Range Improvement As Related To Net Productivity, Energy Flow, And Foliage Configuration[1]

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Highlight

To maximize the conversion of the solar energy received by range vegetation into forms effectively used by domestic animals is an important objective of range managers. In annual-type California range improved by legume introduction and sulfur fertilization, the efficiency of the conversion of annual solar energy income over a three-year period averaged 0.09% by the vegetation and 0.004% by the stockers consuming the fed-off portion of the vegetation. Further study of the manner of display of the photosynthetic surfaces in range vegetation communities to incoming radiant energy will make it possible to identify foliage configurations that will maximize solar energy capture.

Productivity is the rate of generating or transforming a resource per unit time, and it is an attribute of many nonecological systems as well as all ecological systems (ecosystems). Productivity in the ecological context is the time rate of transforming radiant energy from the sun to chemical energy stored by photosynthetic organisms with the resulting generation of organic matter.

From the relatively few long-term records of solar energy receipts that are available, we know that large amounts of energy are received at the earth's surface and that the amounts vary seasonally and from place to place. A primary management objective of ranchers is to maximize the conversion of this energy by range plants; although other qualities of the resulting organic matter, e.g., protein, mineral, or vitamin level, may attain importance in some range situations.

Records of productivity in range ecosystems are few and fragmentary. Nevertheless, it is useful to attempt to compile such information in an example to contrast energy input-output

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[1] *Adapted from a paper presented as part of a symposium on "Range Ecosystems", November 12, 1964, to the annual meeting of the California Section, American Society of Range Management, Ukiah California.*

relations under various levels of resource management. In the example given below some components were not evaluated, and for those, estimates were derived from the observations of others working with related vegetation and consumer types.

Site Description and Productivity Analysis

The study area under consideration is located 30 miles due west of Modesto, California, on the periphery of the San Joaquin Valley at an elevation of 250 ft. The site is on a mature alluvial terrace, and the soil type is Snelling sandy loam. The land has been farmed to dry land winter cereals for grain and hay, but more recently has been used solely for grazing. In the unimproved state the vegetation is largely the annual type with filaree, *Erodium botrys*, and annual species of grass predominating. The climate is the Mediterranean type (Köppen's Csa) with annual precipitation of approximately 16 inches occurring mainly in the winter, with the summer essentially rainless; temperatures are mild in winter and warm to hot in summer (Kesseli, 1942).

In a 7-acre portion of a much larger grazing unit, various experimental treatments involving the introduction of numerous forage species and application of fertilizers were carried out over a 10-year period. In brief these trials demonstrated that marked increases in productivity result from the introduction of a winter annual legume, rose clover *(Trifolium hirtum)* and periodic application of sulfur fertilizer (Love and Sumner, 1952; Williams et al., 1957).

Over a period of three successive years the standing crop of vegetation above ground was measured on replicated plots which had received an initial treatment of gypsum containing 90 lb/acre of sulfur and a seeding of 10 lb/acre of rose clover.[2] The mean annual production of the organic matter sampled at the bloom stage was 2180 lb/acre (Table 1), and this value is used as the base point for the analysis.

In the simplified situation depicted in Fig. 1, two trophic or food levels are highlighted: the producers which comprise the vegetation community and the primary consumers or herbivores, cattle. The next trophic level is man, but his consumption involves export of the livestock products, and hence, is not included in the diagram. Various other consumers were observed, e.g., insects, birds, pocket gophers, and jackrabbits. Their activities were not assessed, but seemed to have little influence during the three years considered in this analysis and are not included in the quantitative aspects of the discussion. Other consumers undoubtedly present, but not discussed here, were the predators and parasites of the livestock and the soil inhabiting decomposers.

Since the vegetation was harvested with a walking sicklebar mower, it is estimated that a stubble amounting to 10% of the above ground portion remained after sampling. Hence the above ground standing crop was 2180/0.9 = 2420 lb/acre. Roots are estimated at 17% of the total biomass based on recent measurements of rose clover and filaree by Ozanne et al. (1965), and thus total plant

Table 1. Effect of range improvement techniques on harvestable forage, legume content of forage, and efficiency of solar energy conversion (SEC) by range vegetation.

	Unimproved		Sulfur fertilization		Rose clover seeding		Rose clover + sulfur	
	Harvest lb/a.	Legume %	Harvest lb/a.	Legume %	Harvest lb/a.	Legume %	Harvest lb/a.	Legume %
1st y.	1080	0	1120	0	1970	29	3080	64
2nd y.	680	0	730	0	1540	38	2270	53
3rd y.	410[1]	0	440[1]	0	940	42	1200	53
Mean	720		760		1480		2180[2]	
SEC. %	0.03		0.03		0.06		0.09	

[1] Rose clover had invaded the unseeded plots by the third year, and these two estimates are extrapolated from quadrats clipped from nearby sites.
[2] Base value for which energy flow example was calculated.

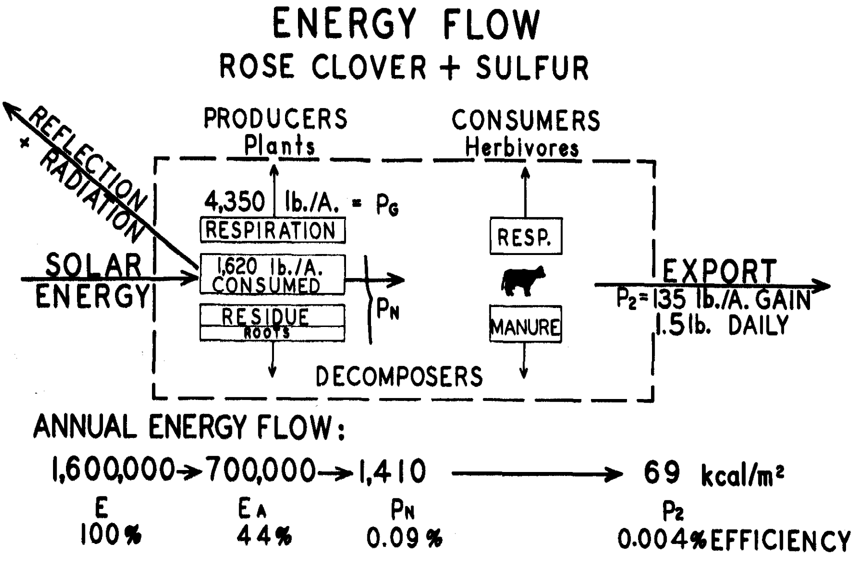

Fig. 1. Productivity, energy flow, and efficiency of solar energy conversion in a range ecosystem modified by introduction of rose clover and application of sulfur fertilizer.

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[2] *The cooperation of W. N. Helphenstine, California Agricultural Extension Service and R. J. Arkley, Soil Morphologist, University of California, Berkeley, in the conduct of this trial is gratefully acknowledged.*

biomass was 2420/0.83 = 2920 lb/acre. If respiration accounted for 33% of gross productivity (Thomas and Hill, 1949), then gross productivity (P_G) amounted to 2920/0.67 = 4350 lb/acre annually. Since net productivity is gross productivity less respiration loss, the net productivity (P_N) was 2920 lb/acre annually.

Some considerations disregarded in the above analysis that may have led to underestimation of productivity are (1) ignoring the possible growth stimulating effects of moderate grazing, (2) not accounting for organic matter contained in plants succumbing prior to sampling, and (3) disregarding the differences in the time that different species reach their peak standing crop (Wiegert and Evans, 1964).

The kind of animals commonly used as primary consumers on this site are steers purchased in the autumn to utilize the winter and spring green forage produced by the annual-type range. If these stockers on the average consume two-thirds of the aboveground standing crop, their consumption amounts to 2420 x 0.67 = 1620 lb/acre. This might be expected to produce an average of 1 lb liveweight gain per 12 lb range forage consumed at a gain level of 1.5 lb per head per day (Lofgreen, 1964; Martin et al., 1958) for a total of 135 lb/acre liveweight gain per year (P_2). This equates to 135/1.5 = 90 grazing days per acre. Each steer may be expected to excrete about 6 lb total solids in liquid and solid manures per day (Anderson, 1957) for a total of 6 x 112 = 672 lb/acre. Losses of energy will occur at the herbivore level due to the respiration involved in the animal's metabolic activities as well as in the export of carcass weight increments to market.

Energy Flow

It was estimated by extrapolation from the nearest weather stations recording solar radiation, that the annual sum of solar energy (E) received at the study site is about 1,600,000 kilocalories per square meter of land surface. Of this total 44% or 700,000 kcal is within the spectrum of wavelengths which plants can use for photosynthesis (E_A). The further partitioning of the energy by the activities of plants has been discussed recently (Loomis and Williams, 1963). In the example presented here, the plant community averaged a conversion of (2920 x 0.112) g/m^2 x 4.3 kcal/g = 1410 kcal/m^2 as the annual net productivity (P_N) averaged for the three year period. Golley's (1961) mean caloric content for green herbs of 4.3 kcal/g of organic matter is used here. The efficiency of solar energy conversion at the producer trophic level then is 1410/1,600,000 = 0.09%.

At the herbivore level in the food chain, the consumption of the plant material described above results in animal gain equivalent in energy to (135 x 2080 kcal/lb) / 4050m^2/acre = 69 kcal/m^2 annually (Lofgreen and Otagaki, 1960). Thus, the secondary productivity (P_2) associated with the consumer or herbivore trophic level has a net efficiency of 69/1,600,000 = 0.004% relative to the available solar energy income.

It is apparent that as the energy from the sun passes down the food chain, the amounts conserved and transmitted to each successive trophic level diminishes markedly. The energy flow is unidirectional, and losses in the form of heat and chemical degradation are irretrievable (Odum, 1963).

The three years comprising the time sample in this study comprise what might be labeled "good" to "poor" in respect to range production. It is of interest that this type of range is subject to violent year-to-year swings in the efficiency of solar energy conversion (Table 1). The annual total of incoming energy is quite stable, however.

Nutrient Relations

Other important considerations are the imports, exports, and cycling of essential nutritional elements. The "cycling" aspect of nutrient exchange is in contrast to the "one-way" degradation of energy in the ecosystem. This account will not go into detail on the cycling of nutrients, but will point out the effect of the alleviation of certain nutritional deficiencies in the soil on the productivity of this range site.

Nitrogen is the primary limiting nutrient on the site. This was corrected in part by the introduction of an adapted legume capable of symbiotic nitrogen-fixation, rose clover (Tables 1 and 2). The addition of sulfur fertilizer alone to the resident plant community was ineffective, because of the precedence of the nitrogen deficiency. However, in the presence of nitrogen-fixing organisms, correction of the sulfur deficiency further enhanced nitrogen-fixation and productivity. The nitrogen-fixing ability of sulfur-fertilized rose clover may be calculated approximately to be 44 − 6 (content of control) = 38 lb/acre nitrogen per annum. Phosphorus was not

Table 2. Effect of range improvement techniques on the nutrient content and annual nutrient removal in forages.

Nutrients in harvested vegetation[1]	Unit	Unimpr.	Sulfur fert.	Rose clover seeding	Rose clover + sulfur
Nitrogen	%	0.9	1.0	1.5	1.9
	lb/acre/year	6	8	22	44
Sulfur	%	0.10	0.14	0.09	0.15
	lb/acre/year	0.7	1.1	1.3	4.0
Phosphorus	%	0.32	0.32	0.27	0.23
	lb/acre/year	2.4	2.6	4.0	5.0

[1] These data are annual means of data from 3 years based on samples drawn from vegetation harvested with sicklebar mower and described further in Table 1.

a limiting factor as may be seen from the phosphorus percentages of the plant tops. They are above the critical level of 0.18% phosphorus for bloom-stage rose clover, and the existence of adequate soil phosphorus has been verified by other work at the site in which phosphorus fertilization was a variable (author's unpublished data).

A major effect of these modifications was to improve the efficiency of solar energy conversion by the producers from 0.03% in the unimproved state to 0.09% for the sulfur-fertilized rose clover treatment (Table 1).

Increasing Productivity By Ecosystem Modification

Odum has called ecosystem modification "ecosystem surgery" to emphasize the frequent drastic consequence for good or ill which may occur. Some modifications of range ecosystems which have had generally favorable effects when knowledgeably used are (1) forage species introduction; (2) the lowering of nutritional barriers; (3) weed and poison plant control; (4) pest control; and (5) grazing management. The first two are illustrated in the above example.

Are there other ways of improving the abysmally low solar-energy conversion efficiencies? Another obvious way is to make use of the peak solar energy income of the summer when our annual-type range is senescent because of protracted drought. By improving the moisture factor through the use of irrigated alfalfa, for example, productivity could be enhanced up to ten times. However, this takes us pretty far from range management.

Yet there is at least one more enticing approach within the range realm. Can we make the light trapping mechanism of our range plant communities more effective? There are certain bits of evidence that suggest a positive answer, and I would like to conclude my paper by a consideration of this thesis.

It has been demonstrated with certain forage species that maximum productivity occurs when there are optimum (or critical) amounts of leaf area relative to land area (leaf area index of Watson, 1958). The existence of these optima is nicely accounted for by Takeda (1961) in a diagram based on photosynthesis and respiration measurements in communities of *Oryza sativa* (Fig. 2). As the amount of leaf area is increased, the rate of gross photosynthesis (and gross productivity) increases rapidly at first, but when the amount of leaf exceeds that necessary for essentially complete light interception, photosynthesis approaches a ceiling value. Respiration is more nearly a linear function of leaf area, i.e., increases proportionately with increasing leaf area. Therefore, dry matter production ($\triangle W=$ net productivity) may attain an optimum value, and then decline with further increases in leaf area due to increased shading of the leaves in the lower portion of the canopy. The optimum leaf area index has been shown to vary seasonally with the amount of solar energy received. Black (1963) has constructed a series of curves based on work with communities of subterranean clover *(Trifolium subterraneum)* which show that the optimum amount of leaf area increases with increasing levels of light intensity (Fig. 3). Moreover, productivity is increased up to the maximum sunlight available in South Australia. Benedict (1941) has observed increased productivity of *Agropyron cristatum, A. smithii,* and *Bouteloua gracilis* also up to the maximum sunlight available at Cheyenne, Wyoming where intensities up to 14,000 ft-c have been measured.

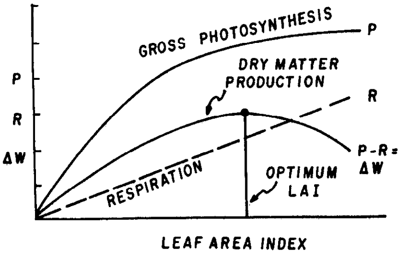

Fig. 2. Relationship between leaf area and dry matter production ($\Delta W=$ net productivity) after Takeda (1961).

Brougham (1958) has demonstrated that the optimum leaf area varies markedly between the two major families of forage species. The optimum leaf area indices for two representative species obtained under comparable light conditions are white clover *(Trifolium repens)* 3.5 and perennial ryegrass *(Lolium perenne)* 7.1. Measurements of the leaf angles and leaf area in horizontal strata in a young pasture containing these two species as dominants show that they also differ markedly in the manner in which their leaf area is displayed (Warren Wilson, 1959). In white clover the leaves are almost horizontal near the top of the canopy, whereas the leaves of perennial ryegrass are nearly vertical (Fig. 4). Moreover, the leaf area distribution curves indicate that a greater proportion of the leaves in white clover are in the upper part of the profile than in perennial ryegrass. Let us attempt to relate this infor-

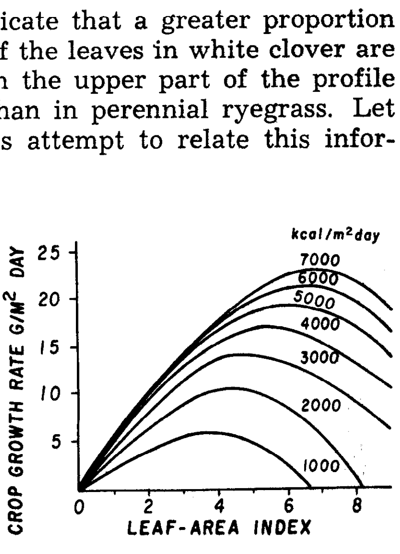

Fig. 3. Relationship of leaf area and crop growth rate (net productivity) at several mean daily solar radiation levels after Black (1963).

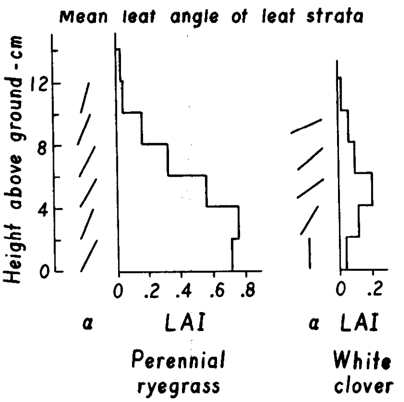

Fig. 4. Foliage angle (*a*) and leaf area index within horizontal strata 2 cm. deep as measured with the inclined point quadrat by Warren Wilson (1959).

mation to the light intercepting ability in two species of closely analogous leaf display characteristics, subterranean clover and Wimmera ryegrass *(Lolium rigidum)*, studied by Stern and Donald (1962). Species dominance was varied in communities of the two species by various levels of nitrogen fertilization. In the clover-dominant, no-nitrogen communities, light intensity fell off much more rapidly as the canopy was penetrated than in the ryegrass-dominant, high-nitrogen communities (Fig. 5). Looking at it from another point of view, we may predicate that in the ryegrass dominant community a more uniform distribution of light interception was attained in the vertical profile of leaf area, and that this is the type of relationship which accounts for the greater optimum leaf area index found by Brougham (1958) for perennial ryegrass than for white clover.

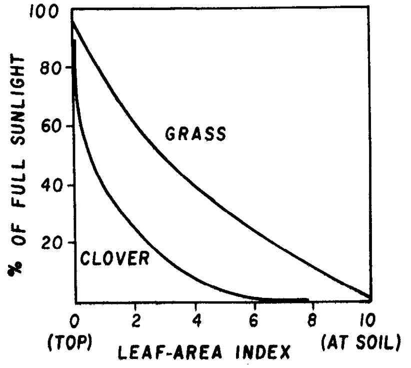

Fig. 5. Relationship of leaf area and light intensity in a clovery sward and a grassy sward after Stern and Donald (1962).

This leads us to a postulation based on data drawn from several workers widely separated geographically, yet through which a consistent thread may be detected. The inference is that plant communities with foliage configurations which allow relatively uniform light interception over the vertical distribution of leaf area, are more efficient in the utilization of solar energy and are likely to have greater net productivities than those with a concentration of horizontally disposed leaves. There is considerable circumstantial evidence in support of this thesis, but now we need the results of a series of integrated studies on all aspects of leaf arrangement that influence competition for light. In a recent review of plant competition Donald (1963) made the very appropriate statement: "Leaf layer density, the dispersion of the leaves, the leaf angle, and the vertical distribution are all aspects of leaf arrangement lending themselves to worthwhile, though difficult, study. Undoubtedly we must also add such leaf features as the reflectivity of the leaf surface, affecting both the back reflection to the sky and the complex reflection patterns within the crop . . . the whole field is wide open for profitable study."

Thus the next breakthrough in our quest for increasing the productivity in range ecosystems may be in ascertaining in detailed, quantitative terms the ideal architectural arrangements of foliage in the multitude of range vegetation types. Then the important task will be learning the necessary techniques for their achievement.

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