

tic grasses of our steppe, *Agropyron spicatum* and *Festuca idahoensis*, and a common grass restricted to the dry mountain parks, *Festuca viridula*, were planted separately in large containers which were imbedded in the soil in a nursery. Seeds of trees characteristic of the dry margin of forest were planted in similar manner for comparison. All grasses germinated shortly after the rainy season was well under way, but none of the tree seedlings emerged until April. On June 1 all root systems were washed free of soil for comparison (Fig. 3). In no case had the tree seedlings penetrated deeper than 140 mm, and the tap roots were virtually devoid of laterals.

The grasses, in contrast, had developed progressively, even if slowly and intermittently, during intervals of above-freezing weather throughout winter. By June 1 each plant had an abundance of adventitious roots 200 mm long, although none had penetrated deeper than 270 mm. Several sturdy tillers had formed and the plants were obviously well enough developed to endure the normal period of enforced aestivation of our summer-dry steppe climate. It has been shown that none of the tree seedlings can survive as many as 10 days after the soil moisture about their roots drops to the wilting coefficient (Daubenmire 1943). Therefore, as far as these grasses are concerned, their superior ability to survive drouth seems related to their ability to germinate in autumn and grow intermittently in winter during periods of favorable weather, and so be sufficiently advanced in their development by the time drouth intensifies in early summer that they can aestivate. Tree seedlings start growth so late that their tap roots are unable to descend rapidly enough to keep ahead of drouth advancing from the surface downward, and so are killed.

Since some of the steppe herbs germinate in spring as do the trees, there must be still other

successful ways of coping with drouth, but these have not yet been investigated.

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## EFFICIENCY OF NET PRIMARY PRODUCTION BASED ON LIGHT INTERCEPTED DURING THE GROWING SEASON

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*Abstract.* Net primary production of a 1-year-old field on the New Jersey Piedmont was 1.08 kcal/cm<sup>2</sup> or 10% of the radiant energy (0.4-0.7  $\mu$ ) intercepted by the vegetation from the last spring frost to the latest date a dominant producer reached its peak standing crop

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biomass; 3.8% of the energy available above the vegetation during the same period; 7.5% of the energy intercepted from the last spring frost to the first fall frost; 3.1% of the energy available above the vegetation during this period; and 1.8% of the energy available yearly. These results are among the first direct determinations of efficiency of net primary production based on interception of radiant energy under field conditions. Interception, the difference between radiant energy available above and below the vegetation, was measured with the Yellott solarimeter, whose small size made possible below-vegetation measurements with minimum disturbance to the cover. Net primary production for shoots was determined on a species basis by the short-term harvest method. Root production was estimated on a community basis by extracting roots from soil samples by a soil-dispersion and chemical flotation technique.

### INTRODUCTION

Estimates of the efficiency of net primary production by terrestrial vegetation under field conditions vary from 0.03% for a desert shrub community (Chew and Chew 1965) to 5.1% for cultivated corn (Yocum, Allen, and Lemon 1964). In general, estimates range from 1.9% to 3.2% for agricultural crops and from 2.2% to 3.5% for forest ecosystems (Hellmers 1964). Bliss (1966) found that herbaceous alpine communities characteristically had efficiencies of 0.14% to 0.76%, and Golley (1965) reported a similar range for an old-field broomsedge community.

These values suggest that natural terrestrial ecosystems usually have efficiencies of net primary production of less than 1% and seldom as great as 3% (Odum 1959, Smith 1966). However, the validity of generalizing from available estimates is questionable since these estimates use inconsistent definitions of efficiency and because no attempt has been made to standardize methodology. Further complications arise because of the many assumptions and rough estimates made by various authors. Frequently such basic parameters as the radiant energy available on site and the caloric content of the vegetation are estimated or assumed, when in fact these quantities can be measured with little difficulty. Perhaps the most common assumption made is that the radiant energy available to the ecosystem under investigation is the same quantity as that measured some distance away. Values recorded at weather stations frequently are used, although such installations often are many miles removed from the study site and in different topographical and meteorological environments.

The short-term harvest method commonly is used to estimate net primary production, and considerable error may result unless frequent sampling is conducted to insure harvesting coincident with the peak standing crop of dominant species comprising the vegetation (Odum 1960). Additional error often is involved if community peak standing crop is used as net production rather than determining peak standing crop and net production on a species basis (Odum 1960, Wiegert

and Evans 1964). Often this oversight is unavoidable for root sampling due to inadequate methodology. However, harvesting shoots on a species basis increases the validity of estimates, particularly when all the dominant producers do not reach peak standing crop biomasses at comparable times (Malone 1968).

We have attempted to avoid the potential errors mentioned above and to provide a more precise estimate of the efficiency of net primary production of a terrestrial ecosystem than previously has been made. Furthermore, this study differs from others in that radiant energy intercepted, as well as that available above the vegetation, was determined. Recent developments in instrumentation have made the measurement of interception possible and are discussed. It is hoped that this research will aid in clarifying the definition of net primary efficiency and lead to standardization of methodology.

### STUDY AREA

The study was conducted during the 1966 growing season in a field adjacent to Hutcheson Memorial Forest, East Millstone, New Jersey (40°30'N, 74°29'W). Climate of this area is modified continental; average yearly precipitation is 112 cm; average date of last frost is April 18 and of first frost October 20; average July maximum temperature is 30°C; January minimum is -6°C (Shulman 1965). Substratum is the Brunswick formation of Triassic shales (Ugolini 1964). The study site was a uniform 20-m by 25-m plot located within a soybean field of approximately 10 ha. The field had been cultivated in 1965 and abandoned after harvest.

### MATERIALS AND METHODS

Efficiency of net primary production is defined in this study as the calories per unit area contained in harvested vegetation divided by the calories of radiant energy available to the vegetation in wavelengths that can be utilized in photosynthesis. Efficiency is calculated for both incident and intercepted radiant energy. Interception is defined as the difference between the light available above and beneath the vegetation; it is not

meant to be an approximation of energy absorption by the vegetation, but rather a useful ecological concept in itself, representing the energy that is available in areas covered by vegetation.

#### *Measurement of insolation*

Insolation was measured at one point above and five points below the vegetation. The below-vegetation stations were chosen to represent the range of variation in vegetation cover. These measurements were made with a recently developed instrument, the Yellott solarimeter, whose small size (6 by 6 by 4 cm) made possible mounting at the ground surface with little disturbance to the vegetation. Two of these instruments were used, each rotated through three of the six light stations, rotations occurring at weekly intervals. A standard meteorological instrument, such as the Eppley pyrhelimeter, was not chosen because such instruments are too large to be easily mounted with their sensitive element at the ground surface without disturbing the vegetation. However, an Eppley pyrhelimeter was maintained throughout the summer at a station above the vegetation adjacent to the study plot. Finally, mean monthly values for 1948 through 1965 from an Eppley pyrhelimeter were obtained from the New Jersey College of Agriculture Experiment Station, approximately 14 km from the study site, and compared with on-site measurements of incident radiant energy.

The Yellott solarimeter uses a silicon photovoltaic cell as its sensitive element. The output of this cell is directly proportional to the intensity of the incident radiant energy. The cell, mounted with a temperature-compensating circuit to negate changes in cell output with changes in temperature, is sealed in a desiccated glass case. Response of the cell is from 0.3 to 1.2  $\mu$ ; response is non-linear to wavelength, peaking at 0.8  $\mu$  (Selçuk and Yellott 1962). (While the selenium photovoltaic cell has a response more like that of the absorption of green plants, this cell suffers from fatigue after exposure to bright light, and is impractical for recording radiant energy for long periods. Although the response curve of the silicon cell is not as desirable for ecological work, this cell does not show fatigue, and therefore makes a usable instrument for recording over long periods.)

The Yellott solarimeters were calibrated with the Eppley pyrhelimeter on site by running the instruments simultaneously at the same location for 10 days. Both kinds of instruments respond to a wavelength band broader than that utilized in photosynthesis. All results reported are corrected to give radiant energy which can be utilized

in photosynthesis (0.4–0.7  $\mu$ ). Yocum et al. (1964) determined this fraction to be 47% of the response of the Eppley pyrhelimeter, and that value is used to correct all readings of this instrument. Correction of the Yellott solarimeter was determined with a graph of the percentage response of the cell vs. wavelength. The areas under the entire response curve and under the part of the curve from 0.4 to 0.7  $\mu$  were determined and the ratio of these two areas calculated. The resulting constant (0.328) was multiplied by each daily reading of each Yellott instrument.

Because the Yellott solarimeter has a non-linear response to wavelengths which peak in the infrared, and because green leaves transmit a greater percentage of infrared than visible radiation (Gates 1965), one would expect the below-vegetation observations to be biased toward the infrared. For example, in the case where energy was equal in intensity but not spectrum above and below the vegetation, one would expect a higher reading from the Yellott instrument below the vegetation. To determine the extent of error resulting from this expected bias, an Eppley pyrhelimeter and one of the silicon cell instruments were compared for the ratio of their responses when unshaded and when shaded by a single green leaf or stalks of green vegetation. This ratio was determined for the Eppley and Yellott instruments for five species: *Geranium hortium*, *Nicotiana glauca*, *Ambrosia artemisiifolia*, *Chenopodium album*, and *Beria* sp.

Determinations were made on both a bright cloudless day and on an overcast day, both in a greenhouse and outside. Statistical analysis of the ratios showed no significant difference between the two instruments at the 5% level. Therefore, it was concluded that the theoretically expected error was negligible under conditions of the study and no correction was necessary for differences in spectral characteristics of the radiant energy above and beneath the vegetation.

Measurement of incident radiant energy began after the last spring frost of 1966 (May 2) and continued until after the first fall frost (October 6). During May, vegetation cover was negligible, and measurements of radiant energy were made only at the above-vegetation station. Rotation of the two Yellott instruments among the six sites above and beneath the vegetation began June 1 and continued until the first frost in the fall.

#### *Shoot-biomass estimation*

Net primary production, exclusive of herbivore consumption, was estimated by harvesting the vegetation at approximately 2-week intervals from June 4 through September 10. Standing crop

biomass of shoots was estimated by clipping all living shoots within fifteen  $\frac{1}{4}$ -m<sup>2</sup> quadrats selected from a table of random numbers. The clipped vegetation was bagged, returned to the laboratory, and sorted into seven different groups. Six of these contained the most frequently encountered species and the seventh contained 18 infrequent species. The samples were oven-dried at 90°C for 24 hours and weighed on a pan balance sensitive to 0.1 g.

Once the peak standing crop biomass of the shoots of each of the species groups was reached, the caloric content of the sampled material was determined by oxygen bomb-calorimetry. For this determination plants from five of the 15 samples were ground in a food mill and duplicate caloric determinations of the ground material were made with a plain oxygen bomb-calorimeter, Parr Model 1300. Appropriate acid and fuse wire corrections were made (Parr Instrument Company 1960).

#### Root-biomass estimation

Coincident with shoot sampling, net primary production of roots was estimated, but on a community basis rather than for each species. At five randomly chosen points soil cores were extracted to a depth of 30 cm by using a soil bucket auger 8 cm in diameter. Roots were removed from the soil by a method of flotation and screening developed for extracting seeds and other organic materials from soil (Malone 1967). Once the peak standing crop of roots had been reached, the five samples comprising the estimate were composited and from this duplicate caloric determinations were made as with the shoots.

When the peak standing crop biomass of the shoots of each species group and the roots on a community basis had been reached and converted to caloric values, an estimate of net primary production for the entire community was available by summing all the estimated values.

#### RESULTS

Corrected weekly means of incident radiant energy were calculated for each station in calories per square centimeter per day. These data indicated that interception of radiant energy by the vegetation was negligible until the middle of June. Mean accumulated radiant energy during the growing season for the dates corresponding to harvest dates of vegetation were determined by multiplying the mean of each weekly run by the days of that run. For periods during which no above-vegetation measurement was made, the grand mean of the two adjacent means was used, and this value multiplied by the number of days

TABLE 1. Mean accumulated radiant energy above, below, and intercepted by the vegetation at intervals of approximately 2 weeks (energy values are in 10<sup>4</sup>kcal/m<sup>2</sup>)

Days from last frost	Above vegetation	Below vegetation	Interception by vegetation
33	6.7	—	—
47	10.5	—	—
61	14.7	12.6	2.1
75	19.1	14.9	4.2
89	23.4	17.5	5.9
103	26.8	19.6	7.2
117	29.9	21.6	8.3
131	32.6	23.3	9.3
158	36.4	26.1	10.3

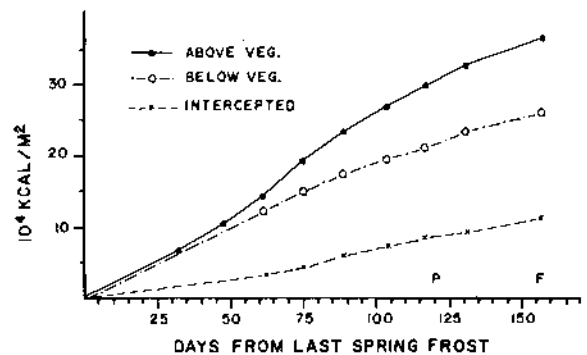


FIG. 1. Mean accumulated radiant energy at intervals of approximately 2 weeks. "P" indicates the latest date that a dominant producer reached its peak standing crop biomass; "F" indicates the date of the first fall frost.

between the actual runs. Accumulated values were then determined by summing the weekly totals from the day of the last frost to the day of each vegetation harvest. These data are listed in Table 1 and presented graphically in Fig. 1.

Values of radiant energy accumulated below the vegetation were also determined from the mean values for each weekly run multiplied by the days of the run. For those weeks during which two below-vegetation stations were measured simultaneously, a grand mean was calculated from the two station means. Radiant energy accumulated below the vegetation was then determined exactly as the above-vegetation radiant energy. Interception was calculated as the difference between the accumulated above-vegetation and below-vegetation values.

Table 2 gives the net primary production for the 1966 growing season including caloric values for each major component of the vegetation. *Ambrosia artemisiifolia* was the most productive species followed in turn by *Raphanus raphanistrum*, *Ipomoea pandurata*, and *Chenopodium album*. Total shoot production was 2,023 kcal/m<sup>2</sup> and community root production was 8,787 kcal/m<sup>2</sup>. Over the entire growing season, total com-

TABLE 2. Net primary production per square meter for the 1966 growing season on the 1-year-old field

Community component	Date of peak standing crop	Caloric value (kcal/g dry wt)	Mean peak standing crop	
			(g dry wt)	(kcal)
Shoots				
<i>Ambrosia artemisiifolia</i> .....	July 30	5.27	123	648
<i>Chenopodium album</i> .....	July 16	5.03	69	347
<i>Ipomoea pandurata</i> .....	July 2	5.21	83	432
<i>Raphanus raphanistrum</i> .....	July 2	4.91	90	442
<i>Setaria glauca</i> .....	August 27	4.95	5	25
<i>Digitalis sanguinalis</i> .....	July 30	4.83	7	34
18 infrequent species.....	July 30	4.98	19	95
Roots.....	August 13	4.52	1,944	8,787
Community net primary production.....			2,340	10,810

munity net production, exclusive of herbivore consumption, was 10,810 kcal/m<sup>2</sup>.

#### DETERMINATION OF EFFICIENCY

Efficiency is the ratio of output (calories in the vegetation) to input (radiant energy); ambiguity arises in the use of the term "efficiency" because input has been defined as energy available over a variety of time intervals. The two most commonly used intervals for temperate regions are the entire year and the period between the last spring frost and the first fall frost. Most studies of forests or tree plantations have considered efficiency of net primary production based on total energy available during the year, while studies of non-forest vegetation have frequently used the energy available during the growing season (Hellmers 1964).

In this study we want to emphasize the value of defining energy input over the growing season. First, this method assures that like intervals are used for the calculation of input and output, which allows for a more realistic comparison of harvest-method data with data obtained from CO<sub>2</sub>-uptake measurements or other short-term methods. Second, a yearly total of radiant energy is unrealistic in relation to intercepted light, since the light intercepted by whatever stalks remain after the growing season clearly provides little information about the use of energy by vegetation. (Because one is impressed with the amount of light intercepted by trees throughout the year, this is not so clearly the case in a forest, but it would be equally questionable in this case to calculate efficiency based on the interception by dormant non-photosynthetic tissue.)

The growing season is defined here as the period in which increases in biomass can be observed, i.e., the interval between the last spring frost and the last sampling date that the biomass of at least one of the dominant species of the vegetation reached its peak standing crop. Effi-

TABLE 3. Efficiency of net primary production for the 1-year-old field in 1966 (Input is calculated from mean daily radiant energy for period multiplied by number of days in period. All efficiencies are based on a net primary production of 108 × 10<sup>2</sup>kcal/m<sup>2</sup>.)

Period of energy input	Input (10 <sup>2</sup> kcal/m <sup>2</sup> )	Efficiency (%)
Last frost to last peak standing crop of a dominant producer species (120 days)		
Above vegetation		
New Brunswick	2,844	3.8
On site	2,839	3.8
Interception	1,085	10.0
Last frost to first frost (157 days)		
Above vegetation		
New Brunswick	3,503	3.1
On site	3,504	3.1
Interception	1,432	7.5
January 1 to December 31 (365 days)		
Above vegetation		
New Brunswick	6,095	1.8
On Site	—	—
Interception	—	—

ciency based on this definition was 3.8% for the 1-year-old field (Table 3). We have also calculated efficiency based on an energy input for both the entire year and the period between frosts since both periods have been used in other studies. These efficiencies are 1.8% and 3.1% respectively (Table 3).

The yearly total of incident radiant energy was estimated from mean monthly values at the nearest meteorological station. In this case the nearest station was the New Jersey College of Agriculture Experiment Station, New Brunswick, approximately 14 km from the study plot. Radiant energy available at the New Brunswick station is comparable to that measured above the vegetation on the old-field site during the growing season. Therefore use of yearly totals from the meteorological station is appropriate.

logical station is considered valid. In this case the station site and the study site have similar topography and weather patterns, but it is risky to generalize from this particular case to situations where a study site and a meteorological station are on different topographic exposures or have different weather patterns.

#### DISCUSSION AND CONCLUSIONS

Efficiency of net primary production of natural terrestrial vegetation is generally considered to be low, and this is substantiated here when efficiency is calculated on the basis of yearly total input. However, efficiency based on the interception of light during the period of incremental standing crop indicates that net production had a comparatively high efficiency, 10%, compared to efficiency based on total radiant energy available throughout the entire year, 1.8%.

What is the meaning of the difference between these two estimates of efficiency? In relation to the total energy input to the earth, the efficiency of net primary production is low, because conditions for primary production are not favorable during much of the year. However, when environmental conditions allow primary production to occur, the efficiency of a 1-year-old field is apparently considerable, in terms of energy intercepted.

Golley (1960) found an efficiency of 1.1% for a field in Michigan that was older than the one in the present study. His estimate of efficiency was based on an energy input from April 1 to October 31, corrected to give energy in the wavelengths utilized in photosynthesis. The nearest comparable estimate in our study is the frost-to-frost efficiency of 3.1% for above-vegetation incident energy. In another study Golley (1965) found an efficiency of 0.3–0.4% for an old-field broom-sedge community, based on the total insolation over the entire year, apparently not corrected for wavelengths utilized in photosynthesis. Assuming this insolation had been measured with an Eppley pyrhelimeter, the corrected value of efficiency would be 0.64–0.85%. The nearest comparable efficiency from our study is for the yearly total input, 1.8%.

Part of the difference between the estimates of efficiencies in Golley's studies and in ours is probably due to the substantial decrease in productivity of old fields after the initial year of abandonment. Odum (1960) found that in subsequent years an old field was only about 60% as productive as during the first year. Assuming the field in our study shows a similar decrease, its approximate efficiency after the first year will be 60% of 1.08 kcal/cm<sup>2</sup>. Assuming the field receives the

same energy input as it did in the first year, the efficiency of net primary production in subsequent years can be estimated as 0.65/35, or 1.9%, based on frost-to-frost energy input, and 0.65/61, or 1.1%, based on the yearly total energy input. Even after these corrections, however, Golley's estimates are still approximately three-fifths of the efficiencies estimated for older stages of the field in our study.

Probably some of this difference is due to our more frequent harvests, which resulted in a more precise determination of the peak standing crop, as Golley admits in the earlier study inadvertently missing the peak and in the later study asserts that quadrats were harvested "almost every month." Missing the peak standing crop biomass probably results in greater error in the estimate of production in old fields than in forests, because so much of the productivity of an old field is tied up with annual rather than stored biomass, so that a greater percentage of old field biomass will be lost to respiration after the peak.

We know of no study exactly comparable to ours, attempting to measure the efficiency of net primary production of natural terrestrial vegetation in relation to interception throughout the growing season. Bray (1961) calculated the efficiency of productivity of a stand of *Picea omorika* studied by Ovington and Heitkamp (1960) by estimating the values of reflection and transmission of light and absorption by non-photosynthetic tissues. Assuming reflection of 2.5%, transmission to the ground of 4%, and absorption by non-photosynthetic tissues of 10%, that is, assuming an absorption of 83.5% of the light incident above the entire forest over the entire year, Bray calculated an efficiency based on absorption of 7.9% for gross production and 4.0% for net production. If we add to Bray's assumptions that approximately two-thirds of the radiant energy was available during the growing season, then the estimated efficiency based on an input of energy during the growing season would be 5.9%; if we assume that one-half of the radiant energy was available during the growing season, then the estimated efficiency is 7.9%. The present study finds an efficiency based on interception of 7.5% for the energy available between frosts and 10.0% for the period between the last frost and last peak standing crop biomass of a dominant producer.

The principal difference between Bray's calculation and the estimate in our study is that Bray assumed a high percentage absorption for a stand of trees, while the interception of a 1-year-old field is expected to be smaller comparatively, and was measured to have a mean value of 40% of the incident radiant energy during the period between

frosts and 34% during the period from last frost to last peak standing crop biomass of a dominant producer.

According to Wassink (1959) beet seedlings raised under optimal conditions and with complete leaf cover of the soil surface gave efficiencies of 9% to 11%. Although in these experiments interception was not actually measured, under conditions of complete cover of the soil surface by leaves interception would be complete except for transmission, which is a relatively minor part of the interception for wavelengths between 0.4 and 0.7  $\mu$ . (Gates 1965). Any transmission by the leaves would increase the estimated efficiency based on intercepted light. Furthermore it has been pointed out that although the annual efficiency of a beet crop is approximately 2.2%, an efficiency calculated after 80–90% of the biomass had been produced, which occurred in 45% of the growing season, was 7–9% based on total energy available to the vegetation (Wassink 1959). These results therefore concur with the results of our study, as far as comparisons are possible.

While no single definition of efficiency as given in Table 3 will suit every ecological purpose, greater clarity and consistency in the use of the term "efficiency" is necessary in the future if useful generalizations concerning the efficiency of net primary production of natural vegetation are to be made. Furthermore, it is advisable wherever possible to use an efficiency for which both the numerator and denominator are defined for like time periods. This will allow meaningful comparisons of estimates of efficiency based on harvest methods with other techniques such as those involving CO<sub>2</sub> uptake.

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