



Simulating vegetational and hydrologic responses to natural climatic variation and GCM-predicted climate change in a semi-arid ecosystem in Washington, U.S.A.

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An ecosystem process model was used to assess likely ecosystem responses to natural climatic variation and GCM-predicted climatic change in the semi-arid north-western U.S.A. Simulated equilibrium conditions between soil water availability and leaf area were compared to long-term natural variations for annual grass and mixed sagebrush/bunchgrass communities subjected to 2°C increases in daily temperature, coupled with 10% increases and decreases in precipitation. Equilibrium simulations suggested that a less productive, invasive grass community would tolerate climate change, whereas a native sagebrush community would not survive the increased temperatures predicted by GCMs. High air temperatures, and the subsequent increases in vapor pressure deficit, caused decreased stomatal conductance, and hence decreased net photosynthesis. High air temperatures also increased maintenance respiration, leading to decreases in net primary production. As the productivity of this community declined, substantial increases in soil water storage occurred. When natural variation of annual weather is incorporated into simulations, both community types were able to survive by adjusting levels of biomass production. Soil water storage was not significantly affected when the vegetation adapted to increased or decreased precipitation through proportional adjustments to leaf area, which in turn dictates evapo-transpiration and soil water drawdown.

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Introduction

Productivity in semi-arid ecosystems is highly dependent on annual climatic fluctuations that determine the temporal and spatial availability of soil water (Martin *et al.*, 1989; Donovan & Ehleringer, 1992). Community vegetation characteristics such as phenology and leaf area in turn determine the timing and magnitude of soil water withdrawal and evapo-transpiration (ET). In order to model the influence of climatic

change on the dynamics of vegetation and ground-water in these ecosystems, it is important to simulate the natural balance that exists between water limitations and vegetation structure. This study incorporates an ecosystem process model, which simulates the dynamics of carbon, nitrogen and water in hydrologically and vegetationally distinct vegetation communities within the sagebrush-steppe biome, to evaluate ecosystem-level responses to both natural climatic variation and projected long-term climatic changes.

Much attention has been given in recent years to the potential for general circulation models (GCMs) to determine the climatic consequences of increasing atmospheric trace gases, primarily CO₂. Hansen *et al.* (1988) represent a consensus among model outputs, predicting mean global surface temperature increases of 2–5°C with doubled atmospheric CO₂ concentrations (also see Manabe & Stouffer, 1980; Schlesinger, 1983, 1984; Schlesinger & Mitchell, 1987; Rowntree, 1988; Mitchell, 1989). Local, regional, and global hydrologic feedbacks to increased temperatures are so numerous and complex, however, that predictions of resulting precipitation changes are far less consistent. Mean global precipitation change estimates range from +15%, due to increased atmospheric moisture (review by Mitchell, 1989), to –21%, due to increased surface albedo that may decrease convective activity (review by Rowntree, 1988). Consequently, predictions of soil water availability resulting from climatic changes are equally variable. Soil moisture relies on interactions of temperature, precipitation, vegetation, and albedo changes, and is highly variable both seasonally and geographically (Schlesinger, 1984; Dickinson, 1986; Schlesinger & Mitchell, 1987; Mitchell, 1989). Because of the agricultural and socio-economic importance of soil water to plant production, however, it may be one of the most important aspects of future climate change (Gleick, 1986).

A key consideration in the assessment of climate change on terrestrial ecosystems is that natural, inter-annual climatic variation may far exceed predictions of mean annual changes caused by increased greenhouse gases. For example, in 59 years of climatic data for our south-central Washington study site, annual precipitation ranged from 91.3 mm to 348.5 mm, a difference of nearly 400%. When viewed in this light, simulating the effects of 10% variations in precipitation predicted by GCMs seems insignificant. However, natural variation acts to create 'average' climatic conditions to which local vegetation may be ideally adapted, and successional response times, for example, exceed the temporal variation of climate (e.g. Woodward, 1987). Changes predicted by GCMs, on the other hand, represent long-term trends that may skew average conditions and create new equilibria between soil water availability and vegetation productivity, or lead to community succession.

Elevated levels of atmospheric CO₂ are a primary constituent of global climate change, and have been found to increase photosynthesis in C₃ plants while decreasing stomatal conductance to H₂O. Cure & Acock (1986), Mooney *et al.* (1991) and Field *et al.* (1992) provide excellent reviews. In general, elevated levels of CO₂ enhance photosynthesis by creating greater internal CO₂ concentrations, thereby increasing the activity of rubisco, and consequently carbohydrate production. While the biophysical mechanism by which stomatal conductance is decreased is still unclear (Field *et al.*, 1992), reductions of 30–50% are commonly found in herbaceous plants (e.g. Mooney *et al.*, 1991). The result of these simultaneous physiological effects is greater efficiency of water use (greater photosynthesis/transpiration ratio), an important factor in water-limited environments.

The objective of this paper is to quantify changes in vegetation biomass and soil water storage of distinct sagebrush-steppe communities under a broad range of long-term climate change scenarios, both with and without direct effects of CO₂. Using the hydrologic equilibrium theory of Grier & Running (1977) and Nemani & Running (1989), we predict changes in vegetation biomass, and suggest a potential for changes in community composition, emphasizing leaf area index (LAI) as a primary control

over photosynthesis, evapo-transpiration, and soil water. Our primary interest is the hydrologic balance of the water-limited intermountain north-western U.S.A., which may determine survival and/or succession of sagebrush–steppe communities.

Methods

Ecosystem model

We use a modification of *FOREST-BGC* (BioGeochemical Cycles), a process-level simulation model that was designed to calculate the cycling of carbon, nitrogen, and water through forest ecosystems (Running & Coughlan, 1988). In a related paper (Kremer & Running, 1996), this modified version of the model was used to simulate the water and nutrient dynamics of three hydrologically and morphologically distinct vegetation communities in the intermountain sagebrush–steppe of south-central Washington. Simulations produced steady state estimates of biomass and soil water storage under contrasting climate years for each of the community types. Seasonal soil water content was predicted with R^2 values of 0.93, 0.94, and 0.98 for cheatgrass, bunchgrass, and sagebrush communities, respectively, while maintaining biomass estimates within 15% of initial, measured values. Complete descriptions of the original model, *FOREST-BGC*, can be found in Running & Coughlan (1988) and Running & Gower (1991).

As a brief summary of the relevant model functions (Running & Nemani, 1991; Running & Gower, 1991), daily precipitation is routed to snowpack or soil, depending on air temperature. A canopy interception fraction based on LAI is subtracted and evaporated, and the remaining water goes into a soil compartment where it is available for transpiration. This model version also incorporates a bare soil evaporation component that reduces the amount of precipitation that is available for transpiration. Based on precipitation/potential evapo-transpiration estimates from Thornthwaite (1948), Stone *et al.* (1983) and Gee *et al.* (1988), an ‘effective precipitation’ of 75% was used, meaning 25% of precipitation is treated as bare soil evaporation, and is not included in soil water recharge. Transpiration is calculated with a Penmon–Monteith equation incorporating radiation and vapor pressure deficit drivers for evaporation. The canopy conductance term is a function of air temperature, vapor pressure deficit, incident radiation, and leaf water potential (determined daily from soil water fraction).

Canopy photosynthesis is calculated by multiplying a CO_2 diffusion gradient by a mesophyll CO_2 conductance and the canopy water vapor conductance, both of which are controlled by radiation and temperature. The model emphasizes LAI as a key structural attribute with substantial control over ecosystem process rates. Carbon available for leaf growth, and the allocation of photosynthate between above- and below-ground portions of the plant is a dynamic function of both water and nitrogen limitations. Leaf growth is modified by leaf water status, which is determined by the ratio of the highest simulated predawn leaf water stress to a defined maximum leaf water stress, set to -5.0 mPa in *ARID-BGC*. This modification allows the model to produce more leaf area the following year if maximum water stress is not reached, but provides a feedback control lowering LAI if maximum water stress is exceeded. Direct effects of CO_2 are simulated by increasing net photosynthesis by 30% after transpiration has been calculated, thus increasing the PSN/transpiration ratio (water use efficiency).

Simulation equilibrium under a given climate was considered to be the point at which a mutual sustainability of available soil water and vegetation biomass has been reached, and induced changes in either or both components would be expected to change the magnitude and/or proportion of this relationship. Equilibriums between

the climate years and simulated above-ground net primary productivity (ANPP) were achieved by repeating annual simulations until there were no changes in ANPP or soil water predictions from year to year. Baseline simulations were performed to establish equilibrium conditions using an 'average' climate year. As a gauge of model robustness, equilibrium conditions were also simulated by repeating climate years which represent extremes of temperature and precipitation. Finally, the model was run with 59 years of actual climate data (i.e. without repeating years), and with the same 59 years modified by GCM conditions. Climate data used is explained in greater detail below.

Study site

ARID-BGC parameterization and validation were performed with data from the Arid Land Ecology Reserve (ALE), a portion of the Department of Energy's Hanford Reservation in south-central Washington. ALE covers approximately 312 km², and represents a mosaic of three distinct vegetation communities, each of which is responsible for substantial variations in spatio-temporal patterns of soil water storage and evapo-transpiration (ET) (Kremer & Running, 1993). Precipitation across the reserve averages 18 cm, most of which occurs in the winter months, with a pronounced mid-summer dry season in most years (Stone *et al.*, 1983). Monthly mean temperatures range from -1.7°C in January to 24.4°C in July. Temperature variation in the winter months is more than twice the magnitude of summer variation (Stone *et al.*, 1983). Potential evapo-transpiration (PET) in this region far exceeds precipitation inputs, and actual ET is generally equal to precipitation (West, 1983; Gee *et al.*, 1988). High PET and fine silt loam soils of high water capacity combine to mitigate the potential for deep soil drainage. However, in extremely wet years or in the absence of vegetation (e.g. anthropogenic disturbance), significant amounts of soil water may pass below the root zone (Gee *et al.*, 1988). Surface runoff is possible during heavy rainfall events, but is typically insignificant with respect to annual hydrologic balances (Gee *et al.*, 1988).

To illustrate the effects of natural, past climate variation and projected future scenarios, we simulate the dynamics of the two most contrasting communities with respect to vegetation biomass and soil water utilization: a sagebrush (*Artemisia tridentata* Nutt.)-dominated community, and a cheatgrass (*Bromus tectorum* L.) community. A thorough description of the structural and hydrologic aspects of each community is provided by Rickard & Vaughan (1988), and Kremer & Running (1993).

Climate data

National Climatic Data Center data for Prosser, Washington, approximately 30 km north-west of ALE, provided the longest continuous, local, daily climate record, from 1931 through 1989. The data reveal high natural variation of daily maximum and minimum air temperature and precipitation. For extreme year simulations, 4 years were chosen from this record to represent extremes in maximum and minimum annual precipitation, and maximum and minimum average daily temperature for the 59-year record. Table 1 summarizes the climatic data for those 4 years. Data from the Hanford Meteorological Station for 1991 were used to represent an 'average' climate year. With respect to annual precipitation, and maximum and minimum daily temperatures, 1991 deviates less than 10% from long-term average conditions at the site. For projected climate change scenarios, daily maximum and minimum temperatures were increased 2°C, and combined with 10% increases or decreases in the magnitude and frequency

Table 1. Precipitation and temperature characteristics of the various climate years used in equilibrium simulations

	Mean (1991)	Max. temp (1934)	Min. temp. (1985)	Max. ppt. (1983)	Min. ppt. (1976)	Temp	GCM Inc.	scenarios Dec.
Precipitation	200	172(-14)	154(-23)	349(+75)	91(-55)	200	220(+10)	180(-10)
Av. max. daily temp.	19.3	20.2(+5)	15.8(-18)	17.4(-10)	17.3(-10)	21.3(+10)	21.3	21.3
Av. min. daily temp.	5.6	5.5(-2)	3.1(-45)	4.0(-29)	3.0(-46)	7.6(+36)	7.6	7.6

Numbers in parentheses represent the percent change from 1991. Climate years were chosen to represent: maximum average annual temperature (1934); minimum average annual temperature (1985); high annual precipitation (1983); low annual precipitation (1976). All GCM scenarios (Temp, Inc, and Dec) include a 2°C increase in daily maximum and minimum temperature. Inc adds 10% precipitation, Dec decreases precipitation by 10%.

of precipitation. Current GCMs do not provide information about the form of precipitation changes, and therefore do not predict, for example, whether an additional 10% precipitation will come in the form of an increased number of events, or as a greater magnitude per event. The climate files were designed so that we could assess the ecological significance, if any, of magnitude *vs.* frequency changes in precipitation. Magnitude changes were incorporated by changing the amount in each event by 10%. Frequency changes used a random number table to select zero precipitation days on which evenly to distribute the increased precipitation, or the precipitation days on which to subtract. For example, because 1991 had 80 precipitation event days, a 10% increase in frequency distributed two additional cm of precipitation (10% of 1991 total) on eight random yeardays, each receiving 0.25 cm.

All climate files were corrected for topographical differences between the meteorological station and ALE using a microclimate simulation model, *MT-CLIM* (Running *et al.*, 1987). *MT-CLIM* uses basic meteorological principles to correct for variations in slope, aspect, elevation, and horizon angle, and generates site-specific daily files of maximum and minimum temperatures, average temperature, relative humidity, insolation, and precipitation.

Phenology

Plant phenological response to future climates will be dictated by complex interactions of soil temperature, soil water availability, radiation, and plant genotypic or phenotypic characteristics. In the sagebrush–steppe region, spring greenup is largely controlled by soil temperature, and summer senescence by soil water and absolute humidity deficits. To assess the effect that both annual climatic fluctuations and increased temperatures of GCM climatic scenarios might have on ecosystem dynamics, we incorporated a simple phenology subroutine that triggers greenup when a specified combination of soil water content and running mean air temperature is achieved. Sims *et al.* (1978) use a 15-day running mean daily air temperature of 4.4°C to signal the beginning of the thermal potential growing season for ALE. This estimate puts the start of the growing season at day 29 in 1992, a year in which the cheatgrass community was first observed to be actively growing on day 30 (Kremer & Running, 1993). Assuming winter soil water accumulation is sufficient, this running mean from Sims *et al.* (1978) provides a reasonable empirical standard on which to base the timing of spring greenup. Vegetation senescence is triggered when soil water deficits reach a user-specified threshold, set here as –3.5 mPa for cheatgrass and –6.5 for sagebrush. A late season daylength threshold prevents errant greenup in the grass version of the model in case warm spells or heavy late summer precipitation occurs when phenotypical growing seasons have expired. To represent the evergreen nature of sagebrush, that version of the model does not contain a daylength trigger, allowing vegetation to photosynthesize whenever temperature and soil moisture conditions permit. Although the temperature, soil moisture, and daylength triggers used in these simulations are purely empirical, all are user-specified, and more general phenological principals may be incorporated if known. The routine creates dynamic phenologic response, altering the length and timing of the growing season from year to year in multiple-year simulations.

Model simulations

Six sets of simulations were performed using *ARID-BGC*:

- (1) Validation of simulated ANPP, using meteorological data for 1971–1974.
- (2) Baseline equilibrium, using 1991 as an average climate year.

- (3) Equilibria using extreme climate years.
- (4) Equilibria of average year modified by GCM scenarios.
- (5) Long-term simulations using 59 years of actual meteorological data.
- (6) Long-term simulations modified by GCM scenarios.

The purpose of each of the simulation sets is as follows.

Validation

ANPP data collected at ALE between 1971 and 1974 provided a test of the ability of the model to simulate ecosystem response to climate variation. The range of precipitation in these 4 years is 147–263 mm, with measured ANPP in the range 950–1440 g m⁻² (Sims *et al.*, 1978; Rickard & Vaughan, 1988). We ran ARID-BGC using climate files for 1971–1974, and compared predicted ANPP for the 4 years to measured field data as an assessment of the models simulation accuracy under variable climatic conditions.

Baseline

Equilibrium leaf area and soil water estimates for 1991 are used as baselines from which to compare extreme year and GCM simulations. Leaf area and soil water values simulated for this equilibrium represent the balance between above-ground biomass and available soil water that is reached through consecutive years of 'average' climatic conditions.

Extreme years

Whereas the extreme years do not represent climatic conditions to which vegetation is expected to equilibrate, they are used to demonstrate (i) robustness of model simulations to a wide range of climatic conditions, and (ii) create a context in which to assess the effects of long-term GCM climate change predictions as they affect natural vegetation/climate equilibriums. Our logic was that if model equilibrium could be reached for each of the vegetation communities under extreme, but repetitive, climate years, we could better evaluate the effects of more subtle, but annually variable, trends brought about by GCM-predicted climates.

Average year with GCM modification

These simulations were run as a comparison to long-term GCM scenarios to reveal differences between simulated vegetational/hydrologic effects of altered average climate conditions vs. those created by incorporating the change into natural variation of annual climates.

Long-term

Simulations were performed for the 59 years of actual site climate data as a means to compare the long-term dynamics of vegetation and soil water under natural and GCM-predicted conditions.

Long-term with GCM modification

These simulations are used to assess the potential for long-term alterations to site water balance or vegetation characteristics that might be expected to lead to community-type shifts or ecological succession within the sagebrush-steppe.

Results and discussion

To narrow the discussion, we note that no significant differences in productivity or soil water storage were simulated by altering frequency, as opposed to magnitude, of precipitation (simulations not shown). That is, productivity differences simulated by varying precipitation were solely dependent on changes in the magnitude of precipitation. This is attributable to the fact that growing season precipitation, even in wet years, is small relative to annual totals in most years (Stone *et al.*, 1983; Gee *et al.*, 1988), and productivity and subsequent drawdown are primarily dependent on winter soil water accumulation (Webb *et al.*, 1978; West, 1983). Also, with LAIs of less than 1.0, interception and subsequent evaporation of rainfall by the canopy are not significant factors, and therefore have little differential effect on changes to frequency vs. magnitude of rainfall events. In these simulations we have used a fairly conservative 10% change in the amount of precipitation, and found that altering the magnitude, as opposed to the frequency, of events had insignificant impact on the simulations. However, if changes in the frequency are more pronounced than changes in magnitude, overall productivity and potential evapo-transpiration may be affected by significant changes in cloudiness, which may in turn affect soil water balances among communities.

For all years of simulation, winter soil water accumulation was sufficient for spring greenup, and onset of the growing season was controlled by mean air temperature. In multiple-year runs the growing period began as early as 1 January for both cheatgrass and sagebrush, as the temperature array for mean calculation is designed to carry over from year to year. In the cheatgrass simulations, the growing season averaged 147 days with a range of 68–196 days. In the sagebrush simulations, the growing season averaged 135 days, with the shortest 66 days. The shorter average growing season in the sagebrush community is a result of greater transpiration that depletes soil water at a greater rate. The ability of sagebrush to carry on photosynthesis at very low leaf water potentials (Rickard & Vaughan, 1988) together with its evergreen characteristics created several multi-year growing periods during long-term simulations, the longest of which spanned 4 years without complete photosynthetic cessation. Daylength and temperature scalars used to calculate photosynthesis (Running & Coughlan, 1988) keep growth and evapo-transpiration at very low levels during winter months, however, and annual productivity during these periods was only moderately greater than during years of near-average growing seasons.

Validation

The model simulated ANPP for a sagebrush-dominated community within 15% of averaged measured values for all 4 validation years, demonstrating necessary sensitivity to year-to-year climate variations. Figure 1 shows predicted and measured values for 1971–1974 ($R^2 = 0.79$).

Equilibrium

Figures 2 and 3 summarize changes in equilibrium conditions from the control year, 1991, under all climate scenarios for cheatgrass and sagebrush communities, respectively. The significance of these runs is that equilibrium conditions were reached for both cheatgrass and sagebrush for all of the extreme years with substantially altered, but reasonable values for photosynthesis, leaf area index, and soil water. To predict equilibrium conditions under such scenarios, however, it must be assumed that the response capability of a given species is robust enough to reach equilibrium through adjustments to productivity without giving way to more xeric or mesic community types.

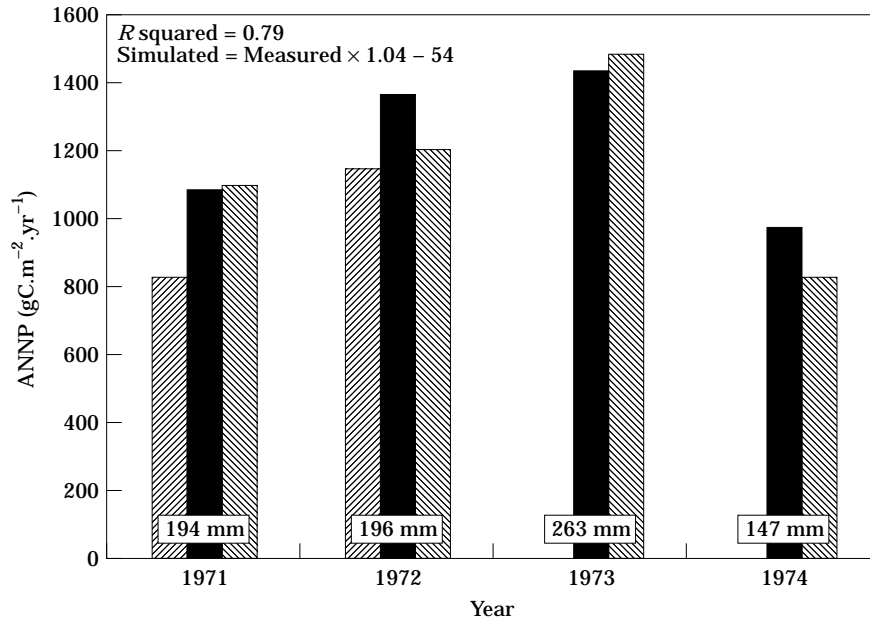


Figure 1. Simulated and measured above-ground net primary production (ANPP) for a sagebrush community at ALE for 4 years for which field data is available. (▨ Sims & Singh, 1978; ■ Rickard & Vaughan, 1988; ▩ Simulated).

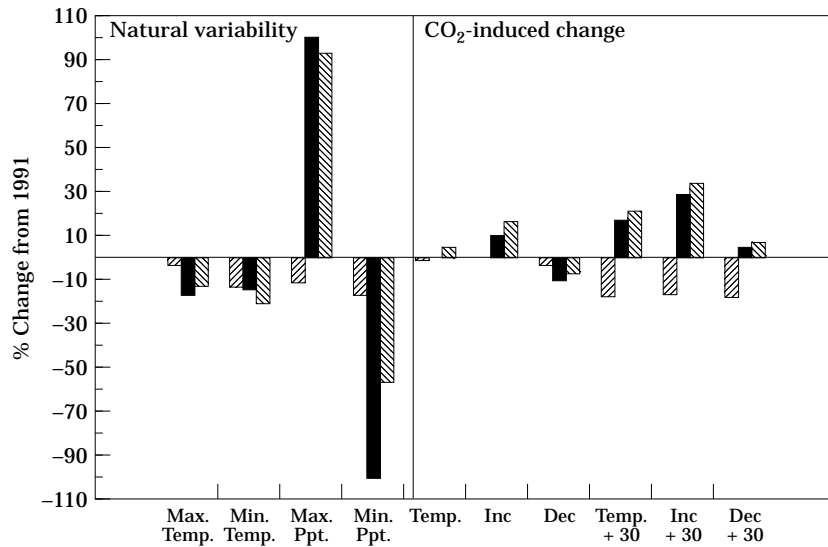


Figure 2. Comparison of the effects of different climate change scenarios on equilibrium soil water storage, leaf area index, and photosynthesis in a cheatgrass community. Abbreviations for GCM scenarios are: Temp = 2°C increase from 1991 in temperature alone, the 'average' year; Inc = 10% precipitation increase with temperature increase; Dec = 10% temperature decrease with temperature increase. + 30 indicates a 30% increase in water use efficiency with these scenarios. (▨ = soil water; ■ = LAI; ▩ = PSN).

Changes in leaf area responsible for the adjusted ET that keeps soil water relatively constant in the extreme precipitation years (1976, 1983 in Fig. 2) may be unrealistic for this community type. For example, with 1983's 348.5 mm of precipitation, nearly twice the average, equilibrium soil water is actually 11% lower than in 1991, but is coupled with an LAI of 0.82 (100% increase). This level of productivity suggests that such a sustained climate extreme might lead to a successional shift in vegetation type rather than a cheatgrass equilibrium. As a comparison, nearby Spokane, WA, (147° 40'N, 117° 26'W) has an average annual precipitation of 407 mm and the same average PET as ALE (Hydrosphere Inc., 1992). This area is an ecotone between sagebrush-steppe and coniferous forest vegetation, and supports ponderosa pine stands with LAIs of up to six (Peet, 1988).

Average year with GCM modification

Cheatgrass. Temperature increase alone increased PSN and soil water drawdown slightly, following the daily air temperature optimum function from Running & Coughlan (1988). Higher maintenance respiration costs associated with warmer temperatures ($Q_{10} = 2.3$) mitigated net gains, however, and overall carbon accumulation differences were insignificant. When precipitation changes are combined with the temperature increase, PSN and subsequent plant productivity respond to the change in available moisture. Under these GCM scenarios, 10% increases or decreases in total precipitation caused proportional 10% changes in leaf carbon accumulation by affecting the amount of water available for plant growth. ET, which is highly sensitive to transpiring leaf area, increased or decreased proportionally, and kept soil water storage within 3% of the control year. Because equilibrium LAIs are reasonable for this community type under all GCM scenarios, these simulations suggest that changes in the magnitude of average precipitation indicated by GCMs are within the adaptive

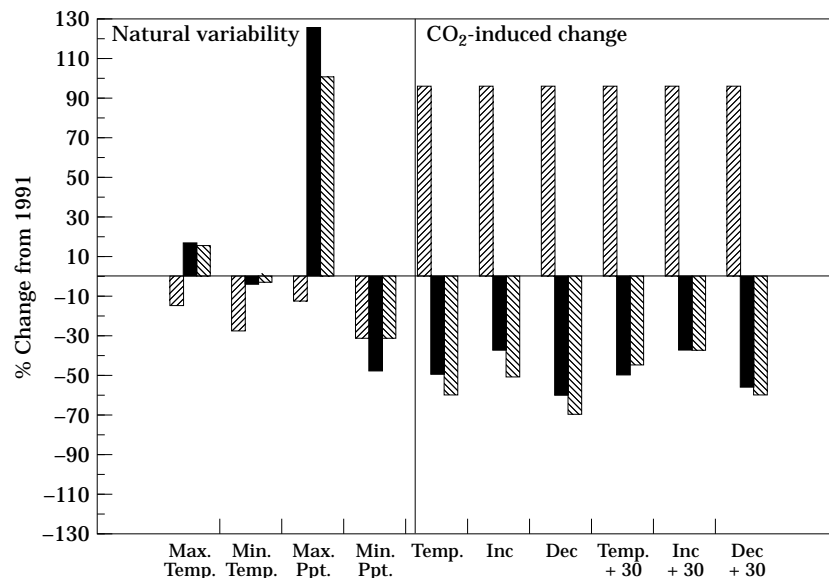


Figure 3. Comparison of the effects of different climate change scenarios on equilibrium soil water storage, leaf area index and photosynthesis for a sagebrush community. Dramatic increases in soil water storage are the result of diminished productivity for this community, and do not account for subsequent invasion and soil water uptake by other plant species. (▨ = soil water; ■ = LAI; ▨ = PSN).

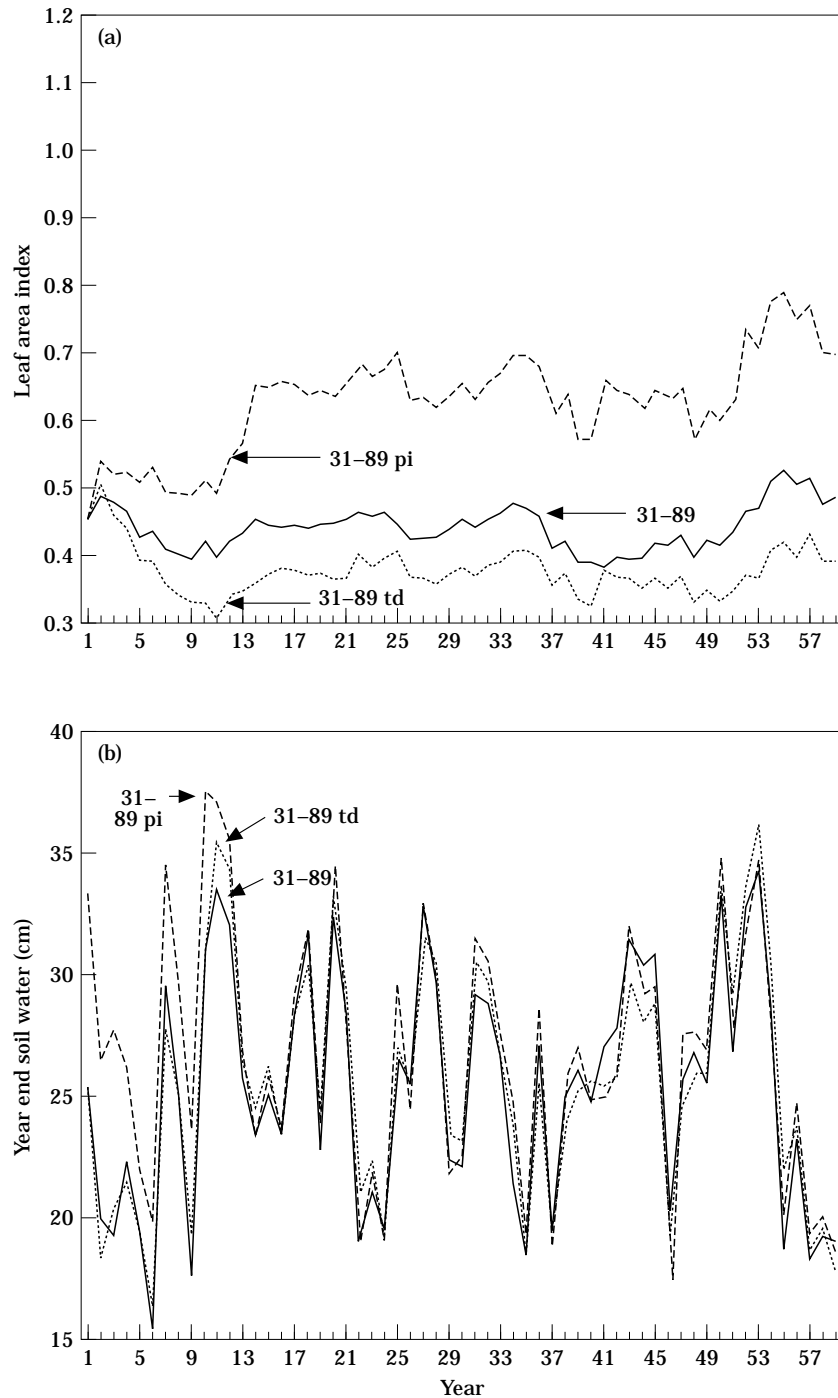


Figure 4 (a,b). Simulated long-term trends in leaf area (a) and soil water (b) for a cheatgrass community. 31-89 represents simulated conditions for the actual 59-year climate record. 31-89td is the 59-year record with the 'Dec' scenario (increased temperature, decreased precipitation), and represents the most deleterious of the GCM climate change scenarios for leaf area production. 31-89pi is the 59-year record with the 'Inc + 30' scenario (increased temperature, precipitation, and water use efficiency), the most favorable for leaf area production. All other GCM scenarios fall within the upper and lower limits set by these two.

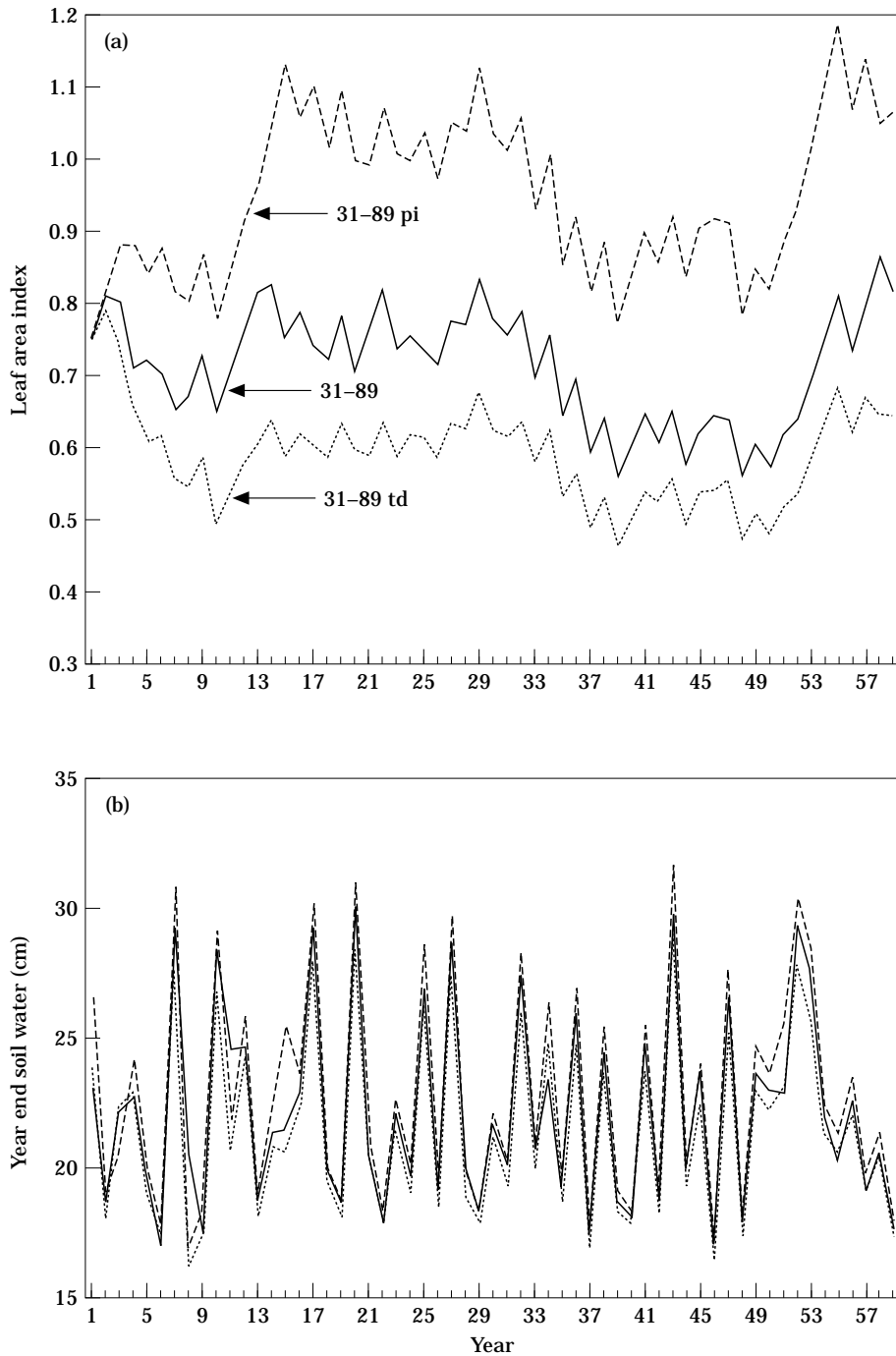


Figure 5 (a,b). Simulated long-term trends in leaf area (a) and soil water (b) for a sagebrush community. 31-89 represents simulated conditions for the actual 59-year climate record. 31-89td is the 59 year record with the 'Dec' scenario (increased temperature, decreased precipitation), and represents the most deleterious of the GCM climate change scenarios for leaf area production. 31-89pi is the 59-year record with the 'Inc + 30' scenario (increased temperature, precipitation, and water use efficiency), the most favorable for leaf area production. All other GCM scenarios fall within the upper and lower limits set by these two.

capability of cheatgrass and may prevent significant variations in soil water or community composition.

When water use efficiency is increased by 30% to simulate direct effects of CO₂, increased LAI decreases soil water storage slightly (15–18% of control) through greater transpiration. But because PSN is more efficient, attenuation of canopy conductance by lower soil water only partially offsets increased productivity. Thus equilibrium is reached with greater biomass and ET, and consequently lower soil water storage. This implies that plants may be able to maintain biomass at greater soil water deficits when water use efficiency is enhanced. Neighbouring sagebrush and bunchgrass communities, which generally have greater water use efficiencies (Toft *et al.*, 1989; Liang *et al.*, 1989) for example, support greater living biomass at higher soil water deficits than cheatgrass (Kremer & Running, 1993).

Sagebrush. Increasing 1991 daily temperatures by 2°C resulted in an annual average that is 1.1°C warmer than the warmest year on record (1983, see Table 1). Under this temperature regime, humidity deficit, and not available soil water, becomes the primary control over stomatal conductance to water vapor. In maintaining substantially higher living biomass than cheatgrass, sagebrush utilizes a lower rate of transpiration (Donovan & Ehleringer, 1992), and incurs considerably higher respiration costs. It is therefore more sensitive to reductions in canopy conductance to H₂O that attenuate photosynthetic rates. High absolute humidity deficits and greater maintenance respiration costs associated with higher daily temperatures in the GCM climates caused severely reduced photosynthesis in the sagebrush community (Fig. 3).

The result of these humidity-scaled photosynthetic rates is an LAI of 0.36, less than half the control equilibrium leaf area. ET drops to 83% of precipitation, and groundwater outflow becomes a significant part of the hydrologic budget (≈ 35 mm per year). Increasing water use efficiency by 30% to simulate direct effects of elevated CO₂ eliminated soil water outflow by increasing LAI, thus increasing ET. PSN, however, remained too low to support realistic biomass levels for this community (Fig. 3), suggesting the potential for vegetation community shifts under GCM climate scenarios.

In any community, a change in the physical environment of this magnitude (i.e. zero soil water deficit), indicates a strong potential for vegetation shifts. Sagebrush communities in this biome, however, are considered native 'climax' vegetation. Once established, they are effective at utilizing the soil water resource to preclude invasion by other species, and occupy a wide range of habitats in the intermountain north-west (Caldwell, 1985). The relationship between temperature, soil water availability, and community sustainability, therefore, may be more robust than our simulations indicate, and established communities may adapt seasonally or genotypically to changing climates.

Long-term simulations

The 59-year simulations, both with and without climate change scenarios, illustrate the importance of accounting for natural climate variation in simulating vegetative and hydrologic consequences of altered climates in sagebrush–steppe plant communities. Figures 4(a,b) and 5(a,b) demonstrate simulated leaf area production and soil water storage that acts to create a dynamic equilibrium between climate and community characteristics when both natural extremes and GCM-predicted climate conditions are present. The GCM temperature increase alone was sufficient to cause severe productivity declines in the sagebrush community equilibrium simulations, as the vegetation was not allowed to recover annually through natural cycles of cooler, wetter years between warmer, dryer ones that may be detrimental to this vegetation type. In

these long-term simulations, however, even the most detrimental scenario (increased temperature, decreased precipitation) created only moderate declines in long-term leaf area (21% average), and no significant changes in soil water (less than 5% variation in average year end storage).

Increasing water use efficiency had a similar effect in both communities. More efficient water use allowed greater productivity before normal soil moisture deficits constrained photosynthesis, resulting in consistently higher leaf area without significant changes to soil water storage.

Thus far we have assessed our long-term estimates of leaf production and soil water storage as a comparison to simulating equilibriums with constant climate conditions, and have consequently made changes appear insignificant, because they indicate productive survival of both community types. However, the range of climate change effects illustrated in Figs 4(a,b) and 5(a,b) are probably far more realistic than those represented by the equilibrium simulations, and should be considered separately. The scope of ARID-BGC does not go beyond an ecosystem process model, and thus cannot be used to suggest community succession or species composition shifts based on changes to productivity. Simulations do, however, provide quantification of substantial changes in LAI and standing biomass of both cheatgrass and sagebrush communities under predicted scenarios of climate change.

GCM climate change-induced variations in cheatgrass leaf area, when integrated over the 59-year simulation period, range from a 14% decrease with elevated temperature and decreased precipitation, to an 18% increase with increased precipitation and water use efficiency (Fig. 4(a)). Under the same scenarios, sagebrush leaf production (LAI) ranges from a 17% decrease to a 34% increase (Fig. 5(a)). Continuous, long-term vegetative production changes of this magnitude in livestock forage, for example, may have considerable economic and ecological consequences. Further research is needed to understand broad scale ecological impacts of productivity changes to individual species, communities, and ecosystems.

Conclusions

Long-term climate change induced by elevated atmospheric CO₂ concentrations may have significant impacts on sagebrush–steppe ecosystems. The extent of changes to ecosystem carbon and water balances will depend upon the capability of the ecosystem to respond to changes in climate, and its response to direct effects of elevated atmospheric gases that create climate change. In this paper, we used two approaches to simulate the potential for differential response of two vegetation communities within a semi-arid ecosystem. Using an equilibrium approach, in which responses to altered climate scenarios were simulated by modifying ‘average’ climatic conditions, a sagebrush community, with relatively high maintenance respiration costs and lower soil water storage, was not able to endure GCM-predicted climate change. High humidity deficits that attenuated PSN, and increased maintenance respiration costs created by elevated temperatures favor lower biomass systems in this semi-arid environment, and indicate a strong potential for vegetational succession. A lower biomass cheatgrass community within the same climate regime was able to reach an equilibrium between productivity and soil water availability under a range of climates without substantial impacts on the hydrologic balance.

Combining the natural climatic variation of long-term simulations with GCM-predicted changes, however, caused relatively modest changes in community leaf area in both communities with virtually no change in soil water storage. Long-term simulations of soil water and leaf area do not indicate a strong potential for community succession or compositional shifts under GCM-predicted climate change in this

ecosystem; more research is required, though, to understand the ecological consequences of the modeled changes in long-term productivity.

The accuracy of our predictions are limited by four primary factors. (1) The spatial resolution of GCMs is too coarse to provide detailed, biome-specific climate scenarios necessary for regional-scale simulations. (2) The response of inter-species competition to subtle, long-term climate change is largely unknown and immeasurable, creating difficulty for predicting ecosystem change, as opposed to vegetational succession. (3) Extrapolating laboratory or field-measured plant response to elevated CO₂, for example, to landscape scales is not yet a reliable science. (4) Inability to validate model predictions of long-term vegetation and hydrologic changes limits us to parameterization using present and past climatic conditions. For these reasons, our projections of ecosystem change should be viewed as best-guess estimates that illuminate the potential for process modeling to provide information about the consequences of climate change. As our knowledge of the ecological processes involved in climate change improves, so will the estimates of its effects on terrestrial ecosystems.

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- Editorial** – A forthcoming issue will contain further articles on global warming.