

PRIMARY PRODUCTIVITY AND WATER USE IN NATIVE FOREST, GRASSLAND, AND DESERT ECOSYSTEMS^{1,2}

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Abstract. The relationship between aboveground net primary production (ANPP) and water use varies significantly among ecosystem types. For both hot deserts and shortgrass prairie-cold deserts which are water limited, ANPP is linearly related to annual water use above a minimum amount of water, estimated at 38 and 170 mm, respectively, needed annually to sustain each system. Once the minimum water to sustain ANPP is reached, ANPP increases an estimated 0.38 g and 1.09 g per 1000 g of additional water in the hot desert and the shortgrass prairie-cold desert. In forest systems not water stressed, ANPP was not related to water use. For grasslands representing a gradient from water stressed toward not water stressed, ANPP correspondingly declined per unit of water used. Classically evaluating water-use efficiency as annual ANPP divided by annual evapotranspiration, forests are the most efficient, 0.9 to 1.8 g ANPP/1000 g water, followed by shortgrass prairie, 0.2 to 0.7, then hot deserts, 0.1 to 0.3.

Key words: deserts; evapotranspiration; forests; grasslands; primary production; water-use efficiency.

INTRODUCTION

The water-use efficiency of vegetation, a much-studied concept in agriculture (Hsiao and Acevedo 1974), has been seldom used to analyze native ecosystems. Basically, water-use efficiency relates primary production and evapotranspiration. The primary production of a population depends on its genetic composition and the abiotic driving variables. Those same abiotic variables and populations of primary producers combine to determine the rate of evapotranspiration. Thus water-use efficiency, the evapotranspirational costs of converting radiant energy to plant biomass, links energy accumulation for ecosystem functions to

an important component of the hydrologic cycle. Therefore, water-use efficiency is valuable for comparing ecosystems of diverse environments and plant forms.

We used water-use efficiency to compare types of 3 native ecosystems: forests, grasslands, and deserts. In addition, we show that production potential has a carryover effect related to the water use of the previous growing season.

METHODS

Most data used here are from investigations conducted throughout the United States for the International Biological Program (IBP). Table 1 lists site names and locations, dominant plant species, and references for detailed descriptions. Site descriptions that follow will be limited to the methods used to collect productivity and evapotranspiration data not previously published.

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TABLE 1. Description and location of major sites of data collection. All sites are from the USA

| Site and state | Latitude (W) | Longitude (N) | Ecosystem type | Dominant plant species | Reference |
|-------------------------------------|--------------|---------------|---------------------|---|---------------------------|
| H. J. Andrews Watershed #10, Oregon | 44°15' | 122°15' | Coniferous forest | <i>Pseudotsuga menziesii</i> , <i>Tsuga heterophylla</i> | Grier and Logan 1977 |
| Hubbard Brook, New Hampshire | 44°10' | 71°35' | Hardwood forest | <i>Acer saccharum</i> , <i>Betula lutea</i> , <i>Fagus grandifolia</i> | Bormann et al. 1970 |
| Walker Branch, Tennessee | 35°58' | 84°17' | Hardwood forest | <i>Carya</i> spp., <i>Quercus alba</i> , <i>Quercus rubra</i> , <i>Quercus prinus</i> , <i>Quercus velutina</i> | Grigal and Goldstein 1971 |
| Coweeta #18, North Carolina | 35°03' | 83°26' | Hardwood forest | <i>Quercus prinus</i> , <i>Acer rubrum</i> , <i>Quercus coccinea</i> , <i>Carya glabra</i> | Day and Monk 1974 |
| Osage, Oklahoma | 36°57' | 96°33' | Grassland | <i>Andropogon scoparius</i> , <i>Sorghastrum nutans</i> | Sims et al. 1978 |
| Cottonwood, South Dakota | 43°57' | 101°52' | Grassland | <i>Agropyron smithii</i> , <i>Buchloe dactyloides</i> | Sims et al. 1978 |
| Dickinson, South Dakota | 46°54' | 102°49' | Grassland | <i>Stipa comata</i> , <i>Agropyron smithii</i> | Sims et al. 1978 |
| Jornada, New Mexico | 32°36' | 106°51' | Grassland | <i>Bouteloua eriopoda</i> | Sims et al. 1978 |
| Pawnee, Colorado | 40°49' | 104°46' | Shortgrass prairie | <i>Bouteloua gracilis</i> , <i>Artemisia frigida</i> , <i>Opuntia polyacantha</i> | Sims et al. 1978 |
| Pantex, Texas | 35°18' | 101°32' | Shortgrass prairie | <i>Bouteloua gracilis</i> , <i>Buchloe dactyloides</i> , <i>Opuntia polyacantha</i> | Sims et al. 1978 |
| Ale, Washington | 46°24' | 119°33' | Grassland | <i>Agropyron spicatum</i> , <i>Artemisia tridentata</i> | Sims et al. 1978 |
| South Curlew Valley, Utah | 41°52' | 112°45' | Cold desert | <i>Artemisia tridentata</i> , <i>Atriplex confertifolia</i> , <i>Sitanion hystrix</i> | Balgh 1973 |
| Silverbell, Arizona | 32°25' | 111°30' | Hot desert | <i>Ambrosia deltoidea</i> , <i>Larrea tridentata</i> , <i>Olneya tesota</i> | Thames 1973 |
| Rock Valley, Nevada | 36°40' | 116°5' | Transitional desert | <i>Ambrosia dumosa</i> , <i>Lycium andersonii</i> , <i>Krameria parvifolia</i> , <i>Larrea tridentata</i> | Turner 1973 |

Forests

For Watershed 10 of the H. J. Andrews Forest in western Oregon, aboveground net primary production (ANPP) was computed by determining each component in the equation, $ANPP = \Delta B + L$, where ΔB is the change in biomass, and L is the annual litter component, an estimate of leaf production. Gross biomass increment in stems and branches was calculated from annual dimensional differences for each community type. Annual foliage production for each species was estimated by regressing leaf production versus stem diameter. Biomass increment of shrubs was estimated by regressing stem production versus stem diameter at the soil surface multiplied by stem length. Net biomass increment was obtained by subtracting mortality losses during the year. Litterfall was determined from 65 litter traps systematically located to sample each community type in proportion to area (Grier and Logan 1978). Assuming that Watershed 10 is a closed system, actual evapotranspiration (AET) was determined by subtracting drainage outflow from precipitation input (R. Fredriksen and D. Harr, *personal communication*).

Aboveground productivity data were taken from

Whittaker et al. (1974) for Hubbard Brook, New Hampshire, and from Monk et al. (1971) for Coweeta, North Carolina, and Walker Branch, Tennessee. Calculated as precipitation minus runoff, AET data for these 3 watersheds, representing the eastern deciduous forests, came from gaged watershed studies—reported for Coweeta, Hubbard Brook, and Walker Branch by Swift et al. (1975), A. C. Federer (*personal communication*) and W. F. Harris (*personal communication*).

Grasslands

For the grassland sites (Pawnee, Pantex, Ale, Jornada, Cottonwood, Dickinson, and Osage, see Table 1), ANPP was determined from aboveground biomass sampled by the harvest technique. Net production was calculated by summing the peak biomass of individual species. AET was estimated from annual precipitation because surface runoff and deep drainage of soil water are negligible under the semi-arid conditions of the shortgrass prairie (Galbraith 1971). Slatyer (1967) made similar assumptions about the water balance of semi-arid areas. For Pawnee, Pantex, Jornada, and Ale, we assumed that precipitation equaled AET, but

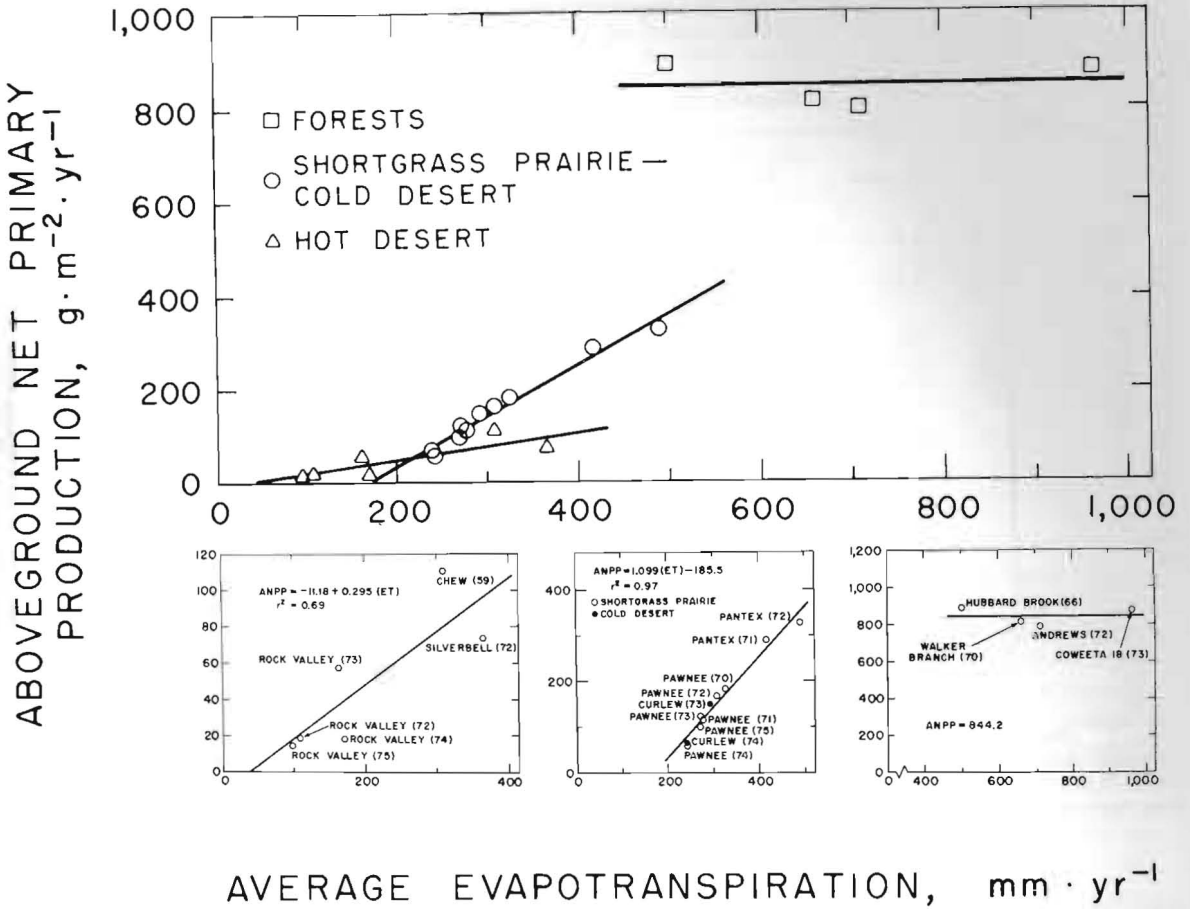


FIG. 1. Aboveground net primary production (ANPP) and water use for hot desert, cold desert, shortgrass prairie, and forests. For the combined linear models, r^2 is .99. Data in Fig. 1A are presented in 1B, 1C, 1D to specify both sites and year of collection.

we reduced precipitation by 4% for Dickinson and by 23% for Osage to allow for stream runoff (Sims et al. 1978).

Deserts

At Curlew Valley, Utah, productivity of perennial plant populations was determined from changes in biomass during the growing season. Nondestructive sampling was used to determine density, mean height, percent cover, and basal area of each dominant perennial on the site. In an adjacent area, destructive harvesting techniques were used to determine the actual relationships among plant components. Balph (1973) and Balph et al. (1974) reported the specific design of the study.

At Rock Valley, Nevada, productivity of perennial plant populations was determined by change in biomass during the growing season. Nondestructive sampling on the site determined primary production of dominant perennials. Regression equations determined by off-site destructive analysis were applied to the on-site perennials. Productivity of winter-active annuals was determined by harvesting during that

growth period. Sampling design was reported by Turner (1973) and Turner and McBrayer (1974).

The productivity of both perennial and annual plant populations at Silverbell, Arizona, was evaluated as those at Rock Valley. Thames (1973, 1974) reported the experimental design. Also, we used the ANPP and water-use data in Chew and Chew (1965) as representative of the Chihuahuan Desert.

At all 3 desert sites, AET was assumed to equal the precipitation. Although horizontal water movement (runon and runoff) occurs, it insignificantly affects year-long ecosystem soil water balance. Vertical drainage also was assumed insignificant as a means of removing water from the rooting zone. Actual measurements of year-long soil moisture dynamics at Curlew Valley (Campbell and Harris 1974) and Silverbell (Evans and Sammis 1975) confirmed that AET and precipitation are equal.

RESULTS

The water use (AET) and productivity (ANPP) data for all systems are shown in Fig. 1. To test for differ-

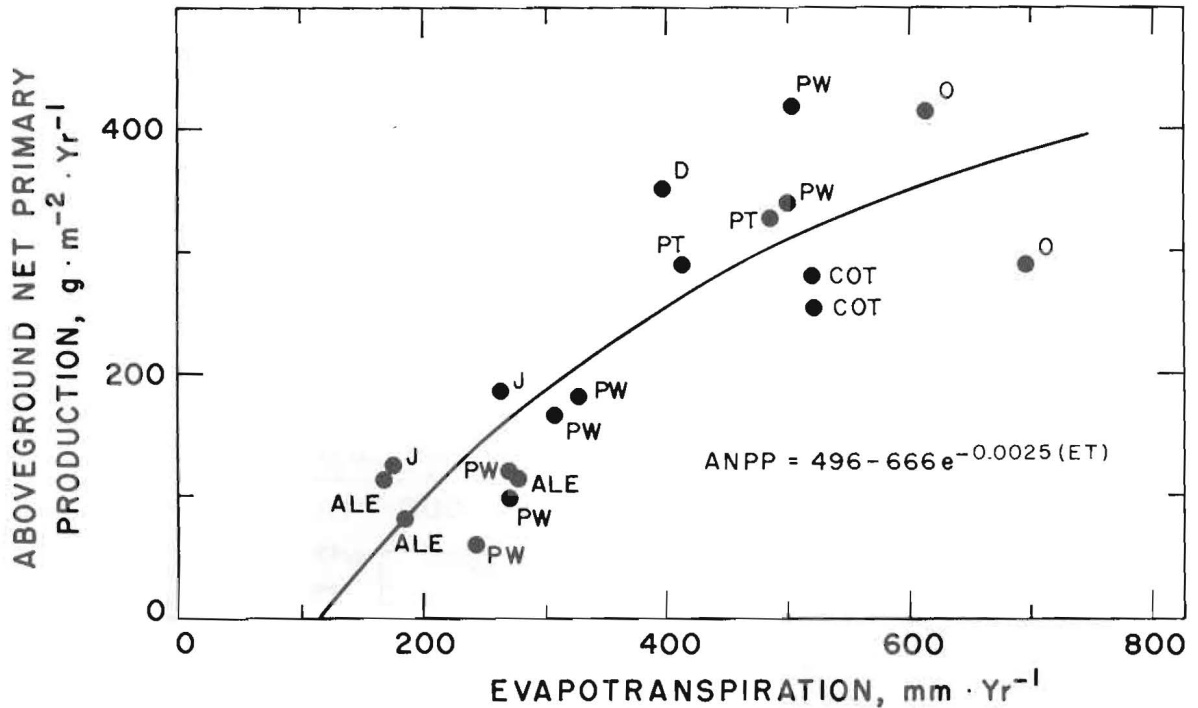


FIG. 2. Aboveground net primary production (ANPP) and actual evapotranspiration (AET) from several United States grasslands sites fully described by Sims et al. (1978). Location and dominant vegetation are listed in Table 1. Site abbreviations are ALE, Ale, Washington, USA; COT, Cottonwood, South Dakota, USA; D, Dickinson, South Dakota, USA; J, Jornada, New Mexico, USA; O, Osage, Oklahoma, USA; PW, Pawnee, Colorado, USA; and PT, Pantex, Texas, USA.

ences among ecosystem types, the data for all sites were examined with the extra-sum-of-squares technique (Draper and Smith 1966). The full linear model is:

$$\text{ANPP} = 844.3 - 1029.8 \chi_1 - 855.5 \chi_2 + 0.0 \chi_3 + 1.09 \chi_4 + 0.30 \chi_5 \quad (1)$$

This equation essentially incorporates 3 linear models to a combined equation with a resultant r^2 of .994. The 3 linear models represent respectively, forests, shortgrass prairie-cold desert, and hot deserts. When extracted from Eq. 1, the 3 linear expressions are:

$$\text{Forest ANPP} = 844.3 + 0.0 (\text{AET}); \quad (2)$$

$$\begin{aligned} \text{Shortgrass prairie-cold desert ANPP} \\ &= 844.3 - 1029.8 + 1.09 (\text{AET}), \\ &= -185.5 + 1.09 (\text{AET}); \quad (3) \end{aligned}$$

$$\begin{aligned} \text{Hot desert ANPP} &= 844.3 - 855.5 + 0.30 (\text{AET}), \\ &= -11.2 + 0.30 (\text{AET}). \quad (4) \end{aligned}$$

In Eq. 1, the variables χ_3 , χ_4 , and χ_5 are AET in mm per year for the forests, shortgrass prairie-cold desert, and hot deserts. Variables χ_1 and χ_2 , dummy variables with values of 0 or 1, are used in combination to specify data for each of the 3 ecosystem types—for ex-

ample, χ_1 was 1 for shortgrass prairie-cold desert data and 0 for all other data.

To test for significant differences among the parameters used from each linear model, we stated a series of alternate hypotheses and used the F statistic which we calculated by comparing the residuals of Eq. 1, relative to the residuals of an alternate linear model derived from an alternate hypothesis.

The first hypothesis was that a single linear model fits all the data as well as the combined linear model—that is, a common intercept and regression coefficient explain the variation just as well as 3 separate intercepts and regression coefficients do. The computed F statistic was 110.0 with 1, 14 df, and the single linear model was, therefore, rejected as an alternative to the combined linear model (Draper and Smith 1966). Successive tests for regression parameters common to all data sets were rejected. The slope parameter and intercepts for the shortgrass prairie-cold desert statistically differed from the hot desert, and the intercept for the forests differed from both hot desert and shortgrass prairie-cold desert. Therefore, the regression parameters in Eqs. 2, 3, and 4 differed significantly from each other, and can be considered as characteristic of each ecosystem type.

The ecosystem types in Fig. 1 are either water limited (deserts, shortgrass prairie) or water abundant

TABLE 2. Relationship between aboveground net primary production (ANPP) and actual evapotranspiration (AET) by shortgrass prairies and cold deserts. Coefficients of determination are shown for 3 regression parameters

| Year of AET relative to year of ANPP | Intercept ^a | Slope ^b | r ² |
|--------------------------------------|------------------------|--------------------|----------------|
| Current | -22.2 | 0.59* | .55 |
| Previous | -14.1 | 0.53* | .44 |
| Current and previous (\bar{x}) | -185.4* | 1.09* | .97 |

^a Annual g ANPP per m².

^b Annual g ANPP/mm AET per m².

* Significant at $P = .05$.

(forests). Figure 2 shows the relationship between AET and ANPP for a series of grassland sites representing a gradient from very water-deficient sites (e.g., Ale, Jornada) toward sites with a water regime favorable for growth (e.g., Osage). For example, annual precipitation averages 230 mm at Jornada and 930 mm at Osage. An exponential model was fitted to the data and gave a smaller error term than a linear model.

In addition, annual data of on-site water use (AET) from the 2 shortgrass prairie sites and the cold desert site were tested with linear regression models to determine which combinations of water use in past and current years best correlated with ANPP. The hypothesis here is that annual water limits productivity on these sites but, further, that primary productivity in any 1 yr is partly related to primary productivity during previous years. As shown in Table 2, water use during the previous year was significantly correlated with current primary production ($r^2 = .44$). Water use during the current year was also significantly related to ANPP of that year ($r^2 = .55$). However, the best correlation ($r^2 = .97$) with ANPP was obtained by summing water use from both the current and the previous years. This highly significant increase in r^2 indicates a strong "carryover" of productivity potential from the previous year. It also shows that data for comparing water use to production should span 2 yr for these "water-limited" sites of shortgrass prairie and cold desert. When computed this way, the shortgrass prairie-cold desert system had a regression coefficient of 1.09 g ANPP/1000 g of water use.

A similar linear analysis for hot desert sites necessarily included annuals as well as perennials (Table 3). For perennials alone, the coefficient of determination varied from 0.62 to 0.69, depending upon whether current or previous water use or the 2 yr combined were correlated with ANPP. When ANPP of annuals was included with the perennial production data, the only significant correlation between ANPP and water use was with current precipitation. The slope of the regression increased from 0.30 to 0.38 g of ANPP per millimetre of water when the production of annuals was added. The regression coefficients did not differ statistically with 90% confidence using the extra-sum-

TABLE 3. Relationship between aboveground net primary production (ANPP) and actual evapotranspiration (AET) by perennials and annuals in hot deserts and transitional deserts. Coefficients of determination are shown for 3 regression parameters

| Year of AET relative to year of ANPP | Intercept ^a | Slope ^b | r ² |
|--------------------------------------|------------------------|--------------------|----------------|
| Perennials | | | |
| Current | -9.6 | 0.31* | 0.64 |
| Previous | -2.6 | 0.23* | 0.62 |
| Current and previous (\bar{x}) | -11.2 | 0.30* | 0.69 |
| Perennials and annuals | | | |
| Current | -5.7 | 0.38* | 0.52 |
| Previous | 26.2 | 0.19 | 0.23 |
| Current and previous (\bar{x}) | 9.7 | 0.28 | 0.38 |

^a Annual g ANPP per m².

^b Annual g ANPP/mm AET per m².

* Significant at $P = .10$.

of-squares technique. In the desert, production by annuals greatly increased during years of higher-than-average precipitation. Annuals contributed significantly to total net production, but annual production alone poorly correlated with annual precipitation ($r^2 = .08$). The seasonal timing of precipitation seemed more critical than total annual precipitation for the growth of annuals. While a carryover of productivity potential from previous years cannot be conclusively demonstrated for desert perennials, the data tend to support the concept. The r^2 value for average water use was slightly better (.69) than for current water use (.64).

Water-use values for the forest systems were averaged for several consecutive years:

| Site | Years | Average AET (mm/yr) |
|------------------------------|-----------|---------------------|
| Hubbard Brook, New Hampshire | 1955-1969 | 514 |
| H. J. Andrews, Oregon | 1969-1973 | 735 |
| Walker Branch, Tennessee | 1969-1972 | 660 |
| Coweeta, North Carolina | 1972-1973 | 964 |

Because the ANPP from each site was determined during only 1 yr, the carryover response could not be examined. Kinerson et al. (1977) showed that ANPP varied <10% a year for a stand of *Pinus taeda*; these data, from 4 consecutive yr, indicate the year-to-year stability of ANPP in a forest not experiencing water stress.

DISCUSSION

For measures of plant frequency, Hyder et al. (1975) showed that precipitation during a previous year affects the performance of plant populations during the year of sampling. For a shortgrass prairie, previous years' precipitation was important in explaining variability in the current year. For example, the frequency of blue grama (*Bouteloua gracilis*) was related to precipitation the previous fall and the 2 previous summers

(Hyder et al. 1975). In contrast to our results, Smoliak (1956) found a very poor relation ($r^2 = .4$) between forage production during the current year and precipitation in the previous year. Using Smoliak's (1956) data on forage production and other data on annual precipitation (Clarke et al. 1943), we correlated forage production with the average annual precipitation of both past and present years—the coefficient of determination was .42, compared to .55 for forage production vs. the current year's precipitation. For a cold-desert site, Blaisdell (1958) calculated coefficients of determination for forage production vs. previous years' precipitation, current year's precipitation, and the average of the current and previous years' precipitation—.03, .29, and .36, respectively. Although bringing in the past years' precipitation explained only a small improvement in the percentage of variability, the trend agrees with our results. In further support of the carryover concept, Cable (1975) found that 64 to 91% of the variation in perennial grass production could be explained by combining rainfall from the previous summer with that of the current summer. He found that this "interaction" alone, not just the current year's rainfall, greatly increased the explained variation.

The carryover of productive potential may be explained by the combined effects of several phenomena. Primarily, 2 favorable yr of precipitation should interact and improve productivity the 2nd yr as a result of increased populations. Favorable precipitation should increase survival of seedlings and tillers, with the opposite responses in years of limited, subnormal precipitation. Population dynamics reported by Hyder et al. (1975) support this hypothesis.

Secondly, 2 favorable yr of precipitation should act to increase carbohydrate reserves available for bud formation. During the 1st yr of favorable precipitation, carbohydrate reserves would increase, making more carbon available for bud formation (i.e., tiller buds in the shortgrass prairie and leaf buds in the cold desert). Subsequently, the potential for rapid initiation of leaves and for greater leaf area would be increased in the 2nd yr's growth. Carbohydrate reserves would be oppositely affected in years of subnormal precipitation.

Finally, precipitation from October to December at Curlew Valley increases the productive potential for the following calendar year. Although the production of new roots slows significantly after September (Caldwell et al. 1975) and moisture absorption slows due to low soil temperatures, the status of soil moisture during the subsequent growing season depends on fall and winter precipitation more than on summer precipitation (Caldwell et al. 1977). Thus, a single period of water impulse, when extensive, apparently extends the period of net photosynthesis and primary production by delaying the onset of severe winter stress in the soil.

The lag in ANPP with respect to annual climatic data probably is not constant among growth forms. Fritts et al. (1971) applied principle component analysis to tree-ring width to separate the effect of current climate and past growth. The variation assigned to past growth varied from 0 to 48% which may be lower than some universal average because trees chosen for analysis of ring width are usually those near the edge of the climatic range; hence, the ring width is most sensitive to current climate.

Computation of water-use efficiency for crop plants is relatively straightforward. Most agricultural plants are annuals and, because yield is of paramount importance, many of these species are not significantly water stressed. Water-use efficiency is simply above-ground yield per unit of evapotranspiration per unit time. Values reported by de Wit (1958) range from 0.9 for alfalfa to 4.3 for sorghum. These data are grams of ANPP per kilogram of transpired water or grams of ANPP per millilitre of water per square metre. Kowal and Kassam (1973) reported an efficiency of 2.56 for maize grown in Nigeria. Similar computations using our data span 0.9 to 1.8 for forest systems, 0.2 to 0.7 for the shortgrass prairie-cold desert systems, and 0.1 to 0.3 for hot deserts. These ratios should be examined because they are frequently regarded as having some meaning concerning water requirements of different vegetation. In general, the trend indicates that forest ecosystems use water more efficiently than shortgrass prairie-cold desert systems which, in turn, are more efficient than hot deserts.

In Fig. 1, water use and primary production have been presented with regard to the carryover of productivity potential. The interpretation of the regression equations of water-stressed systems leads to 2 concepts: (1) that a "minimum" amount of water is needed to sustain productivity; and (2) that productivity increases per increment of water above the minimum requirement. Both concepts can be quantified from data representing hot deserts and shortgrass prairie-cold deserts but, at present, not for forest systems.

Minimum water requirement is defined as the annual water necessary to sustain 0 net primary production. Solving Eq. 4 (hot desert) for 0 ANPP yields an estimate of 38 mm of annual precipitation needed to sustain production of perennials.

$$\text{ANPP} = -11.2 + 0.30 (\text{AET}).$$

For ANPP = 0,

$$\begin{aligned} \text{AET} &= 11.2/0.30 \\ &= 38 \text{ mm/yr.} \end{aligned}$$

When the annuals were included in the linear regression (Table 4), the estimate decreased to 15 mm/yr. For shortgrass prairie-cold desert, the minimum water calculated to sustain production is much higher, 170 mm/yr. Data to support our estimates of minimum water needed to sustain ANPP are not available from

direct observation. The calculations here support the minimum-water concept, but we do not intend the values to be interpreted in a universal sense.

In desert systems, the concept of minimum water is a priori because some arid lands are too dry to support vegetation despite a small amount of annual precipitation. Noy-Meir (1973) discussed the concept of "zero-yield intercept," the value of annual precipitation resulting from a linear fit of annual precipitation against ANPP. He cited values of 25 to 75 mm/yr. For the many types of grasslands studied in the IBP program, long-term averages of precipitation far exceeded 170 mm/yr. Sims et al. (1978) reported values of 250 to 930 mm/yr. Penman (1971), working with irrigation effects on potato yields, predicted 0 productivity at 95 mm of water. While our data are difficult to compare with agricultural crops, Penman's (1971) estimate of water at 0 yield would be higher if his analysis included annual water-use instead of growing season only. Also, his experiments were designed to test fertilizers, and fertilization increases water-use efficiency (Viets 1962).

The increase in ANPP per unit of water above the minimum requirement differs significantly between shortgrass prairie-cold desert and hot deserts. Water-use efficiency of 1.09 g of ANPP per 1000 g of water for the shortgrass prairie-cold desert contrasts with 0.30 for desert perennials and 0.38 for annuals plus perennials. Whittaker and Niering (1975) estimated that the ANPP increases 0.25 g per millimetre of precipitation for the desert-desert grassland sites along a vegetation gradient in the Santa Catalina Mountains of Arizona. Walter (1939) estimated that ANPP for dry grasslands increased 1 gram per millimetre of precipitation in the range of 100 to 550 mm/yr. Estimates for arid and semi-arid systems range from 0.5 to 2.0 for aboveground primary production, and between 1.0 and 6 when belowground production is included (Noy-Meir 1973). Recently Caldwell et al. (1977) reported a water-use efficiency of 1.3 and 2.2 for aboveground and belowground production by cold desert dominants. These values are averages during 1973 and 1974 for communities dominated by *Ceratoides lanata* and *Atriplex confertifolia*. All these estimates agree closely with our data. Thus, on an ecosystem basis, once the minimum water requirement is achieved, vegetation of hot deserts apparently responds less to additional water than does shortgrass prairie-cold desert vegetation.

Two explanations are possible: 1 biological and the other physical (Van Dyne et al. 1978). Biologically, desert perennials may have evolved a more "conservative strategy" in terms of their response to precipitation (Van Dyne et al. 1978). Annual precipitation varies more in deserts than grasslands (Wagner 1978). In years of relatively heavy precipitation, rapid growth would result in a standing crop that would be severely stressed in succeeding years of low precipitation. The

second explanation relates to the higher evaporative potential in deserts compared to grasslands (unpublished data from the same sites listed in Table 1). Precipitation may rapidly evaporate back to the atmosphere from intercepting surfaces, without being used by the vegetation. This reduces the effective water or that used directly by the vegetation. Although this evaporative term will have to be quantified with precipitation data for more frequent intervals, evaporation of intercepted precipitation commonly accounts for $\approx 20\%$ of the total annual precipitation in forest systems (Helvey and Patrick 1965, Krygier 1971). Hillel and Tadmor (1962) reported evaporation as 10–56% of evapotranspiration on desert sites. Both phenomena probably contribute to the relative inefficiency of desert production per unit of water above the minimum requirement. However, the desert perennials clearly are adapted to producing with less water than the perennials of the shortgrass prairie-cold desert.

In the range of our data for forest ecosystems, ANPP is independent of evapotranspiration. Rosenzweig's (1968) model relating AET to ANPP would predict an annual increase in ANPP from 630 to 2500 g/m² for our AET data. Leith's model (Leith and Whittaker 1975) for predicting ANPP from evapotranspiration showed an annual increase of >600 g/m² for our AET data. In both cases, AET was calculated from weather data not necessarily from the same site where ANPP was measured. Although our data base is small, both AET and ANPP are from the same site. We suggest that ANPP and AET are not strongly coupled for systems that are not water stressed. General models that predict ANPP from evapotranspiration estimates only seem to need modification to include other abiotic variables.

Our final point addresses the form of the ANPP *versus* AET as presented in Fig. 1. This relationship indicates that either increments in ANPP are constant with additional water (shortgrass prairie-cold desert and hot desert) or that ANPP is independent of available water (forests). Clearly these relationships by themselves are not general because they do not address the transition between water-limited and water-abundant ecosystems. Analysis of the relationship between ANPP and AET for grassland sites along a gradient of low to high annual AET suggests that the rate of increase in ANPP is a decreasing function of water use (Fig. 2). Water-use efficiency ranges from 1.25 to 0.37, indicating that the grassland vegetation is unable to capitalize upon the additional water at the higher values of available water.

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