

Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales

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Abstract. Correlative approaches to understanding the climatic controls of vegetation distribution have exhibited at least two important weaknesses: they have been conceptually divorced across spatial scales, and their climatic parameters have not necessarily represented aspects of climate of broad physiological importance to plants. Using examples from the literature and from the Sierra Nevada of California, I argue that two water balance parameters—actual evapotranspiration (AET) and deficit (D)—are biologically meaningful, are well correlated with the distribution of vegetation types, and exhibit these qualities over several orders of magnitude of spatial scale (continental to local). I reach four additional conclusions. (1) Some pairs of climatic parameters presently in use are functionally similar to AET and D; however, AET and D may be easier to interpret biologically. (2) Several well-known climatic parameters are biologically less meaningful or less important than AET and D, and consequently are poorer correlates of the distribution of vegetation types. Of particular interest,

AET is a much better correlate of the distributions of coniferous and deciduous forests than minimum temperature. (3) The effects of evaporative demand and water availability on a site's water balance are intrinsically different. For example, the 'dry' experienced by plants on sunward slopes (high evaporative demand) is not comparable to the 'dry' experienced by plants on soils with low water-holding capacities (low water availability), and these differences are reflected in vegetation patterns. (4) Many traditional topographic moisture scalars—those that additively combine measures related to evaporative demand and water availability—are not necessarily meaningful for describing site conditions as sensed by plants; the same holds for measured soil moisture. However, using AET and D in place of moisture scalars and measured soil moisture can solve these problems.

Key words. Bioclimatology, climate, climatic indices, forest physiognomy, moisture scalars, Sierra Nevada, water balance.

INTRODUCTION

Growing interest in the possible biotic consequences of climatic change has led to a resurgence in studies of the climatic controls of vegetation distribution. Such studies are generally seen as falling into two broad categories: ecophysiological and correlative (Woodward, 1987; Prentice *et al.*, 1992; Martin, 1992; Cramer, 1997). All else being equal, ecophysiological studies—those based on detailed knowledge of the physiology and life-history traits of plant species or functional types (e.g. Bunce, Chabot & Miller, 1979; Woodward, 1987; Prentice *et al.*, 1992; Neilson, 1995)—offer the best opportunity for predicting climatically-induced changes in the distribution of plant species and vegetation types. However, correlative studies, by revealing broad and sometimes unanticipated relationships between climate and vegetation distribution, play an important role by identifying potentially significant and previously overlooked physiological mechanisms.

In practice, the distinction between ecophysiological and correlative studies often is blurred. Even as physiological mechanisms are better and better understood, ecophysiological studies still depend on empirical

correlations to determine quantitative relationships between physiologically important factors and vegetation distribution (e.g. Woodward, 1987; Prentice *et al.*, 1992). Conversely, correlative studies have an ecophysiological basis when they focus on climatic parameters thought to be of broad physiological importance to plants in general (e.g. Stephenson, 1990; Shao & Halpin, 1995).

This paper aims to compare and critique some climatic parameters used in correlative studies of climate and vegetation distribution. Correlative approaches have exhibited at least two important weaknesses: (1) they have been conceptually divorced across spatial scales, and (2) their climatic parameters have not necessarily represented aspects of climate of broad physiological importance to plants. At continental and global scales, correlations usually have been between the physiognomy of dominant vegetation and measures related to energy supply (temperature, potential evapotranspiration, or radiation), water supply (precipitation), their ratios, or parameters related to the climatic water balance (e.g. Leith, 1956; Holdridge, 1967; Mather & Yoshioka, 1968; Budyko, 1974; Whittaker, 1975; Box, 1981, 1995; Sowell, 1985; Woodward, 1987; Stephenson, 1990; Prentice *et al.*, 1992; Tchekabkova *et al.*,

1993). In contrast, correlative studies at local to regional scales have tended to be floristic rather than physiognomic, and often have used climatic surrogates rather than measured climate (particularly in mountainous regions). In studies at these finer scales, elevation often is used as a surrogate for temperature, precipitation, and insolation. Surrogates for differences in local water balances independent of elevation have included factors such as soil depth and drainage (e.g. Velázquez, 1994) and synthetic 'topographic moisture' scalars (e.g. Whittaker & Niering, 1965; Parker, 1982a, 1991; Peet, 1981, 1988; Allen, Peet & Baker, 1991).

The second major weakness in correlative studies is that, generally, their climatic parameters have not necessarily represented aspects of climate of broad physiological importance to plants (Tuhkanen, 1980). For example, many studies at continental and global scales have been based on the implicit but false assumption that energy and water act independently on plants (Stephenson, 1990). Similarly, studies at local to regional scales often have not adequately considered the interactions of energy and water. One consequence of the lack of consistent focus on climatic parameters of broad physiological importance has been that, even among studies at similar spatial scales, different researchers have tended to use a wide and inconsistent range of parameters (e.g. see Tuhkanen, 1980; Stephenson, 1990; Shao & Halpin, 1995). As yet, there is no generally-accepted subset of climatic parameters used in a majority of correlative studies.

Here I examine these problems in greater detail and demonstrate that two water balance parameters—actual evapotranspiration (AET) and deficit (D)—have several properties that make them broadly useful in correlative studies of climate and vegetation distribution. I present arguments supporting six conclusions.

- (1) AET and D are biologically meaningful measures of climate.
- (2) Some pairs of climatic parameters presently in use are functionally similar to AET and D; however, AET and D may be easier to interpret biologically.
- (3) Several well-known climatic parameters are biologically less meaningful or less important than AET and D, and consequently are poorer correlates of the distribution of vegetation types. Of particular interest, AET is a much better (and probably more meaningful) correlate of the distributions of coniferous and deciduous forests than minimum temperature or other climatic parameters.
- (4) The effects of evaporative demand and water availability on a site's water balance are intrinsically different. For example, the 'dry' experienced by plants on sunward slopes (high evaporative demand) is not comparable to the 'dry' experienced by plants on soils with low water-holding capacities (low water availability). These differences are reflected in vegetation patterns.
- (5) A corollary of the preceding conclusion is that many traditional topographic moisture scalars—those that additively combine measures related to evaporative

demand and water availability—are not necessarily meaningful for describing site conditions as sensed by plants; the same holds for measured soil moisture. We therefore should not always expect adjacent sites with similar values of topographic moisture scalars, or similar measured soil moistures, to support similar vegetation types.

- (6) The distributions of vegetation types are well correlated with AET and D across several orders of magnitude of spatial scale, from continental to local. AET and D therefore can help eliminate the conceptual divorce among correlative studies at different spatial scales.

Each of these conclusions is addressed in a separate section. Several supporting examples, particularly for the fourth conclusion, come from new analyses of data from the Sierra Nevada of California.

REVIEW: THE CLIMATIC WATER BALANCE

For a plant to use external energy for growth, water must be available; otherwise the energy will act only to heat and stress the plant. For a plant to use water for growth, energy must be available; otherwise water simply will percolate through the soil or run off, unused. The primary effects of climate on plants, therefore, are determined by the interactions of energy and water (Stephenson, 1990). The climatic water balance describes these interactions. In water balance calculations, energy is represented by potential evapotranspiration (PET—which I will also call 'evaporative demand'), and available water (W) is defined as the total amount of liquid water reaching the soil, minus the net change in water stored in the soil (Stephenson, 1990). The interactions of evaporative demand and available water (PET and W) are described by three water balance parameters: AET, D, and surplus (S). Interpretation of these parameters is greatly aided by diagrams showing the seasonal interactions of demand and availability, with annual totals of the parameters appearing as areas under curves (Fig. 1). Relationships among water balance parameters can be expressed in two equations: $W = AET + S$ and $PET = AET + D$. The first equation describes conservation of water; the second can be viewed as describing conservation of energy (Stephenson, 1990).

Unfortunately, AET has had two conflicting definitions (Stephenson, 1990). Following the implicit definition of Thornthwaite & Mather (1955) and later authors using their approach, I define AET as the evaporative water loss from a site covered by a hypothetical standard crop, given the prevailing water availability. (A standard crop is a continuous sward of short green plants that completely shade the ground and exert negligible resistance to evaporative water loss; cf. Rosenberg, Blad & Verma, 1983.) Though most natural vegetation does not behave as a standard crop, the value of this definition of AET is that it estimates the simultaneous availability of biologically usable energy and water at a site, independent of actual vegetation (Major, 1963; Rosenzweig, 1968). The other commonly-used definition of AET (which is not used in this paper) is

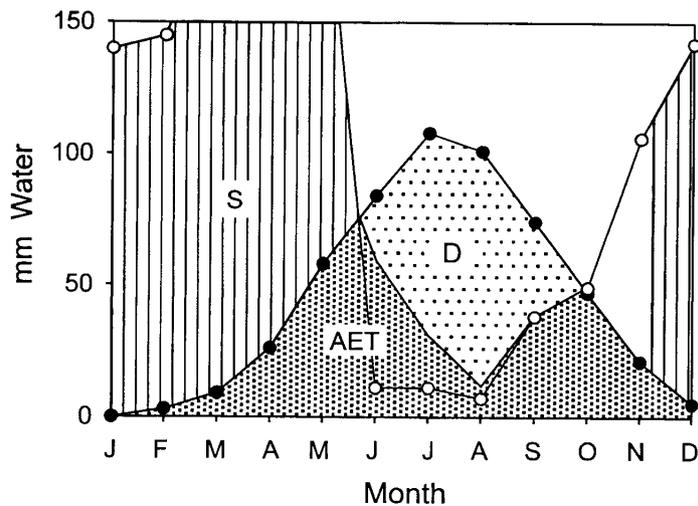


FIG. 1. The annual water balance of a site on level ground, soils of 0.5 m depth, at 2000 m elevation, and in the wet Kaweah watershed of the southern Sierra Nevada (data from Stephenson, 1988). From October through May, water supply (rain plus snowmelt, ○) exceeds evaporative demand (potential evapotranspiration or PET, ●); during this period, actual evapotranspiration (AET, dense stippling) equals PET. In October and November, excess water replaces soil water used during the summer; the white area between the water supply and PET curves represents soil-water recharge. From November through May, after soil water has been replenished, the difference between water supply and PET is surplus (S, vertical stripes). From June through September, PET exceeds water supply. During this period, AET equals water supply plus water extracted from the soil (which is shown as the curve between the water supply and PET curves). Deficit (D, light stippling) is the difference between PET and AET.

the evaporative water loss from the actual soil and vegetation of a site—whatever that vegetation may be—given the prevailing water availability (cf. Woodward, 1987; Neilson, 1995).

Deficit, as I use the term, refers to climatic water deficit, and must be distinguished from soil water deficit. Climatic water deficit (D) is evaporative demand not met by available water—a measure of how much more water could have been evaporated or transpired from a site covered by a standard crop, had that water been available (Stephenson, 1990). It is therefore a measure of absolute drought that is independent of the actual vegetation of the site. In contrast, soil water deficit is the difference between the field capacity of a soil and its water content at a particular point in time.

S is a measure of excess water in the environment. It is the amount of water that leaves a site covered by a standard crop, through runoff or subsurface flow, without being evaporated or transpired. Because S usually is of only indirect physiological importance to plants (Stephenson, 1988, 1990), it receives little attention in this paper.

Throughout this paper, local scales are defined as those modified by site-specific variations in soils, topography, proximity to water, and so on—generally 0.1 ha to more than 100 ha (cf. Major, 1951). Regional scales are those influenced by broadly similar climatic patterns—generally watersheds up to small portions of continents. Continental and global scales are self-explanatory.

BIOLOGICAL INTERPRETATION OF AET AND D

Because AET estimates the simultaneous availability of biologically usable energy and water in the environment, it

reflects the magnitude and length of conditions favourable to plant growth (Major, 1963; Rosenzweig, 1968). In contrast, D is related to the magnitude and length of drought stress experienced by plants—heat stress that cannot be regulated by transpiration, metabolic costs that cannot be met by active photosynthesis, and potential for cell damage or death (e.g. Kramer & Kozlowski, 1979; Jones, 1992; Larcher, 1995). Accordingly, AET and D are useful for explaining several natural patterns. The distribution of vegetation types at continental and global scales is well correlated with AET and D (Fig. 2; Stephenson, 1990; Frank & Inouye, 1994). AET is highly correlated, over a broad range of ecosystems, with tree species richness (Currie & Paquin, 1987; Currie, 1991; but see Latham & Ricklefs, 1993), organic litter decomposition rates (Meentemeyer, 1978; Berg *et al.*, 1993), and ecosystem productivity (Rosenzweig, 1968; Leith, 1975, 1976). AET also has proved useful in explaining the organic content, acidity, weathering rates, and distribution of soil types (Arkley, 1967). It is because AET and D describe climate as the interactions of energy and water, and not just their absolute amounts, that they successfully explain several patterns and processes in nature (Stephenson, 1990).

PAIRS OF CLIMATIC PARAMETERS FUNCTIONALLY SIMILAR TO AET AND D

Shao & Halpin (1995), exploring the relationship between the distribution of six eastern North American tree and shrub species and sixteen pairs of climatic parameters (including AET and D), found that the species' distributions were best correlated with AET and annual sum of growing degree days (GDD). Since environmental energy (in this

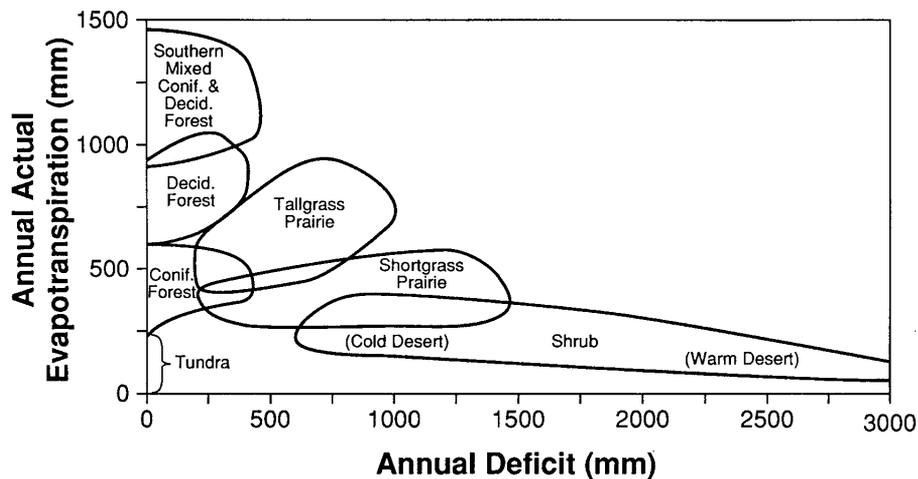


FIG. 2. The distribution of the major North American plant formations relative to annual AET and D (from Stephenson, 1990).

case represented by cumulative GDD) is strongly correlated with PET (Rosenberg, Blad & Verma, 1983), the pair of parameters AET and GDD should be functionally similar to the pair AET and PET. (Supporting this contention, the correlation between species distributions and AET and PET was nearly identical to that of AET and GDD [Shao & Halpin, 1995].) The pair of parameters AET and PET, in turn, should be functionally similar to the pair of parameters that is the main topic of this paper: AET and D. When plotted on a graph with AET and D as perpendicular axes (e.g. Fig. 2), a given value of PET uniquely defines a line with slope -1 and y -intercept PET (because, by definition, $PET = AET + D$). On such a graph, a line representing constant AET intersects a line representing constant PET at the uniquely corresponding values of AET and D.

Supporting the contention that the pair of parameters AET and PET (and, by extension, AET and GDD) is functionally similar to AET and D, discriminant analysis shows that the relative abilities of AET and PET *v.* AET and D to distinguish among North American vegetation types are identical (Table 1). In contrast, however, Shao & Halpin (1995), using the kappa statistic to compare actual and predicted distribution maps of their six woody species, found that the pair AET and GDD and the pair AET and PET both were better correlated with species distributions than AET and D. However, the differences were significant for only one of the four models they explored ($P < 0.05$; Wilcoxon signed ranks test), and may not hold generally among physiognomic types and at broader geographic scales (as in Table 1).

Taking inspiration from the work of Specht (1972, 1981) and others, some authors have used the parameter AET/PET (the ratio of actual to potential evapotranspiration) in studies of vegetation distribution at continental and global scales. AET/PET commonly has been used in conjunction with GDD, among other parameters (Prentice *et al.*, 1992; Beerling, Huntley & Bailey, 1995; Huntley *et al.*, 1995; Bugmann, 1996; Sykes, Prentice & Cramer, 1996). Skarpe (1996) used, among several other parameters, AET/PET and mean temperature of the warmest month. In these

examples, AET/PET is paired with a measure of energy—cumulative GDD or mean temperature of the warmest month. As suggested earlier, because environmental energy is strongly correlated with PET (Rosenberg, Blad & Verma, 1983), the pairs of parameters listed above are functionally similar to AET/PET and PET. The pair of parameters AET/PET and PET, in turn, should be functionally similar to AET and D. When plotted on a graph with AET and D as perpendicular axes (e.g. Fig. 2), a given value of AET/PET uniquely defines a line of slope AET/D (always ≥ 0) which passes through the origin; a given value of PET uniquely defines a line with slope -1 and y -intercept PET. These lines intersect at uniquely corresponding values of AET and D.

Supporting the preceding argument, discriminant analysis shows that the relative abilities of AET/PET and PET *v.* AET and D to distinguish among North American vegetation types are similar (Table 1). Though the ability of AET/PET and PET to discriminate among vegetation types was somewhat lower than that of AET and D for two of the three combinations of vegetation types tested (Table 1), the differences were statistically indistinguishable at $P = 0.05$. Importantly, the pair AET/PET and PET, like AET and D (and AET and PET), is significantly better at distinguishing among vegetation types than several pairs of parameters used in earlier studies (Table 1; see the next section).

In his studies of the climatic controls of the distribution of boreal tree species and Canadian vegetation types, Lenihan (1993; Lenihan & Neilson, 1993) used, among other parameters, summertime AET and what he called 'soil moisture deficit'. His 'soil moisture deficit'—PET minus AET (Lenihan & Neilson, 1993)—is identical to what I call climatic water deficit (D); thus the close relation between Lenihan's parameters and those that are the main topic of this paper are obvious. However, it may be generally preferable to use annual AET rather than summertime AET; the former is meaningful in both warm and cool regions, whereas the latter tends to be meaningful only in cool regions (as in Lenihan's work). Similarly, it is generally

TABLE 1. Percentages of North American sites for which physiognomy was correctly classified by nearest-neighbour discriminant analysis, using various pairs of climatic parameters (after Stephenson, 1990).

Parameters‡		All North American formations (241 sites)	Minus transition formations and coastal prairie (198 sites)	Coniferous forest and deciduous forest only (91 sites)
AET, D	(Stephenson, 1990)	58.9	80.3	95.6
AET, PET	(Shao & Halpin, 1995)	58.9	80.3	95.6
AET/PET, PET	(modified from Prentice <i>et al.</i> , 1992)	55.6	75.3	95.6
min T, D	(modified from Woodward, 1987)	51.5	67.2*†	81.3*†
log PET, log P	(Holdridge, 1967)	52.7	68.2*	81.3*†
T, P	(Leith, 1956; Whittaker, 1975)	51.9*	70.2*	81.3*†
PET, PET/P	(modified from Budyko, 1974)	53.5	66.7*†	82.4*†
PET, 100 (P/PET-1)	(Mather & Yoshioka, 1968)	45.6*†	65.7*†	82.4*†
D/PET, S/PET	(Thorntwaite, 1948; see Mather, 1974, 1985)	39.0*†	52.0*†	83.5*†

NOTE: Some numbers differ slightly from those published in Stephenson (1990), apparently due to recent changes in the SAS (1996) algorithm used for nearest-neighbour discriminant analysis. Nearest-neighbour discriminant analysis results in a greater misclassification rate than parametric discriminant analysis, but was necessary because the data strongly violated the assumptions of parametric discriminant analysis (Stephenson, 1990).

* Significantly fewer correct classifications than for AET and D, or AET and PET ($P < 0.05$ or better; chi-square analysis [1 d.f.] of the number of sites classified correctly by one pair of parameters but incorrectly by the other).

† Significantly fewer correct classifications than for AET/PET and PET ($P < 0.05$ or better, as above).

‡ AET, actual evapotranspiration; D, deficit; PET, potential evapotranspiration; min T, mean temperature of coldest month; P, precipitation; T, temperature; S, surplus. All parameters except min T are annual means.

preferable to use climatic water deficit (PET minus AET—the parameter used by Lenihan) rather than soil water deficit (the difference between the field capacity of a soil and its water content). It is not unusual for two regions with identical soil water deficits (nearly complete soil water depletion) to have very different climatic water deficits and to support different vegetation types. In North America, for example, regions with complete soil water depletion and very high climatic water deficit support warm desert shrublands, whereas regions with complete soil water depletion but lower climatic water deficit may support shortgrass prairie (Stephenson, 1990). Annual AET and D, as they are defined in this paper, are therefore more universally applicable than summertime AET or soil water deficit.

Though the pairs of parameters discussed in this section are functionally similar to AET and D, I believe that the latter are easier to interpret biologically. Unlike AET and D, measure of absolute environmental energy by themselves (such as GDD or PET) cannot be interpreted in physiologically meaningful ways without knowledge of simultaneous water availability (relative or absolute), and vice versa. Similarly, the relative measure AET/PET by itself is difficult to interpret. Use of AET/PET in some studies may partly be motivated by its appearance in an equation used to estimate leaf area index (LAI) (Specht, 1972, 1981). However, AET/PET by itself is not directly related to LAI; soil water dynamics must also be known (Specht, 1972, 1981). AET/PET also has been presumed to be linearly related to net photosynthesis (Specht, 1981), and therefore

has been viewed as an integrated measure of the annual amount of growth-limiting drought stress (or, conversely, moisture availability) on plants (e.g. Prentice *et al.*, 1992; Beerling, Huntley & Bailey, 1995; Huntley *et al.*, 1995; Bugmann, 1996; Skarpe, 1996; Sykes, Prentice & Cramer, 1996). However, given the strong correlation between net primary production and AET alone (Rosenzweig, 1968), the latter interpretations seem likely to be true only when PET is relatively constant. Ultimately, AET or absolute drought (D), instantaneous or integrated, are likely to be physiologically more interpretable than relative moisture availability or drought (such as reflected in AET/PET or D/PET) (e.g. Rosenzweig, 1968; Kramer & Kozlowski, 1979; Jones, 1992; Larcher, 1995).

PROBLEMS WITH SOME OTHER CLIMATIC PARAMETERS

Studies of the climatic controls of vegetation distribution at continental and global scales traditionally have used climatic measures related to energy supply (temperature, potential evapotranspiration, or radiation), water supply (precipitation), their ratios, or related indices. Elsewhere I have demonstrated that these approaches have shared an important problem: they could not distinguish between climates that were similar in annual energy and water supplies but different in their seasonal timing (Stephenson, 1990). Thus they implicitly but falsely assumed that the effects of energy and water on plants were independent. Not surprisingly, then, the distributions of vegetation types

at a continental scale are better correlated with AET and D (or functionally similar pairs), which describe the interactions of energy and water, than with parameters that do not consider interactions (Table 1; Stephenson, 1990).

Because it is frequently invoked as the primary controller of forest physiognomy (e.g. Woodward, 1987; Woodward & Williams, 1987; Arris & Eagleson, 1989; Prentice *et al.*, 1992; VEMAP Members, 1995; Haxeltine & Prentice, 1996), minimum temperatures merits particular attention. While there is no doubt that minimum temperature *per se* affects some plant distributions (Woodward, 1987), it may play only a minor role in determining forest physiognomy. For example, the vast expanses of evergreen coniferous forests in the Pacific Northwest grow where minimum temperatures seemingly should favour broadleaved deciduous forests (Fig. 3; Waring & Franklin, 1979; Woodward, 1987; Prentice *et al.*, 1992). Some authors have suggested that this exception may be due to a special circumstance; namely, summer drought in the Pacific Northwest may shift dominance to coniferous trees (Waring & Franklin, 1979; Woodward, 1987; Prentice *et al.*, 1992). However, Fig. 3 clearly demonstrates that drought *per se* does not determine forest physiognomy; temperate deciduous forests often occur at summer water deficits at least as severe as those experienced by coniferous forests of the Pacific Northwest (Fig. 3; Stephenson, 1990). More important, coniferous forests of the wettest (and warmest) coastal regions of the Pacific Northwest experience, on average, little or no summer water deficit (Fig. 3; Stephenson, 1990; Lenihan & Neilson, 1993).

Another explanation of forest pattern, with a plausible physiological mechanism, is available: site potential for primary production, not minimum temperature, controls the distribution of coniferous and deciduous forests (Bond, 1989; Stephenson, 1990; see also Reich, Walters & Ellsworth, 1992; Reich *et al.*, 1995). In North America, absolute drought (annual D) does not determine forest physiognomy; it only determines whether forest of any kind occupies a site (Stephenson, 1990). Forests occur where annual D is less than about 400 mm, grasslands and shrublands where it is greater (Fig. 2). Forest physiognomy, in contrast, is related to AET, which is a measure of site potential for primary production (Major, 1963; Rosenzweig, 1968). Deciduous forests are favoured when site potential for primary production is relatively high; specifically, annual AET must be greater than about 600 mm (Figs 2 and 3). Coniferous forests, on the other hand, are favoured by low AET, which can be achieved in three ways (Stephenson, 1990): sites may have (1) an annual water supply that is adequate for deciduous forest, but an annual energy supply that is too low (boreal forests of Canada and the northernmost United States, coastal forests of the Pacific Northwest, and high elevation coniferous forests of the inland west of the United States), (2) an annual energy supply that is adequate for deciduous forest, but an annual water supply that is too low (some coniferous forests of the inland west of the United States), or (3) annual energy and water supplies that are both adequate for deciduous forest, except they are asynchronous (coniferous forests of the inland Pacific Northwest, and some low elevation forests of the inland west of the United States). The physiological

mechanism by which site potential for primary production might determine forest physiognomy is discussed elsewhere (Chabot & Hicks, 1982; Bond, 1989; Stephenson, 1990; Kikuzawa, 1991; Reich, Walters & Ellsworth, 1992; Reich *et al.*, 1995).

THE DIFFERING EFFECTS OF EVAPORATIVE DEMAND AND WATER AVAILABILITY

Unlike the studies discussed in the preceding two sections, studies of the climatic controls of vegetation distribution at local to regional scales often have used climatic surrogates rather than direct measures of climate (or indices derived from them). A fundamental problem with many of these surrogates is that they additively combine measures related to evaporative demand and water availability into a single synthetic 'topographic moisture' scalar. This section sets the stage for a demonstration (presented in the next section) of the problems with topographic moisture scalars by demonstrating that (1) the effects of changing evaporative demand on a site's water balance are qualitatively different from the effects of changing water availability, and (2) these differences are reflected in the distribution of vegetation types.

I will make these points using examples from Sequoia National Park, in the southern Sierra Nevada of California. Six sequential subsections briefly examine (1) study site and methods, (2) the effects of evaporative demand on local water balances, (3) the effects of water availability on local water balances, (4) predicted patterns of forest distribution in the southern Sierra Nevada, based on the different effects of evaporative demand and water availability on local water balances, (5) observed patterns of forest distribution in the southern Sierra Nevada, and (6) related studies.

Study site and methods

Sequoia National Park is dominated by a Mediterranean-type climate with dry summers and wet winters (Major, 1977; Stephenson, 1988). The Kaweah watershed of the Park is relatively wet; the Kern watershed, lying to the east in the rain shadow of the Great Western Divide, is relatively dry, receiving only one half to two thirds of the annual precipitation received by the Kaweah watershed (Stephenson, 1988). Locally within both watersheds, water availability is modified by soil water-holding capacity, and evaporative demand is modified by slope aspect and steepness.

Like most mountainous areas, the Sierra Nevada generally lacks the climatic measurements (such as windspeed, humidity, and solar radiation) needed for the most accurate methods of calculating site water balances (Rosenberg, Blad & Verma, 1983). I therefore used the empirical Thornthwaite method (Thornthwaite, Mather & Carter, 1957), which requires only knowledge of temperature and precipitation and has provided good estimates of evapotranspiration as high as 3750 m in the Rocky Mountains (Sharpe, 1970). As elaborated elsewhere (Stephenson, 1988), I used data from twenty-three weather stations and twenty-two snow measurement stations to

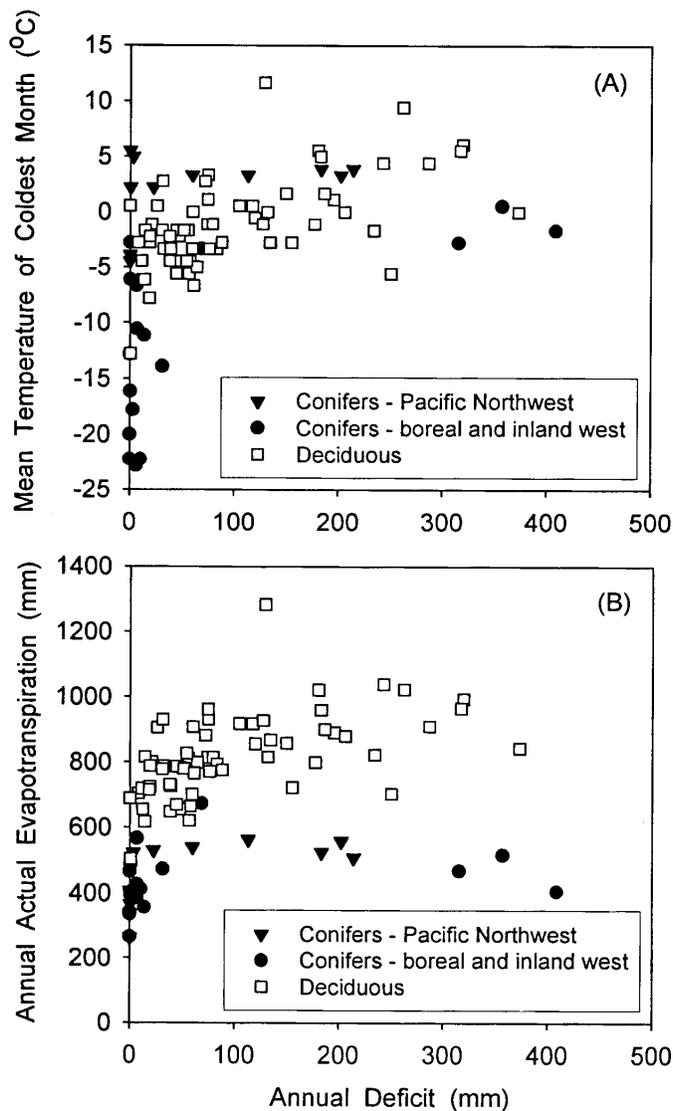


FIG. 3. The distribution of North American coniferous and deciduous forests relative to minimum temperature, AET, and D (cf. Fig. 2). AET and D are climatic measures calculated independently of the actual forest types occupying the sites (see the text). (A) While mean temperature of the coldest month (which is a strong correlate of absolute minimum temperature; Prentice *et al.*, 1992) separates most coniferous forests of the Pacific Northwest from other coniferous forests (a floristic distinction within a physiognomic type), it does not separate coniferous from deciduous forests (physiognomic types). Coniferous and deciduous forests also fail to be distinguished by annual D (a measure of absolute drought), by itself or interacting with minimum temperature. (B) In contrast, the distributions of coniferous and deciduous forests are well correlated with annual AET. (Climatic data are from Eagleman, 1976; forest type data are from the sources listed in Stephenson, 1990. For clarity, mixed forests of coniferous and deciduous trees have been excluded.)

derive watershed-specific lapse rates for temperature, precipitation, and time and rate of snow melt. I then used these lapse rates in conjunction with the Thornthwaite method to derive curves describing elevational changes in AET and D within each watershed, sequentially assuming soil depths of 0, 0.5, and 1.0 m. Water balances of individual forest stands within a watershed were calculated by classifying their soils as either deep (>0.5 m) or shallow (<0.5 m). Local effects of slope aspect and steepness on evaporative demand were classified according to the amount of direct-beam solar radiation potentially reaching a stand (Frank & Lee, 1966). For simplicity, stands with potential

radiation values less than that of level ground were called 'north-facing', whereas those with values greater than level ground were called 'south-facing'. Extreme north-facing and south-facing slopes were arbitrarily assigned PET values 0.9 and 1.1 times that of level ground, respectively.

Forest vegetation data came from 179 tenth-hectare stands, ranging from lower to upper treeline (about 1500–3400 m elevation). Stand locations were chosen independent of forest type by using topographic maps to locate sample sites covering a broad range of elevation, slope steepness, and slope aspect within the two watersheds. Relative basal areas of tree species were used to classify

TABLE 2. Species composition and elevational ranges of the five major forest types sampled in Sequoia National Park, southern Sierra Nevada, California.*

Forest type	Species with >10% basal area	% basal area	Typical elevational range of type (m)
Ponderosa pine forest	<i>Pinus ponderosa</i> Laws.	35%	1500–1900
	<i>Abies concolor</i> (Gordon & Glend.) Lindley	32%	
	<i>Quercus kelloggii</i> Newb.	15%	
	<i>Calocedrus decurrens</i> (Torrey) Florin	12%	
White fir forest	<i>A. concolor</i>	61%	1700–2400
	<i>P. lambertiana</i> Douglas	20%	
	<i>A. magnifica</i> Andr. Murray	13%	
	<i>Sequoiadendron giganteum</i> (Lindley) Buchholz†		
Jeffrey pine forest	<i>P. jeffreyi</i> Grev. & Balf.	51%	1800–2500
	<i>C. decurrens</i>	21%	
	<i>A. concolor</i>	12%	
Red fir forest	<i>A. magnifica</i>	72%	2300–3100
	<i>A. concolor</i>	13%	
Foxtail pine–Lodgepole pine forest	<i>P. contorta</i> Loudon	55%	2600–3400
	<i>P. balfouriana</i> Grev. & Balf.	45%	

* Data are from Stephenson (1988).

† Where giant sequoia (*Sequoiadendron giganteum*) occurs, its basal area overwhelms all others, and therefore was not included in calculations for this table.

TABLE 3. Numbers of sampled forest stands by forest type and factors affecting the local water balance.

Forest type	Wet watershed				Dry watershed	
	Deep soil		Shallow soil		Deep soil	
	North slope	South slope	North slope	South slope	North slope	South slope
Ponderosa pine forest	6	4	0	1	0	1
White fir forest	18	12	0	0	0	0
Jeffrey pine forest	0	5	4	5	7	12
Red fir forest	13	11	1	1	4	1
Foxtail pine–Lodgepole pine forest	0	1	8	4	13	14

stands into eight forest types and eighteen forest sub-types, based on a quantitative key derived from classifications performed by TWINSPAN (Stephenson, 1988). I dropped from analysis those categories of forest stands with too few representatives to draw meaningful conclusions—those in forest types represented by eight or fewer stands, those occurring at wet meadow edges, and those occurring on shallow soils in the dry Kern watershed. This left 146 stands in five major forest types: ponderosa pine, white fir, jeffrey pine, red fir, and foxtail pine–lodgepole pine (Tables 2 and 3). The names and compositions of these forest types are essentially identical to those identified by Rundel, Parsons & Gordon (1977), with the exceptions that I refer to their ‘white fir–mixed conifer’ forest simply as white fir forest, and I lump foxtail pine and lodgepole pine forests (recognizing the abundance of stands containing both species).

I tested the relationships among forest composition, elevation, and slope aspect both by chi-square analysis of Table 3 and by regressing the elevations of stands in fifteen

forest sub-types in the two watersheds against the amount of direct-beam solar radiation potentially received by the stands (Stephenson, 1988). Forest sub-types, rather than types, were used in regressions because the elevational bands occupied by types were so broad as to obscure subtle differences in elevation between north- and south-facing slopes.

As a yardstick for comparison in the following examples, different water balances are compared to that of a reference site on soil 0.5 m deep, on level ground, at 2000 m elevation, and in the wet Kaweah watershed (Fig. 1). This reference site has a calculated annual AET of 330 mm and annual D of 200 mm.

Effects of evaporative demand

On graphs with AET and D plotted as perpendicular axes, the effects of changing evaporative demand on a site’s water balance (assuming constant water availability) always will be limited to the lower left and upper right quadrants

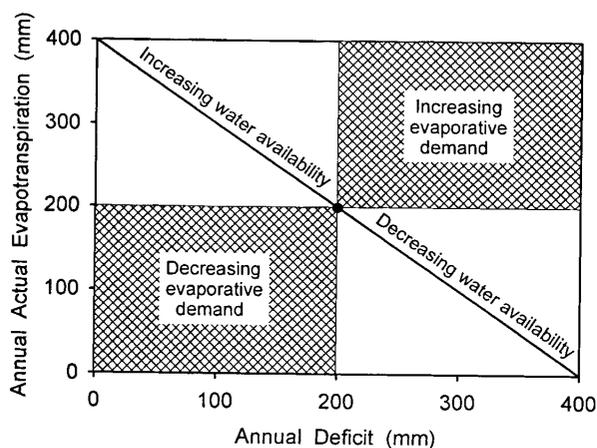


FIG. 4. The differing effects of evaporative demand and water availability on a site's water balance. The point at the middle of the graph represents the water balance of a site with annual AET and D both of 200 mm. Decreasing evaporative demand (assuming constant water availability) can only decrease the site's AET, D, or both; the reverse holds for increasing evaporative demand. The effects of changing evaporative demand are therefore limited to the crosshatched areas. In contrast, the effects of changing water availability (assuming constant evaporative demand) always will be limited to a diagonal line of slope -1 and y -intercept PET (see the text).

defined by perpendicular lines passing through the point representing the site's unmodified water balance (Fig. 4). This is because a decrease in evaporative demand (PET) can only result in no change or a decrease in AET, D, or both; the reverse holds for an increase in evaporative demand. At 2000 m elevation in the wet watershed, increasing northern exposure (that is, decreasing insolation, hence decreasing evaporative demand) leaves annual AET unchanged, while reducing annual D by 54 mm (Fig. 5). In contrast, increasing southern exposure increases both AET (by 13 mm) and D (by 40 mm) (Fig. 5).

In the same (wet) watershed, the water balance on a north-facing slope is similar to that of a site on level ground at higher elevation, whereas the water balance of a south-facing slope is similar to that of a site on level ground at lower elevation (Fig. 5). This is easily explained; both the increased insolation on a south-facing slope and increased temperature at lower elevation act to increase evaporative demand, and both primarily cause an increase in annual D (e.g. see Shreve, 1915; Mowbray & Oosting, 1968). Thus, the effects of changing slope aspect (changing evaporative demand) on site water balances are similar to the effects of changing elevation.

Effects of water availability

In contrast, the effects of changing water availability (assuming constant evaporative demand) always will be limited to a diagonal line of slope -1 and y -intercept PET (Fig. 4). This is because, by definition, $PET = AET + D$; the diagonals thus represent isolines of constant PET (Stephenson, 1990). Since a change in water availability alone does not affect PET, any increase in AET is mirrored

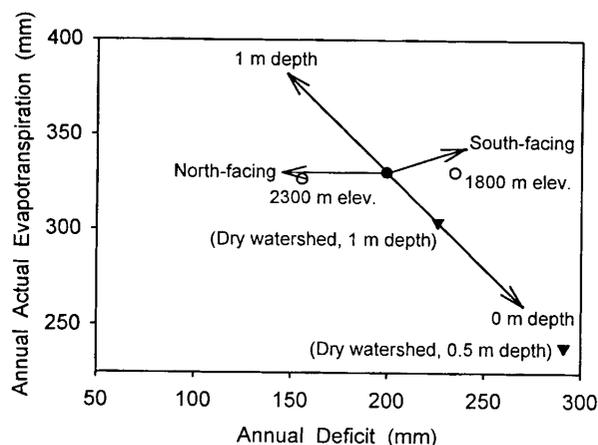


FIG. 5. The effects of slope aspect, soil depth, elevation, and watershed on site water balance in the southern Sierra Nevada. The solid circle at the intersection of the vectors represents conditions on level ground, 0.5 m soil depth, at 2000 m elevation, and in the wet Kaweah watershed (as in Fig. 1). Endpoints of the vectors labelled 'North-facing' and 'South-facing' represent the local effects of changing evaporative demand associated with slope aspect, whereas the endpoints labelled '1 m depth' and '0 m depth' represent the local effects of changing water availability—in this case, soils of 1 m and 0 m depths, respectively. Open circles represent sites on level ground, 0.5 m soil depth, and in the wet watershed, but at 2300 m and 1800 m elevation, respectively. Triangles represent sites on level ground, 0.5 m and 1.0 m soil depth, at 2000 m elevation, but in the dry Kern watershed.

by an equivalent decrease in D, and vice versa. The magnitude of change along the diagonal is a function of both the magnitude of change in water availability and its seasonal interaction with evaporative demand. At 2000 m elevation, increasing soil depth from 0.5 m to 1.0 m (that is, increasing water availability) increases annual AET by 52 mm and decreases annual D by the same amount (Fig. 5). In contrast, decreasing soil depth to near 0 m decreases annual AET by 70 mm and increases D by the same amount (Fig. 5).

Further illustrating the effects of water availability, water balances of sites on deeper soils (0.5 to 1.0 m) in the dry watershed are similar to those on shallow soils (0 to 0.5 m) in the wet watershed (Fig. 5). Thus, the regional effects of decreased precipitation in the dry watershed are similar to the local effects of shallow soils in the wet watershed. Both limit available water, and both cause a decrease in AET mirrored by an identical increase in D.

Predicted forest patterns

The preceding subsections show that evaporative demand and water availability always have different effects on a site's water balance, and I have implied that these differences should be reflected in the composition of local vegetation. For example, a 'dry' south-facing slope should not necessarily support the same vegetation type as a 'dry' site on shallow soil. The distribution of forest types in the southern Sierra Nevada supports these expectations, as I demonstrate in this and the next subsection.

TABLE 4. Pairwise comparisons of expected and observed forest types on sites defined by factors affecting the local water balance.*

Watershed	Soil depth	Slope aspect	Expected forest types	Observed forest types†
wet	deep	NORTH	similar	similar ($P=0.09$)
wet	deep	SOUTH		
wet	shallow	NORTH	similar	similar ($P=0.31$)
wet	shallow	SOUTH		
dry	deep	NORTH	similar	similar ($P=0.22$)
dry	deep	SOUTH		
wet	SHALLOW	all	different	different ($P<0.00001$)
wet	DEEP	all		
WET	deep	all	different	different ($P<0.00001$)
DRY	deep	all		
WET	SHALLOW	all	similar	similar ($P=0.98$)
DRY	DEEP	all		

* Factors being compared in each pair are shown in capital letters.

† P -values are from chi-square analysis (Norusis, 1993) of the data presented in Table 3; P -values >0.05 are taken to indicate that forest types in the comparisons are not significantly different. In individual comparisons, rows with fewer than a total of five observations were eliminated from the analysis.

By examining diagrams showing the relative effects of watershed, soil depth, elevation, and slope aspect on site water balances (e.g. Fig. 5; similar patterns tend to hold at all elevations), I defined four expected patterns of forest composition. First, when all elevations are considered within a given watershed and on a given soil depth, there should be little or no difference in forest types found on north- and south-facing slopes. This is because the effects of slope aspect on local water balances are similar to those of elevation (Fig. 5); within a given watershed and on a given soil depth, then, a specific forest type should be found on both north- and south-facing slopes, only at different elevations. Since the expectation of no difference in forest types with slope aspect was supported (see Tables 3 and 4, and below), I lumped slope aspects in the following analyses.

The second expected pattern is that, when all elevations are considered within a given watershed, the composition of forest stands on deep and shallow soils should differ. This is because at all elevations, sites on shallow soils have substantially lower AET and higher D than sites on deep soils (Fig. 5). Third, on soils of similar depths, the composition of forest stands in the wet and dry watersheds should differ. As in the preceding example, this is because at all elevations the lower precipitation of the dry watershed yields substantially lower AET and higher D than in the wet watershed (Fig. 5). Finally, we would expect forest composition on shallow soils in the wet watershed to be similar to that on deep soils in the dry watershed. The water balances of such sites are similar; one is arid because of low soil water-holding capacity, the other because of a

rainshadow. In both cases water availability is decreased, leading to similar decreases in AET and increases in D (Fig. 5).

Observed forest patterns

Expectations were confirmed in all comparisons (Table 4). Forest types did not differ significantly between north- and south-facing slopes ($P=0.09$ to 0.31), though there was some indication that Jeffrey pine forest may be somewhat more common on south-facing slopes, white fir forest on north-facing slopes (Table 3). As expected, when watershed and soil depth were held constant the primary effect of slope aspect was on the elevation of forest types. Of the fifteen forest sub-types considered, fourteen showed a positive relation between the elevation of the sub-type and potential direct-beam solar radiation (however, only three of these were statistically significant at $P<0.05$; Stephenson, 1988). On average, the elevation of a forest sub-type was about 200 m higher on a steep south-facing slope than a steep north-facing slope (Stephenson, 1988). (The observed elevational difference is less than the >500 m difference suggested by Fig. 5, which is based on arbitrary assumptions of differences in PET on north- and south-facing slopes.)

Forest types differed by soil depth within a watershed ($P<0.00001$), and between watersheds on soils of similar depths ($P<0.00001$). Also as expected, forest types on shallow soils in the wet watershed were similar to those on deep soils in the dry watershed ($P=0.982$). The distributions

TABLE 5. Combinations of factors used in some topographic moisture scalars*.

Scalar name (and authors)	Factors affecting evaporative demand		Factors affecting water availability				
	Aspect or est. solar radiation	Slope exposure	Slope position	Slope config.	Slope steepness	Soil water-holding cap.	Proximity to water
Topographic moisture gradient (Whittaker, 1956, 1960, 1967, 1978, Whittaker & Niering, 1965)	1	2	3				4
Topographic-moisture gradient (Kessell, 1979)	1	3	2				
Topographic potential moisture index (Parker, 1980)	1		1	3	3	3	
Site moisture scalar (Peet, 1981)	1	3	3			2	
Elevation/solar irradiation scalar (Wentworth, 1981)	1	2	3				
Topographic relative moisture index (Parker, 1982a,b, 1988, 1991)	1		1	3	3		
Topographic-moisture gradient (Vankat, 1982)	1		3		2		3
Radiation index (Parker, 1989)	1	2		2			
Topographic moisture index (Allen, Peet & Baker, 1991)	1	1	4	3			

*Numerals represent rank order of weight given to the factors used in creating the scalars. For example, for Whittaker's 'topographic moisture gradient', slope aspect is given the greatest weight in the scalar, whereas proximity to water is given the least. Slope configuration, slope steepness, and soil water-holding capacity were not used in Whittaker's scalar, and therefore have no ranking.

of the forest types relative to annual AET and D are shown in Fig. 6.

Related studies

The effects of evaporative demand described above are similar to those reported by Shreve (1915), who noted that measured evaporative demand in the Santa Catalina Mountains of Arizona decreased with both increasing northern aspect and with increasing elevation. As expected, vegetation types in the Santa Catalina Mountains were found at their lowest elevation on north-facing slopes, and highest elevation on south-facing slopes; the elevational difference between aspects was as much as 500 m (Shreve, 1915; see also Whittaker & Niering, 1965). The general pattern has long been known; vegetation types often occur at higher elevation on sunward slopes than on shaded slopes (e.g. Hall, 1902; Shreve, 1915; Weaver & Clements, 1938; Woodbury, 1947; Oosting, 1956; del Moral & Watson, 1978; Vankat, 1979; Peet, 1988). The pattern is sometimes apparent in 'mosaic diagrams' when a particular moisture scalar is strongly influenced by slope aspect (e.g. Whittaker & Niering, 1965; Peet, 1981, 1988; Wentworth, 1981; Allen, Peet & Baker, 1991). Roise & Betters (1981) have provided a simple mathematical model that can be used to describe the relationship between slope aspect and the elevation of vegetation types.

In contrast to the effects of evaporative demand,

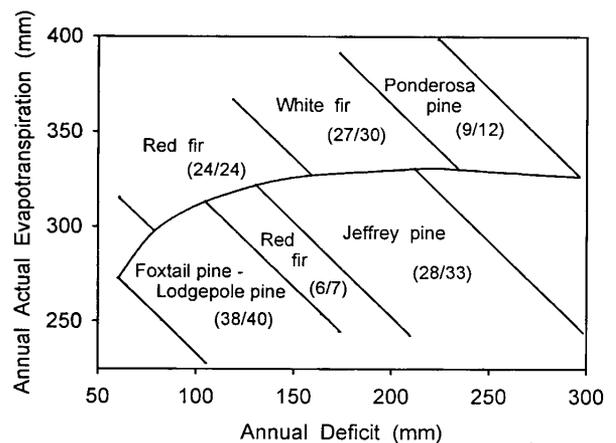


FIG. 6. The distribution of forest types in the southern Sierra Nevada relative to annual AET and D (cf. Fig. 2). Diagonal lines represent constant PET and elevation. The curved central line represents changes in AET and D, at a constant soil depth of 0.5 m in the wet Kaweah watershed, that occur with elevation; elevation increases from right to left along the curve. Areas above the curve are on deep soils (>0.5 m depth) in the wet watershed; areas below the curve are either on shallow soils (<0.5 m depth) in the wet watershed, or on deep soils in the dry Kern watershed. Denominators of the fractions are the number of stands sampled in that forest type; numerators are the number of correctly classified stands—those falling within the boundaries indicated for the types.

differences in site water balances caused by changing soil depth (water availability) in the Sierra Nevada are not similar to those caused by slope aspect or elevation; consequently, entirely different suites of forest types occur on deep soils and shallow soils within a watershed. While other studies in mountainous regions have focussed less on water availability by itself, there is a general tendency for different suites of vegetation types to occur along riparian zones (high water availability) than on adjacent uplands (lower water availability) (e.g. Whittaker & Niering, 1965; Peet, 1988).

PROBLEMS WITH TOPOGRAPHIC MOISTURE SCALARS AND MEASURED SOIL MOISTURE

'...required soil moisture [for plants] may result from favourable atmospheric precipitation, limited evaporation on a northern slope, or soil structure and the proximity of groundwater.' Walter (1985) p. 29.

Statements such as Walter's seem so obvious as to border on trivial. Both intuition and measured soil moisture tell us that sites with high precipitation, on shaded slopes, on soils with high water-holding capacity, or close to groundwater are wetter than their opposites. A seemingly logical conclusion is that sites can be arranged conceptually along a single moisture gradient, meaningful for describing, understanding, and predicting the distribution of plant species or vegetation types. Thus, following Whittaker's lead (Whittaker, 1956, 1960, 1967, 1978; Whittaker & Niering, 1965), many investigators have inferred local moisture conditions by combining, into a single topographic moisture scalar, measures of site factors known to affect both evaporative demand and water availability (Table 5).

However, as suggested by the preceding section, sites having similar values of Whittaker-style moisture scalars (as well as similar measured soil moistures) can exert physiologically different effects on plants. Suppose we define a simple moisture scalar as the sum of values reflecting soil water-holding capacity (ranging from 0 for high-capacity soils to 2 for low-capacity soils) and slope aspect (ranging from 0 for north-facing slopes to 2 for south-facing slopes). The moisture scalar therefore ranges from 0 (very wet: high-capacity soils on north-facing slopes) to 4 (very dry: low-capacity soils on south-facing slopes). Now consider two sites, one on soil with intermediate water-holding capacity (e.g. 0.7 m depth) on a south-facing slope (scalar value of $1 + 2 = 3$), the other on soil with low water-holding capacity (e.g. 0.2 m depth) on flat ground (scalar value of $2 + 1 = 3$). These sites have identical moisture scalar values of 3, and therefore lie toward the dry end of the scale. Also assume that at the beginning of the growing season the water content of soils at both sites was near field capacity, and at the end of the growing season it is near the permanent wilting point. Soil at the first site is dry because, over the course of the growing season, high evaporative demand eventually used up an intermediate amount of available water. Soil at the second site is dry because lower evaporative demand used up the small amount of available water. Over

the course of the growing season, then, plants at the first site had available to them a greater cumulative amount of simultaneously-available energy and water than plants at the second site. Thus, in spite of the sites having similar instantaneous soil moisture contents at the end of the growing season (as reflected by both the moisture scalar and measured soil moisture), the first site has an intrinsically higher potential for primary production (measured as AET) than the second (e.g. see Fig. 5).

Thus, within a region, the cumulative 'dry' experienced by plants on shallow soils is physiologically different from the cumulative 'dry' experienced by plants on south-facing slopes. We therefore should not necessarily expect to find the same vegetation type in both environments—and in fact we do not, as illustrated by the distribution of forest types in the southern Sierra Nevada. The annual water balances of the sites are not comparable; the difference between the environments can be represented meaningfully by a vector (as in Fig. 5), but not by a scalar. Though scalars can summarize instantaneous soil moisture content, two dimensions (AET and D) are needed to summarize the physiologically-relevant moisture dynamics that led to a particular instantaneous moisture content.

Within given regions, some topographic moisture scalars have worked well in spite of additively combining terms related to evaporative demand and water availability. This may be because most scalars are heavily dominated by one set of factors—usually those related to evaporative demand (Table 5). In some cases, then, it may be that moisture scalars have been useful in spite of, not because of, the addition of factors related to water availability. Loucks (1962) recognized the problem of mixing terms in scalars, and therefore formed separate scalars related to evaporative demand ('local climate') and water availability ('moisture regime'). However, as discussed by Loucks, values of separate demand and availability scalars are only useful within small regions of essentially uniform climate.

VEGETATION DISTRIBUTION ACROSS SPATIAL SCALES

As summarized in the preceding sections, AET and D help explain the distribution of vegetation types over several orders of magnitude of spatial scale—from global and continental (Stephenson, 1990; Frank & Inouye, 1994) to local (Stephenson, 1988 and this paper). At progressively finer scales, different suites of factors modify site water balances that otherwise are products of factors operating at broader scales. For example, the general type of water balance found in the Sierra Nevada (summer-dry, winter-wet) is determined by subcontinental-scale climatic patterns. This broad, subcontinental-scale water balance determines the physiognomy of vegetation—in this case, evergreen coniferous forest (Fig. 2). The subcontinental-scale water balance is in turn modified by factors operating at a regional scale, such as rainshadows. Regional effects determine broad patterns of floristic composition within the physiognomic type. On deep soils in the southern Sierra Nevada, forest types dominated by fir mostly occur in the wet Kaweah watershed; those dominated by pine mostly occur in the dry

Kern watershed (Table 3; Fig. 6). Regional water balances, in turn, are further modified by factor operating at local scales, such as slope aspect and soil water-holding capacity. These local modifications sometimes exactly counteract regional influences on floristic composition; for example, in the southern Sierra Nevada forest types dominated by pine, not fir, occur on shallow soils in the wet watershed (Table 3). Even though different aspects of the physical environment are influencing water balances at each scale (continental, regional, and local), their effects on vegetation are linked through the water balance, as represented by AET and D.

DISCUSSION AND CONCLUSIONS

No single set of climatic parameters has been widely accepted as a standard in correlative studies of vegetation distribution (e.g. see Tuhkanen, 1980). In part, this is because our understanding of the climatic controls of vegetation distribution is still maturing. I suggest that the field of parameters can be narrowed to those representing aspects of climate that (1) are of broad physiological importance to plants under a wide range of climatic conditions (meaning that the parameters must consider the interactions of energy and water), (2) are well correlated with vegetation distribution (which should automatically follow), and (3) exhibit these characteristics over a broad range of spatial scales. AET and D form one set of parameters meeting these criteria.

However, parameters not meeting all of the above-mentioned criteria have performed well in many published studies. In some cases this is because the parameters work well under conditions unique to a given study, but may lack generality (Tuhkanen, 1980). For example, for regions in which the seasonal timing of water availability relative to demand is spatially relatively consistent, changes in availability or demand will be approximately paralleled by changes in AET and D. However, unless AET and D (or functionally similar parameters) are explicitly used, problems will arise at spatial scales large enough to include climates similar in absolute annual water availability and demand, but different in the seasonal timing of the two (Stephenson, 1990). Similarly, topographic moisture scalars, even if their effectiveness were not harmed by combining terms related to water availability and demand, cannot be compared meaningfully among regions (Loucks, 1962).

Many researchers performing correlative studies have acknowledged that the interactions of energy and water are important, yet have not calculated water balances. Is it impractical to expect widespread use of AET and D, given that some of the data needed to accurately calculate site water balances (e.g. solar radiation, humidity, wind speed) often are lacking? I suggest that in many cases it may be better to use even the crude (and sometimes maligned) Thornthwaite or Holdridge methods of calculating site water balances, which require only knowledge of temperature and precipitation, than to not consider the interactions of energy and water at all.

Though I have emphasized the importance of the direct physiological effects of AET and D in determining vegetation distribution, some important effects may be

indirect. For example, site productivity and decomposition rates, both of which are strongly related to AET, may influence fire frequency and intensity. Fire frequency and intensity, in turn, can exert tremendous influence on life-form or species composition (Stephenson, 1990; Barton, 1993). Through its influence on litter decomposition rates and parent-material weathering rates, AET also affects soil fertility. Thorough studies of mechanisms therefore must include the indirect effects of the climatic water balance, particularly as it affects disturbance regimes and soil properties.

While AET and D are useful measures of climate across spatial scales, by themselves they are neither complete nor perfect. Other aspects of climate, such as temperature extremes, undoubtedly play a role in controlling plant distributions. Additionally, while more closely representing physiologically important aspects of climate than many other measures of climate, AET and D still are imperfect measures of climate as it is sensed by plants. As I have suggested elsewhere (Stephenson, 1990), future research might explore replacing AET and D with two related measures of the interactions of energy and water in the environment: (1) integrated solar radiation over periods when soil moisture is adequate for a predefined 'standard crop' to maintain open stomata, and (2) integrated solar radiation over periods when soil moisture is inadequate for the same crop to maintain open stomata.

Clearly, correlative studies continue to play a role in expanding our understanding of the climatic controls of vegetation distribution. For example, correlations I have summarized here show that the distributions of coniferous and deciduous forests are more strongly related to annual AET than to minimum temperature, suggesting that forest physiognomy may be determined by site potential for primary production, not temperature. Such correlations can help focus ecophysiological research aimed at further elucidating mechanisms.

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REFERENCES

- Allen, R.B., Peet, R.K. & Baker, W.L. (1991) Gradient analysis of latitudinal variation in Southern Rocky Mountain forests. *J. Biogeogr.* **18**, 123–139.

- Arkley, R.J. (1967) Climates of some great soil groups of the western United States. *Soil Sci.* **103**, 389–400.
- Arris, L.L. & Eagleson, P.S. (1989) Evidence of a physiological basis for the boreal-deciduous forest ecotone in North America. *Vegetatio*, **82**, 55–58.
- Barton, A.M. (1993) Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. *Ecol. Monogr.* **63**, 367–397.
- Berling, D.J., Huntley, B. & Bailey, J.P. (1995) Climate and the distribution of *Fallopia japonica*: use of an introduced species to test the predictive capacity of response surfaces. *J. Veg. Sci.* **6**, 269–282.
- Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., Calvo de Anta, R., Couteaux, M., Escudero, A., Gallardo, A., Kratz, W., Madeira, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V., Muñoz, F., Piussi, P., Remacle, J. & Virzo de Santo, A. (1993) Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.
- Bond, W.J. (1989) The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Linn. Soc.* **36**, 227–249.
- Box, E.O. (1981) *Macroclimate and plant form*. Junk, The Hague.
- Box, E.O. (1995) Factors determining distributions of tree species and plant functional types. *Vegetatio*, **121**, 101–116.
- Budyko, M.I. (1974) *Climate and life*. Academic Press, New York.
- Bugmann, H. (1996) Functional types of trees in temperate and boreal forests: classification and testing. *J. Veg. Sci.* **7**, 359–370.
- Bunce, J.A., Chabot, B.F. & Miller, L.N. (1979) Role of annual leaf carbon balance in the distribution of plant species along an elevational gradient. *Bot. Gaz.* **140**, 288–294.
- Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf life spans. *Annu. Rev. Ecol. Syst.* **13**, 229–259.
- Cramer, W. (1997) Using plant functional types in a global vegetation model. *Plant functional types* (ed. by T.M. Smith, H.H. Shugart and F.I. Woodward), pp. 271–288. Cambridge University Press, Cambridge.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant species richness. *Am. Nat.* **137**, 27–49.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**, 326–327.
- del Moral, R. & Watson, A.F. (1978) Gradient structure of forest vegetation in the central Washington Cascades. *Vegetatio*, **38**, 29–48.
- Eagleman, J.R. (1976) *The visualization of climate*. Lexington Books, Lexington, Mass.
- Frank, D.A. & Inouye, R.S. (1994) Temporal variation in actual evapotranspiration of terrestrial ecosystems: patterns and ecological implications. *J. Biogeogr.* **21**, 401–411.
- Frank, E.C. & Lee, R. (1966) *Potential solar beam irradiation on slopes*. U.S. Dept. Agric., Forest Service, Research Paper RM-18.
- Hall, H.M. (1902) A botanical survey of San Jacinto Mountain. *Univ. Calif. Publ. Bot.* **1**, 1–140.
- Haxeltine, A. & Prentice, I.C. (1996) BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochem. Cycles*, **10**, 693–709.
- Holdridge, L.R. (1967) *Life zone ecology*, rev. edn. Tropical Science Center, San Jose, Costa Rica.
- Huntley, B., Berry, P.M., Cramer, W. & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J. Biogeogr.* **22**, 967–1001.
- Jones, H.G. (1992) *Plants and microclimate*, 2nd edn, Cambridge University Press, Cambridge.
- Kessell, S.R. (1979) *Gradient modeling: resource and fire management*. Springer-Verlag, New York.
- Kikuzawa, K. (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am. Nat.* **138**, 1250–1263.
- Kramer, P.J. & Kozlowski, T.T. (1979) *Physiology of woody plants*. Academic Press, New York.
- Larcher, W. (1995) *Physiological plant ecology*, 3rd edn. Springer-Verlag, Berlin.
- Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.
- Lenihan, J.M. (1993) Ecological response surfaces for North American boreal tree species and their use in forest classification. *J. Veg. Sci.* **4**, 667–680.
- Lenihan, J.M. & Neilson, R.P. (1993) A rule-based vegetation formation model for Canada. *J. Biogeogr.* **20**, 615–628.
- Lieth, H. (1956) Ein Beitrag zur Frage der Korrelation zwischen mittleren Klimawerten und Vegetationsformationen. *Ber. Dtsch. Bot. Ges.* **69**, 169–176.
- Lieth, H. (1975) Modeling the primary productivity of the world. *Primary productivity of the biosphere* (ed. by H. Lieth and R.H. Whittaker), pp. 237–263. Springer, New York.
- Lieth, H. (1976) The use of correlation models to predict primary productivity from precipitation or evapotranspiration. *Water and plant life* (ed. by O.L. Lange, L. Kappen and E.-D. Schulze), pp. 392–407. Springer, New York.
- Loucks, O.L. (1962) Ordinating forest communities by means of environmental scalars and phytosociological indices. *Ecol. Monogr.* **32**, 137–166.
- Major, J. (1951) A functional, factorial approach to plant ecology. *Ecology*, **32**, 392–412.
- Major, J. (1963) A climatic index to vascular plant activity. *Ecology*, **44**, 485–498.
- Major, J. (1977) California climate in relation to vegetation. *Terrestrial vegetation of California* (ed. by M.G. Barbour and J. Major), pp. 11–74. Wiley, New York.
- Martin, P. (1992) Vegetation responses and feedbacks to climate: a review of models and processes. *Clim. Dyn.* **8**, 201–210.
- Mather, J.R. (1974) *Climatology: fundamentals and applications*. McGraw-Hill, New York.
- Mather, J.R. (1985) The water budget and the distribution of climates, vegetation and soils. *Publ. Climatol.* **38**, 1–36.
- Mather, J.R. & Yoshioka, G.A. (1968) The role of climate in the distribution of vegetation. *Ann. Ass. Am. Geogr.* **58**, 29–41.
- Meentemeyer, V. (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465–472.
- Mowbray, T.B. & Oosting, H.J. (1968) Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. *Ecol. Monogr.* **38**, 309–344.
- Neilson, R.P. (1995) A model for predicting continental-scale vegetation distribution and water balance. *Ecol. Appl.* **5**, 362–385.
- Norusis, M.J. (1993) *SPSS for Windows: Base system user's guide, release 6.0*. SPSS Inc., Chicago.
- Oosting, H.J. (1956) *The study of plant communities*, 2nd edn. W.H. Freeman & Co., San Francisco.
- Parker, A.J. (1980) Site preferences and community characteristics of *Cupressus arizonica* Greene (Cupressaceae) in southeastern Arizona. *Southwest Nat.* **25**, 9–22.
- Parker, A.J. (1982a) The topographic relative moisture index: an approach to soil-moisture assessment in mountain terrain. *Phys. Geogr.* **3**, 160–168.
- Parker, A.J. (1982b) Environmental and compositional ordinations of conifer forests in Yosemite National Park, California. *Madroño*, **29**, 109–118.

- Parker, A.J. (1988) Stand structure in subalpine forests of Yosemite National Park, California. *For. Sci.* **34**, 1047–1058.
- Parker, A.J. (1989) Forest/environment relationships in Yosemite National Park, California, USA. *Vegetatio*, **82**, 41–54.
- Parker, A.J. (1991) Forest/environment relationships in Lassen Volcanic National Park, California, U.S.A. *J. Biogeogr.* **18**, 543–552.
- Peet, R.K. (1981) Forest vegetation of the Colorado Front Range. *Vegetatio*, **45**, 3–75.
- Peet, R.K. (1988) Forests of the Rocky Mountains. *North American terrestrial vegetation* (ed. by M.G. Barbour and W.D. Billings), pp. 63–101. Cambridge University Press, Cambridge.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.
- Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62**, 365–392.
- Reich, P.B., Koike, T., Gower, S.T. & Schoettle, A.W. (1995) Causes and consequences of variation in conifer leaf life-span. *Ecophysiology of coniferous forests* (ed. by W.K. Smith and T.M. Hinckley), pp. 225–254. Academic Press, San Diego.
- Roise, J.P. & Better, D.R. (1981) An aspect transformation with regard to elevation for site productivity models. *For. Sci.* **27**, 483–486.
- Rosenberg, N.J., Blad, B.L. & Verma, S.B. (1983) *Microclimate: the biological environment*, 2nd edn. Wiley, New York.
- Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *Am. Nat.* **102**, 67–74.
- Rundel, P.W., Parsons, D.J. & Gordon, D.T. (1977) Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. *Terrestrial vegetation of California* (ed. by M.G. Barbour and J. Major), pp. 559–599. Wiley, New York.
- SAS (1996) *Release 6.12*. SAS Institute, Inc. Cary, NC.
- Shao, G. & Halpin, P.N. (1995) Climatic controls of eastern North American coastal tree and shrub distributions. *J. Biogeogr.* **22**, 1083–1089.
- Sharpe, D.M. (1970) The effective climate in the dynamics of alpine timberline ecosystems in Colorado. *Publ. Climatol.* **23**, 1–82.
- Shreve, F. (1915) *The vegetation of a desert mountain range as conditioned by climatic factors*. Cargenie Institute of Washington Publ. no. 217, Washington, D.C.
- Skarpe, C. (1996) Plant functional types and climate in a southern African savanna. *J. Veg. Sci.* **7**, 397–404.
- Sowell, J.B. (1985) A predictive model relating North American plant formations and climate. *Vegetatio*, **60**, 103–111.
- Specht, R.L. (1972) Water use by perennial evergreen plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* **20**, 273–299.
- Specht, R.L. (1981) Growth indices—their rôle in understanding the growth, structure and distribution of Australian vegetation. *Oecologia*, **50**, 347–356.
- Stephenson, N.L. (1988) *Climatic control of vegetation distribution: the role of the water balance with examples from North America and Sequoia National Park, California*. Ph.D. dissertation, Cornell University, Ithaca.
- Stephenson, N.L. (1990) Climatic control of vegetation distribution: the role of the water balance. *Am. Nat.* **135**, 649–670.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.* **23**, 203–233.
- Tchebakova, N.M., Monserud, R.A., Leemans, R. & Golovanov, S. (1993) A global vegetation model based on the climatological approach of Budyko. *J. Biogeogr.* **20**, 129–144.
- Thorntwaite, C.W. (1948) An approach toward a rational classification of climate. *Geogr. Rev.* **38**, 55–94.
- Thorntwaite, C.W. & Mather, J.R. (1955) The water balance. *Publ. Climatol.* **8**, 1–86.
- Thorntwaite, C.W., Mather, J.R. & Carter, D.B. (1957) Instructions and tables for computing potential evapotranspiration and the water balance. *Publ. Climatol.* **10**, 183–311.
- Tuhkanen, S. (1980) Climatic parameters and indices in plant geography. *Acta Phytogeogr. Suecica*, **67**, 1–105.
- Vankat, J.L. (1979) *The natural vegetation of North America*. John Wiley & Sons, New York.
- Vankat, J.L. (1982) A gradient perspective on the vegetation of Sequoia National Park, California. *Madroño*, **29**, 200–214.
- Velázquez, A. (1994) Multivariate analysis of the vegetation of the volcanoes Tláloc and Pelado, Mexico. *J. Veg. Sci.* **5**, 263–270.
- VEMAP Members (1995) Vegetation/ecosystem modeling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochem. Cycles*, **9**, 407–437.
- Walter, H. (1985) *Vegetation of the Earth and ecological systems of the geo-biosphere*, 3rd edn. Springer-Verlag, Berlin.
- Waring, R.H. & Franklin, J.F. (1979) Evergreen coniferous forests of the Pacific Northwest. *Science*, **204**, 1380–1386.
- Weaver, J.E. & Clements, F.E. (1938) *Plant ecology*, 2nd edn. McGraw-Hill, New York.
- Wentworth, T.R. (1981) Vegetation on limestone and granite in the Mule Mountains, Arizona. *Ecology*, **62**, 469–482.
- Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecol. Monogr.* **26**, 1–80.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**, 279–338.
- Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biol. Rev.* **49**, 207–264.
- Whittaker, R.H. (1975) *Communities and ecosystems*, 2nd edn. Macmillan, New York.
- Whittaker, R.H. (1978) Direct gradient analysis. *Ordination of plant communities* (ed. by R.H. Whittaker), pp. 7–50. Dr W. Junk, The Hague.
- Whittaker, R.H. & Niering, W.A. (1965) Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology*, **46**, 429–452.
- Woodbury, A.M. (1947) Distribution of pigmy conifers in Utah and Northeastern Arizona. *Ecology*, **28**, 113–126.
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge University Press, Cambridge.
- Woodward, F.I. & Williams, B.G. (1987) Climate and plant distribution at global and local scales. *Vegetatio*, **69**, 189–197.

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