). This apparent anomaly is probably due to the very high correlation between C/N and OC (Table 4) and the positive correlation of NPPa to OC.

Equations developed from the Arizona and inland California soils data are not good for the coastal California soils. In the Fort Bragg area, soil drainage has the greatest influence on NPPa, which is so poorly correlated with 0C that the model is not useful. The best equation for the well drained soils of Arizona and inland California (Table 3, 15 DF) overestimates the NPPa of all the pygmy forest soils, which are mostly poorly drained; it underestimates the NPPa of all but one of the Bishop pine forest soils, which are mostly moderately well drained; and it greatly underestimates the NPPa of all but one of the coastal redwood forest soils, which are well drained. The coastal fog may be an important factor too, since the NPPa predictions are poor even for the well drained soils of the Fort Bragg area.

Table 4-Correlations of continuous variables with one another. Correlation coefficients (r) for 13 Arizona and seven inland California soils are on the lower left and those for 15 coastal California soils are on the upper right. Coefficients with absolute values greater than 0.444 (0.514 for the coastal set) are significant ($p = 0.05$) and those greater than 0.561 (0.641 for the coastal set) are highly significant ($p = 0.01$).

	NPPa	OC	MART	Clay	C/N	pH
NPPa		0.502	-0.443	0.135	0.415	-0.180
CC	0.883		-0.618	0.197	0.544	-0.092
MAAT	-0.880	-0.760		0.160	-0.706	0.549
Clay	-0.154	0.068	0.246		-0.079	0.177
C/N	0.788	0.869	-0.772	-0.167		-0.658
pH	-0.612	-0.454	0.754	0.143	-0.388	
AET	0.608	0.559	-0.570	-0.142	0.597	-0.463
FET	0.787	0.705	-0.823	-0.044	0.650	-0.833

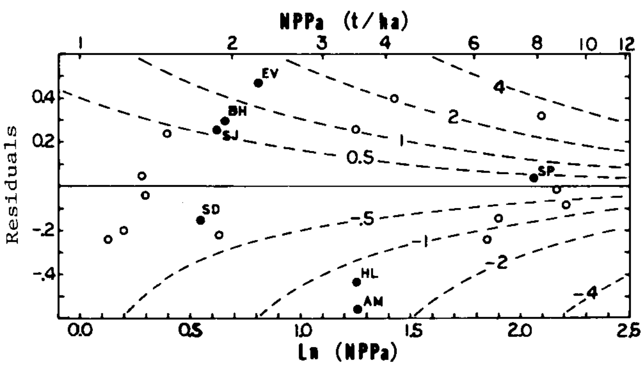

Figure 2-Residuals (actual minus predicted values) from Ln(NPPa) = 1.4846 + 0.6731 Ln(OC) - 0.2952 pH - 0.0103 Clay + 0.0194 C/N (Eq. 5) for the 13 Arizona and 7 California soils. The horizontal axis represents predicted values and the dashed lines represent conversions of residuals to NPPa by taking their antilogarithms.

A plot of the residuals (Fig. 2) shows how actual NPPa relates to values predicted from the best equation for Arizona and inland California soils (Table 3, 15 OF). The inland California values are evenly distributed between positive and negative deviations. There are positive and negative values for both annual grassland and chamise-chaparral soils. The NPPa of the Spanish Peak red fir site is based on the average productivity over the first 120 years following deforestation, whereas the NPPa of the Arizona sites are based on the current productivity averaged over the last five years, yet the residual for the Spanish Peak site is very small. However, 8.4 t/ha is only a minimum figure for the NPPa of the Spanish Peak site, because carbon lost as CO_2 from completely decomposed organic matter was not accounted for in estimating NPPa from the model of Stangenberger (1978). The NPPa of forest stands may be affected more by stand condition, as reported by Grier and Logan (1977), than by differences between successional and mature stands. In fact, it may even be more appropriate to compare sites by mean NPPa over a successional period, as for two of the chamise-chaparral stands as well as for the Spanish Peak red fir stand. Cyclical repetitions of disturbance and succession may be more a rule than an exception for plant communities (White, 1979).

CONCLUSIONS

Soil parameters were found useful for estimating the NPPa of well drained Arizona and inland California soils, assuming that the Ln(NPPa) is related to the Ln(OC) and functions of AET or soil properties which affect the rate of soil organic matter decay. Even though organic carbon in the soil is only a fraction of that in an ecosystem, its quantity may be the best organic matter parameter for estimating NPPa in all except mature ecosystems because it is less readily affected by perturbations of the environment. Soil organic matter may vary little through a cycle of disturbance and succession, whereas there may be extreme changes in the quantities of litter above ground (Turner and Long, 1975).

The best equation for predicting the NPPa of 13 Arizona and 7 California soils would be Ln(NPPa) = -.7148 + 0.6774 Ln(OC) + 0.0346 FET -.0147 clay (R^2=0.881, 5E=0.2957). However, Chow's test indicates (F=5.32, with 9 and 7 degrees of freedom) that this regression is significantly different ($p < 0.05$) from a similar regression (same variables) for the 13 Arizona soils alone. Therefore, equation 5 (Table 3, 15 OF), which is suitable for either the 13 Arizona soils alone or in combination with the 7 inland California soils, is considered to be better because it is more widely applicable:

$$\mathrm{Ln(NPPa)} = 1.4846 + 0.6731\ \mathrm{Ln(OC)} - 0.2952\ \mathrm{pH} - 0.0103\ \mathrm{Clay} + 0.0194\ \mathrm{C/N}. \quad (5)$$

This equation appears to be good for predicting the NPPa in chamise-chaparral and annual grassland ecosystems, but there is insufficient data for judging its accuracy in estimating the productivity of forest ecosystems at higher altitudes in California. Better and more universally applicable equations can be developed only when much more soils data can be coordinated with NPPa measurements.

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