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EFFECTS OF LAND COVER, WATER REDISTRIBUTION, AND TEMPERATURE ON ECOSYSTEM PROCESSES IN THE SOUTH PLATTE BASIN

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Abstract. Over one-third of the land area in the South Platte Basin of Colorado, Nebraska, and Wyoming, has been converted to croplands. Irrigated cropland now comprises 8% of the basin, while dry croplands make up 31%. We used the RHESSys model to compare the changes in plant productivity and vegetation-related hydrological processes that occurred as a result of either land cover alteration or directional temperature changes (−2°C, +4°C). Land cover change exerted more control over annual plant productivity and water fluxes for converted grasslands, while the effect of temperature changes on productivity and water fluxes was stronger in the mountain vegetation. Throughout the basin, land cover change increased the annual loss of water to the atmosphere by 114 mm via evaporation and transpiration, an increase of 37%. Both irrigated and nonirrigated grains became active earlier in the year than shortgrass steppe, leading to a seasonal shift in water losses to the atmosphere. Basin-wide photosynthesis increased by 80% due to grain production. In contrast, a 4°C warming scenario caused annual transpiration to increase by only 3% and annual evaporation to increase by 28%, for a total increase of 71 mm. Warming decreased basin-wide photosynthesis by 16%. There is a large elevational range from east to west in the South Platte Basin, which encompasses the western edge of the Great Plains and the eastern front of the Rocky Mountains. This elevational gain is accompanied by great changes in topographic complexity, vegetation type, and climate. Shortgrass steppe and crops found at elevations between 850 and 1800 m give way to coniferous forests and tundra between 1800 and 4000 m. Climate is increasingly dominated by winter snow precipitation with increasing elevation, and the timing of snowmelt influences tundra and forest ecosystem productivity, soil moisture, and downstream discharge. Mean annual precipitation of <500 mm on the plains below 1800 m is far less than potential evapotranspiration of 1000–1500 mm and is insufficient for optimum plant productivity. The changes in water flux and photosynthesis from conversion of steppe to cropland are the result of redistribution of snowmelt water from the mountains and groundwater pumping through irrigation projects.

Key words: climate change; Colorado; ecosystem dynamics; hydrology; land cover change; land use change; RHESSys model; South Platte River; water redistribution.

INTRODUCTION

The interface between the Great Plains and the Rocky Mountains in Colorado is a complex region where large areas of shortgrass steppe have been converted to dryland and irrigated croplands. In addition, there has been a 30-yr trend of increasing temperatures throughout the Great Plains and the western United States, in keeping with general circulation model scenarios of increasing atmospheric CO_2 concentrations (Lauenroth and Sala 1992, Karl et al. 1993, Watson et al. 1996). Both land cover change and globally forced climate alterations influence regional ecosystem processes, although not necessarily in the same way or with the same magnitude. Direct and indirect effects of both may combine in unexpected ways.

Effects of climate change

Temperature changes can affect regional vegetation productivity and hydrology by enhancing or reducing evapotranspiration (ET) and by lengthening or shortening the growing season. Where there is ample precipitation and soil moisture available during the growing season, an increase in ET from warming will not impair, and may enhance, primary production. At high

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elevations in the mountains, tundra and coniferous forest growth are limited by temperature, not moisture (Peet 1989), so warming is expected to enhance net primary productivity. In the Great Plains, however, annual potential evapotranspiration (PET) is >1000 mm and exceeds the mean annual precipitation of <500 mm (Sims 1989). Warming is expected to increase the ratio of ET to precipitation unless there are substantial concurrent increases in annual precipitation. Between the plains and the subalpine forest belt there is a mid-elevation transition zone of montane conifers at 1800–2500 m, where complex topography influences exposure and microclimate, and soil moisture is strongly controlled by aspect and soil texture. In this elevational region, growth is enhanced or reduced with warming, depending on location (Stohlgren and Bachand 1997).

In the shortgrass steppe, additional precipitation would enhance plant production, and long-term net primary productivity records confirm that wet years are more productive than dry years (Sala et al. 1988). Because PET rises with air temperature, however, areas with increased precipitation may still experience a reduction in water supplies with warming if ET exhausts available water (Watson et al. 1996).

Precipitation to the central Rocky Mountains comes primarily as winter snow, and mountain river runoff is dominated by snowmelt (Baron 1992, Rango 1995). Climate warming in temperate mountainous regions is projected to have a greater influence on the timing of snowmelt than on the volume of snowmelt runoff (Rango 1995, Baron et al. 1998). Simulations of Rocky Mountain hydrologic responses suggested that discharge will decrease somewhat (~5%) with increased temperatures, except in small glacierized basins where discharge is projected to increase slightly (Rango 1995, Baron et al. 1998). In contrast to the dampened response to temperature, discharge responds almost linearly to changes in winter precipitation (Nash and Gleick 1993, Rango 1995, Baron et al. 1998). In this respect, high-elevation catchments operate differently from lower elevation and more temperate watersheds, where forest ET competes with stream flow (Sala et al. 1988, Likens and Borman 1995, Schindler 1997). Many Rocky Mountain watersheds have their headwaters (and the bulk of their snowpack) in alpine tundra or talus fields, where melt begins before ET becomes important. Because of this, plant water requirements are somewhat uncoupled from stream flow.

Effects of land and water use changes

Land use change in the short grass steppe exerts a strong negative influence on ecosystem carbon balance at all elevations, through harvest, loss of soil organic matter, and erosion (Burke et al. 1991). Land cover alterations in the mountains, such as those brought about by logging, can cause short-term increases in stream discharge through re-allocation of soil water from transpiration to runoff and through lowered evaporative surface area (Goudie 1990). Irrigated agriculture and urbanization are major land uses that spatially redistribute water resources from river channels to fields and reservoirs. In the South Platte River Basin, ~80% of the annual surface water supply is used within the basin for urban and agricultural needs (Dennehy et al. 1993). A large volume of ground water is also extracted from aquifers of the South Platte Basin and applied to irrigation. South Platte aquifers are regularly replenished from mountain snowmelt, and thus differ from groundwater aquifers whose waters are Pleistocene remnants.

Subtle ecologic and hydrologic changes may occur through changes in regional climate driven by land use and land cover. Changes in vegetation canopy characteristics such as leaf area, albedo, evapotranspiration rates, and roughness can influence regional and global climate, as suggested both by observations (Barnston and Schickedanz 1984, Meher-Homji 1991) and model simulations (Shukla and Mintz 1982, Shukla et al. 1990, Chase et al. 1996, Zhang et al. 1996). Using a climate version of the mesoscale atmospheric model, RAMS, Copeland and colleagues suggested that significant changes in temperature, humidity, wind speed, and precipitation may have occurred in Colorado due to land use change (Copeland et al. 1996, Pielke et al. 1992). Short-term (three-day) and fine-grid (6.5-km) RAMS simulations for the Colorado Front Range under scenarios of pre-European settlement shortgrass steppe vs. current land use also showed substantial differences in precipitation, temperature, and cloud cover from land use change alone (Chase et al. 1998, Stohlgren et al. 1998).

Understanding the effects of land use, water redistribution, and climate change is important in developing a better appreciation of the ecologic, social, and economic limits on the region. While there is a body of literature addressing direct ecologic and hydrologic responses to climate and land use, not nearly enough is known about more subtle consequences, such as the feedbacks between land surface processes and climate variability (Lubchenko et al. 1991, Pielke et al. 1997, Steyaert et al. 1997). Using RHESSys, the Regional Hydro-Ecological Simulation System (Band et al. 1993), we asked how sensitive regional ecosystem dynamics are to both land cover change and climate alteration. We compared fluxes of carbon and water from the South Platte River Basin under potential natural vegetation, under current land cover, and in response to changes in temperature.

Study region

Headwaters of the 62 900-km^2 South Platte River begin at 4000 m elevation along the Continental Divide and flow 720 km to its confluence with the North Platte River in Nebraska (Fig. 1). Seventy percent of Colorado's population, more than two million people, live in the basin (Dennehy et al. 1993). Precipitation in the

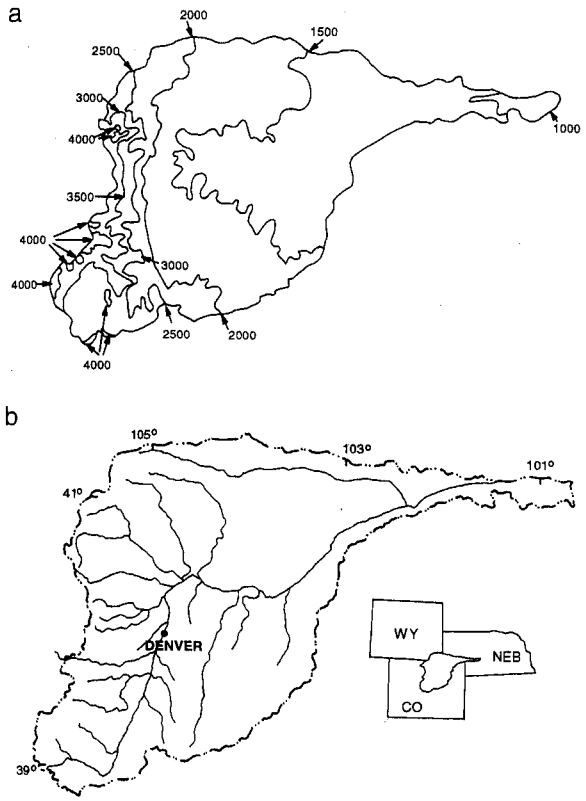

FIG. 1. South Platte River Basin of Colorado, Wyoming, and Nebraska. (a) Digital elevation map (redrawn from EROS Data Center DEM, Sioux Falls, South Dakota); (b) hydrologic and political features (redrawn from Dennehy 1993).

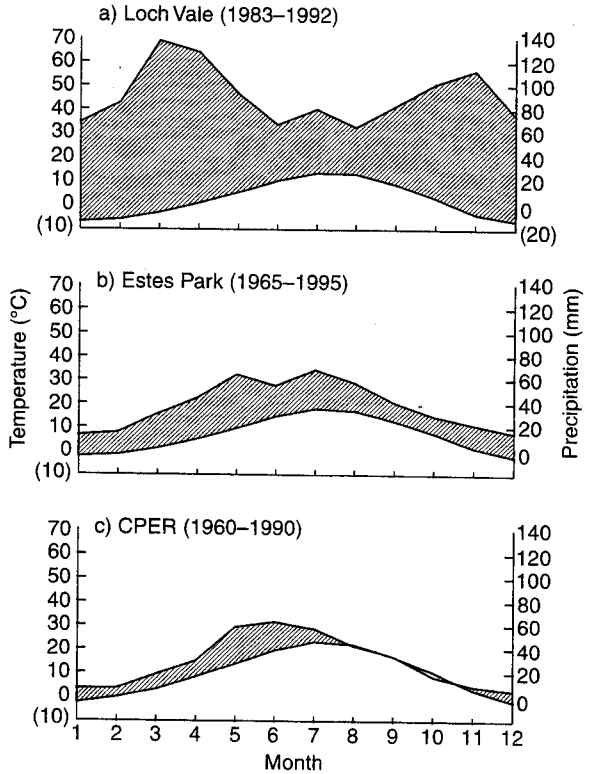

FIG. 2. Climate diagrams for three elevations within the South Platte River basin: (a) Loch Vale Watershed (3146 m); (b) Estes Park (2295 m); and (c) Central Plains Experimental Range (CPER, 1650 m), showing years of record from which each graph was derived. Hatched areas represent relative humidity season when actual evapotranspiration is less than potential. Mean annual temperature and precipitation are (a) 2.5°C, 1099 mm; (b) 6.3°C, 432 mm; and (c) 9.2°C, 334 mm, respectively. Data are from (a) Loch Vale database (Baron 1992), (b) Colorado Climate Data (1992), and (c) Shortgrass Steppe Long-Term Ecological Research (1996).

mountains is >1000 mm annually, compared with 300–400 mm on the plains (Fig. 2). Because PET for the plains is greater than precipitation, water often limits primary productivity, and there is rarely subsurface runoff, except for return flow from irrigated croplands (Sala et al. 1988, Sims 1989). Currently, precipitation supplies 24 680 × 10^6 m^3/yr to the South Platte River Basin (Dennehy et al. 1993). Imported water, mostly from the Colorado and Arkansas River basins, adds an additional 494 × 10^6 m^3/yr (Dennehy et al. 1993). While a water budget for the South Platte Basin is beyond the scope of this paper, this amounts to a substantial seasonal and spatial redistribution of water resources.

METHODS AND DATA LAYERS

Methods

RHESSys is a spatial data and simulation system that uses geographic information system techniques to transform spatial data into a landform description, and has a set of process models, FOREST-BGC and TOPMODEL, that compute water and carbon flux through watersheds (Band et al. 1993). FOREST-BGC is a stand-level model of forest carbon and water budgets that has been parameterized for use in both forested and grassland landscapes (Running and Coughlan 1988, Hunt et al. 1996). In this version of FOREST-BGC, C_3 and C_4 physiological processes were not delineated. FOREST-BGC is coupled with TOPMODEL, a quasi-distributed hydrological model (Beven and Kirkby 1979) to model watershed hydro-ecological processes (Band et al. 1993). Daily weather (temperature maxima and minima, precipitation) was extrapolated to each hillslope with MTCLIM-3D (Thornton et al. 1997). RHESSys has been applied to hydrological investigations, forest productivity, regional-scale water and carbon budgets, climate change scenarios, and nitrogen leaching (Running et al. 1989, Band et al. 1991, 1993, 1996, Running and Nemani 1991, Band 1993, 1994, Creed et al. 1996). RHESSys offers spatially distributed daily output. The model is fully described in Band et al. (1993), and modifications are described below.

To better represent steep mountain watersheds, we modified the original spatial framework described in Band et al. (1993) to resolve temperature and precip-

TABLE 1. Land cover types in the South Platte River Basin.

Cover type	Potential vegetation Area (km²)	(%)	Current vegetation Area (km²)	(%)
Alpine	2 031	3.3	1 948	3.2
Coniferous	11 296	18.3	8 956	14.5
Deciduous	1 040	1.7	732	1.2
Shortgrass	47 211	76.7	25 983	42.2
Dry crops†	···	···	18 941	30.8
Wet crops	···	···	5 018	8.1
Total	61 578	100.0	61 578	100.0

† During the growing season, land area listed as dry crops is split evenly between cropland and fallow land.

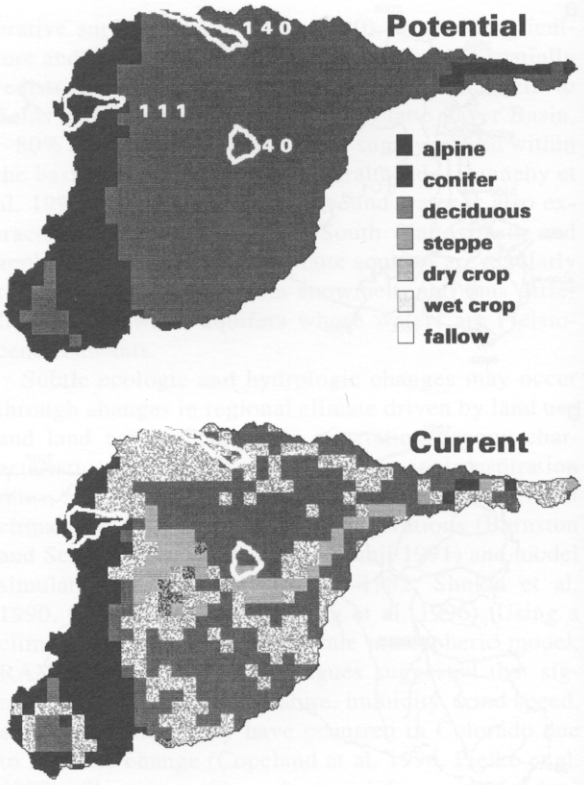

FIG. 3. Land cover classifications for the South Platte River basin. The top panel shows potential vegetation (derived from Küchler [1975]); the bottom panel shows current vegetation (Loveland et al. 1991). Grid size is 10 km. Stippled areas of current classification represent mixed vegetation types within a grid: dry crop and fallow, or wet crop and deciduous. The three hillslopes discussed in the text are outlined: Hillslope 111 is mostly alpine and coniferous forest; Hillslope 140 was converted from steppe to mostly dry crop and fallow; and Hillslope 40 was converted from steppe to mostly wet crop (refer to Table 5).

itation gradients on each hillslope and a snow redistribution option to imitate wind redistribution of snowpack (Lammers et al. 1997; M. D. Hartman, C. Tague, L. E. Band, J. S. Baron, R. L. Lammers, and D. W. Cline, *unpublished manuscript*). The micrometeorology model, MTCLIM-3D, extrapolated base station meteorology to each 200-m elevation band for each hillslope. This allowed temperature and precipitation to vary on hillslopes with wide topographic gradients.

Canopy interception of rain, hence the amount of moisture routed to evaporation rather than to soils for transpiration, is directly proportional to LAI (leaf area index, the total [two-sided] leaf area per unit area of ground). This results in high model sensitivity to changes in LAI. For example, an increase of LAI from 2 to 6 when native grasses are converted to crops increases interception from ~30 to 100% for precipitation events of <2 mm.

Soils were kept wet for irrigated crops during the growing season (15 April–15 August) by adding water daily at twice the PET rate. Irrigation water was added directly to the top of the soil, so that it entered soil via the soil litter layer.

Data layers

Elevation was derived from the 1 km resolution U.S. conterminous digital elevation model (DEM) accompanying the EROS Data Center 1-km AVHRR/NDVI data set (Eidenshink 1992). The South Platte Basin was divided into 136 individual hillslopes with a terrain-partitioning algorithm (Band et al. 1993). This is done by extracting a drainage network from the DEM, wherein nested subcatchments are delineated based on stream links. Stream links are the unbranched reaches of stream channels between stream junctions or the source. The terrestrial part of each subcatchment is partitioned into areas that contribute drainage waters to each side of a stream link (Band et al. 1996). Hillslopes were necessarily coarse at the scale of the entire South Platte Basin, and each hillslope contained more than one well-defined catchment, especially in mountainous areas of high topographic relief. Slope, aspect, and the wetness index were calculated by digital terrain analysis from the digital elevation data layer. Saturated hydraulic conductivity (K_o) was derived as a linear function of the wetness index (W):

$$K_o = 100 - 5W.$$

This equation provides for a gradation in soils from coarser to finer moving downslope. The hydraulic conductivity generated gave a mean value of 67 cm/d, with a standard deviation of 8.9 cm/d (Lammers 1998).

Potential land cover was derived from Küchler's natural vegetation map to represent pre-agricultural conditions (Küchler 1975, VEMAP Members 1995, Kittel et al. 1995). This map was initially developed with 10-km resolution; each vegetation grid was divided into 100 equal 1-km pixels for our simulations. Current land cover was obtained from the EROS Data Center (EDC) 1-km AVHRR data base for the conterminous United States (Loveland et al. 1991), with the following modification: for cells where the Loveland et al. (1991) current land cover map indicated natural vegetation, the natural vegetation type from Küchler (1975) was used to provide consistency between the two maps (T.

TABLE 2. Leaf area index (LAI) and phenology of land cover types simulated for the South Platte Basin.

Vegetation	Min. LAI	Max. LAI	Phenology†
Alpine	0.01	1.00	Onset: 1 May Max. dates: 30 Jun–1 Aug
Coniferous	5.00	5.00	No seasonal variation
Shortgrass	0.00	0.60	Onset: 1 May Max. dates: 30 May–16 Jul
Dry crops			
Wheat	0.00	4.00	Onset: 16 Mar Max. dates: 15 May–9 Jun
Fallow (weeds)	0.00	0.03	Onset: 10 Jul Max. dates: 9 Aug–31 Oct
Wet crops	0.00	6.00	Onset: 15 Apr Max. dates: 15 May–16 Jul

† Phenology is presented for current climate scenarios. Green-up began 2 wk earlier with each +2°C, or 2 wk later with a −2°C.

Kittel and D. Ojima, *unpublished data*). In this region of distinct vegetation gradients based on precipitation and elevation, the coarse-resolution map by Küchler (1975) is probably fairly good. Several investigators have conducted validation studies of the EDC data base, and found that the land cover classification performed well (Zelt et al. 1995, Merchant et al. 1996, Zhu et al. 1996).

Most of the difference between current and potential land cover occurred through conversion of steppe grasses to dry crops (a wheat–fallow system where only half the land is planted at any time), or to irrigated crops (mostly corn) (Table 1). Other vegetation changes that occurred were conversion of some coniferous forests in the foothills and some deciduous forests along river corridors to croplands (Fig. 3). Because deciduous forests made up <2% of total land cover for the South Platte, we do not report on deciduous forest processes. Soil rooting depth was derived from available water capacity maps of the State Soil Geographic Database (STATSGO) (Lytle 1993, Lammers et al. 1997).

LAI values and phenology were assigned to land cover types based on published literature values for all vegetation types except wheat (Table 2; Dickinson et al. 1986). LAI values for wheat were calculated from aboveground live wheat biomass (from Metherell et al. 1993), while wheat phenology for current climate, including green-up and harvest, was taken from Shanahan (1982). Maximum LAI was set to 6.0 for irrigated cropland. Maximum LAI for shortgrass steppe was 0.6, and for dryland wheat maximum LAI was set to 4.0. Half of the land area under dryland wheat is fallow at any given time, and we assigned a small LAI of 0.03 to weedy vegetation cover on fallow land during the late summer and fall (Metherell 1992). LAI for coniferous forests was constant at 5.0, while tundra increased LAI from a minimum of 0.01 to 1.0 over a growing season. Vegetation phenology for alpine, grassland, and dry crop vegetation types was cued to temperature, so that green-up began 2 wk earlier with every +2°C temperature increase, or 2 wk later with a −2°C temperature decrease.

We used weather data for calendar year 1992 from 119 weather stations for temperature, and from 177 weather stations for precipitation in the South Platte Basin, to drive the models (Colorado Climate Data 1992, Thornton et al. 1997). Colorado climate is notoriously variable, and 1992 was no exception (Hansen et al. 1978). Precipitation in February, April, and May was 50% of the 30-yr mean, while precipitation in March, June, and August was 200% of the 30-yr mean. Temperatures from February through May were 2–8°C greater than the 30-yr average; they were 2–4°C less than the average from June through August (Colorado Climate Data 1992). Climate change simulations were made by altering the minimum and maximum daily temperature of the 1992 weather file by −2° and +4°C. These two temperature scenarios were chosen based on RHESSys simulations for a high-elevation watershed at the headwaters of the South Platte Basin (Baron et al. 1998). The cooler temperatures represent trends that have been observed for the Colorado Front Range over the past four decades (Williams et al. 1996, Stohlgren et al. 1998). Simulations of +2°C warming in the headwater basin caused little change in model output from control runs, but a +4°C warming showed dramatic differences in processes, suggesting that a temperature threshold had been passed (Baron et al. 1998). We did not vary precipitation for these simulations because uniform changes in precipitation would never occur in our domain, and the complexities involved with attempting meaningful seasonal and spatial precipitation regimes were very great.

RESULTS

Effects of land cover change by land cover type

Annual summaries.—Annual basin-wide net photosynthesis and transpiration increased by by >80% due to the change in vegetation between potential and cur-

TABLE 3. Ecosystem processes by land cover for current climate simulations under current vs. potential natural land cover.

	Steppe	Dry crop†	Wet crop	Current basin total‡	Potential basin total‡
Net photosynthesis§					
Annual	411	496	1389	528	293
May	90	209	404	124	56
Transpiration‖					
Annual	140	162	509	182	99
May	30	70	145	42	18
Evaporation‖					
Annual	210	209	460	238	207
May	16	22	88	27	18

† Dry crop is the combined model output for dry crop and fallow fields.

‡ Basin totals are areally weighted averages.

§ Net photosynthesis is measured in g $C \cdot m^{-2} \cdot mo^{-1}$ for May, and g $C \cdot m^{-2} \cdot yr^{-1}$ for annual values.

‖ Transpiration and evaporation are measured in mm/mo for May, and mm/yr for annual values.

rent land cover (Table 3). Evaporative losses, however, increased by only 15%. Individual land cover types showed dramatic response (Table 3). Irrigated (wet) crops showed substantially greater photosynthesis and transpiration than dry crops or the original steppe vegetation. Evaporation from wet croplands was 120% greater than that from steppe. Evaporation from nonirrigated crops differed from steppe by 3% or less. There was little change in alpine tundra or coniferous forest processes between current and potential land cover scenarios; their data are not shown.

Summaries for May.—An examination of these same processes for the month of May showed great basin-scale differences in photosynthesis and transpiration rates between potential and current vegetation (Table 3). May was chosen as a representative month because vegetation is photosynthetically active in all South Platte vegetation types by that time of the year, yet rates of water fluxes and photosynthesis were expected to differ depending on climate variability. Both the wet crop and dry crop reach maximum LAI of 6 and 4, respectively, by 15 May (day 135). However, shortgrass steppe does not reach its maximum LAI of 0.6 until 1 June (day 152), so it is still gaining leaf area through May. The shift in phenology from steppe to crops more than doubled net photosynthesis and water lost through transpiration for May of current vs. potential vegetation for the entire basin. Basin-wide evaporation in May increased by 50% due to land cover change.

Individual land cover types behaved very differently with land use change (Table 3). Dry crop photosynthesis and transpiration were more than twice as high as shortgrass steppe in May, with wet crop photosynthesis and transpiration nearly five times as high. Dry crops and wet crops evaporated 6 mm and 73 mm more than steppe, respectively.

Substantial spatial differences in photosynthesis and transpiration are evident between potential and current land cover on 1 June (Plate 1). Most of the change, as expected, occurred on the plains where there was conversion of steppe to croplands. Irrigated crops showed large increases in photosynthesis and transpiration, while the wheat–fallow showed increases or decreases in photosynthesis and transpiration rates depending on location.

Effects of temperature changes by land cover type

Annual results.—Cooler temperatures were beneficial to the dry and irrigated crops, but caused a decrease in native tundra, conifer, and steppe vegetation productivity (Table 4). Basin-wide, the increase in net productivity was only 3%, so the overall effect of cooling was slight to negligible. Warming was quite detrimental to carbon gain across all vegetation types except tundra, due to increased plant respiration. The loss was most pronounced for dry crops, where net photosynthesis decreased by 27% compared with the current climate. Warmer spring temperatures at the highest elevations allowed tundra a longer growing season, causing photosynthesis to increase by 9%. Annual productivity for the entire South Platte Basin declined by 16%.

Annual transpiration rates decreased by almost 30% for alpine and coniferous vegetation types at cooler temperatures. Cooler temperatures also decreased transpiration rates in the steppe and grassland crops by 2–16%. Less water was evaporated throughout the basin with cooler temperatures, with the greatest decrease (27%) occurring in tundra, and 13–22% less water evaporated from the other vegetation types. The net basin-wide effect of cooling was a 9% decrease in transpiration and a 15% decrease in evaporation. Climate warming had the opposite effect on basin-wide ET. The amount of water transpired from tundra, coniferous, steppe, dry crop, and wet crop vegetation increased by 50, 25, 8, 15, and 6%, respectively, over the current climate control runs. Evaporation increased with warming for all vegetation types. The overall effect of basin warming was slightly more water transpired than under current climate, but 28% more water evaporated.

Results for May.—Carbon production was strongly suppressed with cooler temperatures (Table 4). The basin-wide decline was 25%; alpine and steppe produced 73–83% less carbon with a −2°C cooling. Results for temperature warming were mixed. Warming was highly beneficial to alpine vegetation, and increased spring productivity by >200%. Steppe productivity also increased with warming, but conifer and crop vegetation decreased photosynthesis, again due to increased plant respiration. There was a 5% decrease in basin-wide productivity with warming. There is variation within the mountain vegetation types that is obscured by the monthly summary for May: the highest elevation tundra and coniferous forest shows increased productivity with warmer temperatures on the 1 June snapshot,

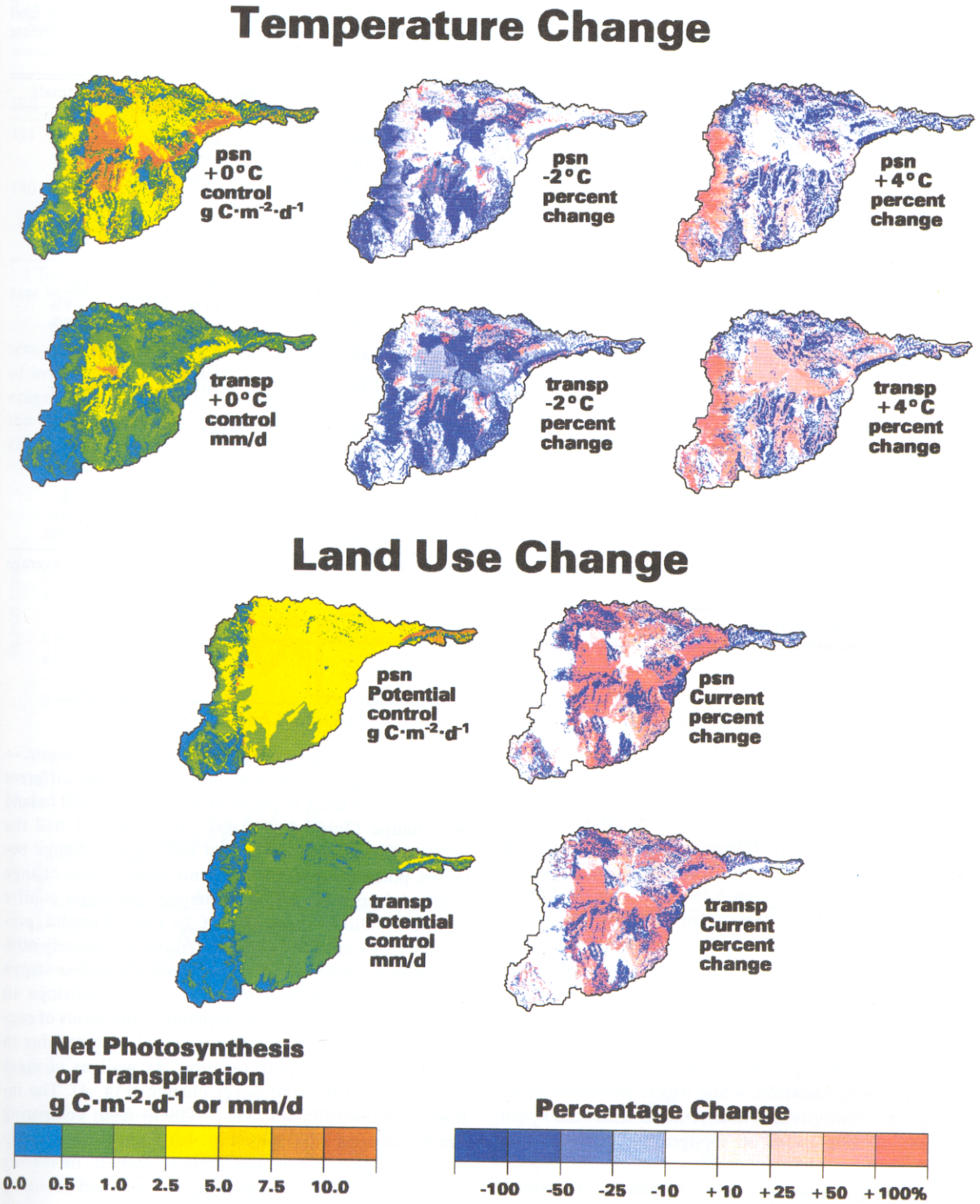

PLATE 1. Responses of net photosynthesis and transpiration to temperature changes (top) and land use change (bottom) for 1 June 1992. Images on the left represent net photosynthesis (psn, in g $C \cdot m^{-2} \cdot d^{-1}$) and transpiration (transp, in mm/d). Images on the right represent percentage deviation away from current values for temperature change scenarios, and percentage deviation away from potential values for land use change scenarios. In percentage change images, warm colors depict an increase, while cool colors depict a decrease in carbon fixed or water transpired. White represents little or no change ($\pm 10\%$) from the original values.

TABLE 4. RHESSys model output of annual and May net photosynthesis, transpiration, and evaporation for current land cover classes of the South Platte River Basin. Values shown are for the control scenario, generated from 1992 climate data. Percentages are deviations from the control run for −2°C and +4°C climate change scenarios.

Output	Alpine	Coniferous	Steppe	Dry crop†	Wet crop	Basin total‡
Net photosynthesis§						
Annual	269	326	411	458	1389	528
−2°C	−12%	−3%	−6%	+16%	+2%	+3%
+4°C	+9%	−21%	−9%	−27%	−12%	−16%
May	23	61	90	105	404	124
−2°C	−83%	−13%	−73%	−15%	−1%	−25%
+4°C	+104%	−13%	+29%	−39%	−7%	−5%
Transpiration‖						
Annual	34	95	140	160	509	182
−2°C	−29%	−27%	−16%	−2%	−11%	−9%
+4°C	+50%	+25%	+8%	−15%	+6%	+3%
May	3	15	30	35	145	42
−2°C	−89%	−33%	−80%	−23%	−10%	−33%
+4°C	+223%	+33%	+53%	−29%	+10%	+12%
Evaporation‖						
Annual	139	222	210	206	460	238
−2°C	−27%	−13%	−13%	−13%	−22%	−15%
+4°C	+43%	+23%	+19%	+20%	+50%	+28%
May	14	30	16	18	88	27
−2°C	−64%	−13%	−19%	−5%	−23%	−19%
+4°C	+78%	+13%	+13%	+5%	+55%	+30%

† Because half of the area under dry crops is fallow at any given time, values reported for this category are the average of model results for crop and fallow land.
‡ Basin totals are areally weighted averages.
§ Net photosynthesis is measured in g $C \cdot m^{-2} \cdot mo^{-1}$ for May, and g $C \cdot m^{-2} \cdot yr^{-1}$ for annual values.
‖ Transpiration and evaporation are measured in mm/mo for May, and mm/yr for annual values.

while lower elevation coniferous forests display negative changes in net photosynthesis (Plate 1).

May transpiration responded strongly to warming and cooling in alpine, coniferous, and steppe vegetation (Table 4). Both wet and dry crops transpired less with cooling, and dry crops transpired less with warming. The actual amount of water transpired, except for irrigated crops, ranged from 3 to 35 mm in the control runs, so the amount of water transpired per square meter from each vegetation type in May was small. Transpiration rates for 1 June show the extent of spatial variation; irrigated crops transpire the most water, while tundra and conifers transpire the least (Plate 1). Dry cropland showed spatial variation in response to warming or cooling; some areas showed no response to temperature variation, while others increased or decreased productivity and transpiration with both warming and cooling based on topographic characteristics (Plate 1).

May evaporation was most responsive to climate change in tundra, decreasing 64% and increasing 136% with cooling and warming, respectively (Table 4). Conifers and the grasses (except dry crop) showed less of a response to temperature, but evaporation decreased with cooling and increased with warming. The amount of water transpired in May was greatest from irrigated crops. Basin-wide, warming and cooling changed evaporative losses by 20–30%.

Individual hillslope responses

Influence of topographic location and climate.— Three hillslopes were selected to represent different land covers to track ecosystem processes related to land use change (Table 5, Fig. 3). Hillslope 111 had the greatest elevational range, but only slight change between potential and current land covers. The change resulted from conversion of steppe and some conifer to wheat–fallow, and a loss of 26 km^2 of tundra, presumably by conversion to conifer. Approximately 60% of hillslope 140 was converted from shortgrass steppe to dry and fallow cropland, and 88% of hillslope 40 was converted to irrigated cropland. Time series of ecosystem processes by hillslopes reveal changes due to climate and geographic location, as well as changes brought about by land cover change (Fig. 4). The influence of location was very evident from comparing runoff between hillslopes (Fig. 4a). Runoff from mountain hillslope 111 was driven by snowmelt, increasing in early May (day 120), peaking in June, and declining through July (Fig. 4a). Runoff from the dry crop and steppe hillslope 140 was driven by rainfall, and surface flow only occurred for a short while during and after rain events. Runoff from the irrigated crop hillslope 40, which was driven by irrigation and rainfall, was sustained and high during the period of irrigation.

The dynamics of soil moisture were different between mountains and plains (Fig. 4b). Water content

TABLE 5. Descriptions of three (out of 136) hillslopes selected to show effects of land use change on ecosystem dynamics. Soil rooting depths are means, with standard deviations in parentheses.

Hill	Elevation range (m)	Total area (km^2)	Soil root depth (cm)	Days (length) of growing season†	Potential vegetation types (km^2)	Current vegetation types (km^2)
111	1815–3900	731	46 (13)	89–300 (211) 89–300 (211)	alpine (307) coniferous (413)	alpine (281) coniferous (414)
140	1628–2083	641	60 (0)	120–226 (106) 77–226 (149)	steppe (11) steppe (641)	dry/fallow (36) steppe (270) dry/fallow (371)
40	1394–1488	417	58 (3)	120–226 (106) 104–226 (122)	steppe (417)	steppe (52) wet crop (365)

† Top numbers are potential vegetation growing season; bottom numbers are current vegetation growing season. Days of year begin 1 January.

was a function of porosity and depth, as well as amount of available water. Mountain soils in hillslope 111 averaged 46 cm in depth. These soils were dry through the winter, and began to gain moisture around day 95 (April 5). The volumetric soil water content ranged from 10 to 24% (40% is saturation) between early April and the end of August (Fig. 4b). Plains soils in hillslopes 40 and 140 ranged from 50 to 60 cm depth. They exhibited their highest soil moisture content in the spring and winter, and lowest during the growing

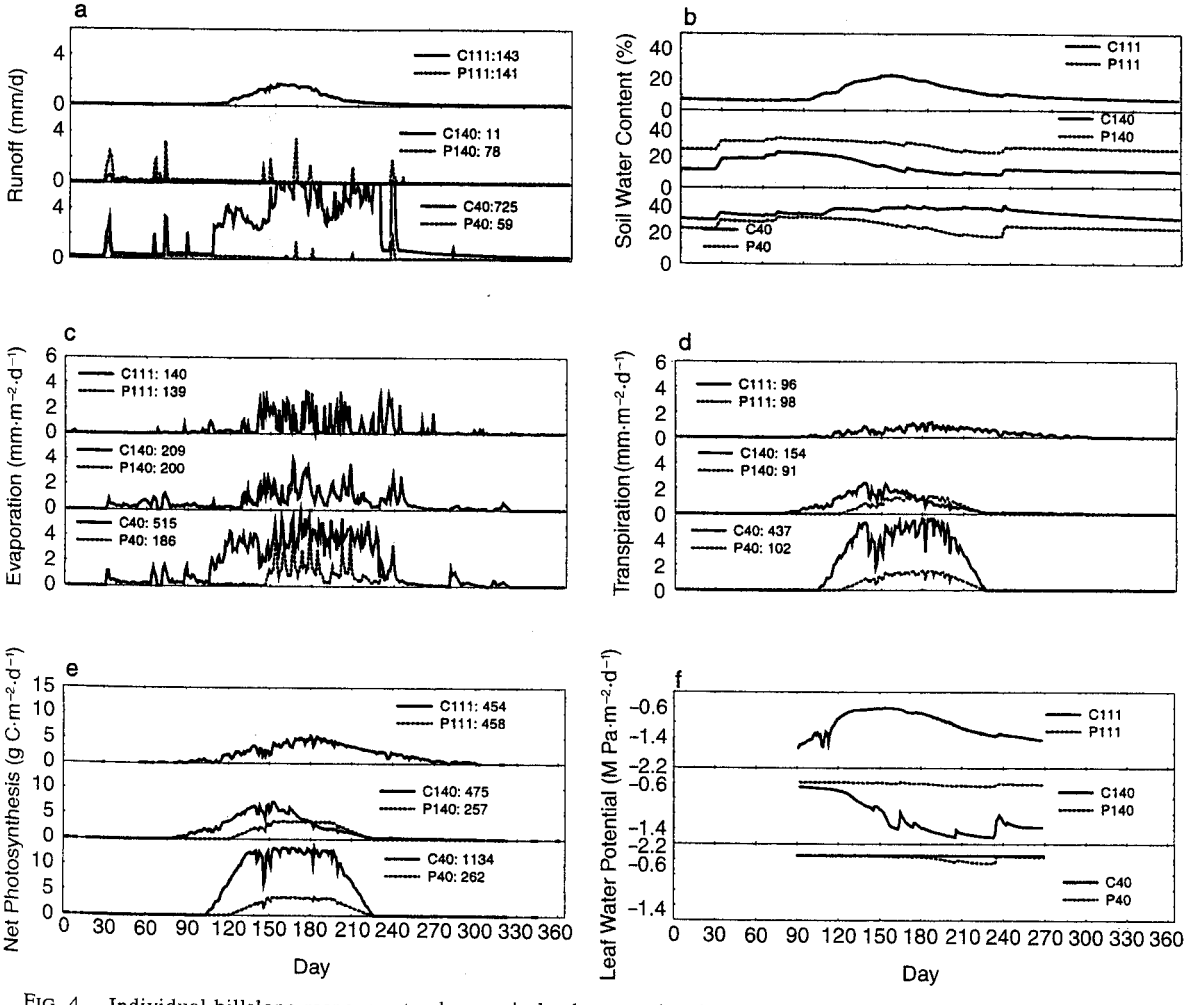

FIG. 4. Individual hillslope responses to changes in land cover, showing (a) hillslope outflow, (b) soil water content, (c) evaporation, (d) transpiration, (e) net photosynthesis, and (f) leaf water potential. Solid lines are potential land cover; dotted lines are current land cover. Notation in key is Potential, or Current, hillslope number, and annual total of each variable. Please refer to Fig. 3 and Table 5 for locations of hillslopes and land cover types.

season. One can see the effect of individual rain storms. Water losses through evaporation and transpiration from the mountain hillslope were less than those from the other two hillslopes (Fig. 4c, d). Transpiration in the mountains was less seasonally dynamic than transpiration from the plains hillslopes, but the total amount of water transpired was similar between mountain and steppe potential vegetation.

Mountain hillslope 111 had a 211-d growing season, with photosynthesis beginning at lower elevations around day 89 (beginning of May) and continuing until day 300 (end of October) (Fig. 4e). Elevational differences can be clearly seen in the upper left corner of Plate 1, where the highest elevations show 0.0–2.5 g $C \cdot m^{-2} \cdot d^{-1}$, compared with 2.6–5.0 g $C \cdot m^{-2} \cdot d^{-1}$ in the lower elevation reaches of the basin. The steppe grasses had a shorter growing season due to water stress, beginning on day 120 (beginning of May) and ending on day 226 (10 August).

The simulated predawn leaf water potentials provide an estimate of water stress by describing stomatal resistances, and thus constrain the upper limits of daily transpiration. Transpiration occurred freely through most of the growing season in the mountain hillslope, rising in the spring and declining at the end of summer. Explanations for simulated leaf water potentials for the grass vegetation types are more complex (Fig. 4f). Low LAI values for steppe create low water demand, so that potential vegetation did not undergo much, if any, water stress. There were great differences in leaf water potentials between wheat–fallow in hillslope 140 and irrigated crops in hillslope 40, due to soil water availability. Greater LAI but no additional water supply induced negative leaf water potentials in the dry crops of hillslope 140, whereas unlimited irrigation water kept leaf water potentials high in wet crops of hillslope 40.

Influence of land use change.—There was little land cover change to hillslope 111, and these small changes did not alter runoff or soil water content (Fig. 4a, b). In contrast, large differences occurred on the plains hillslopes. There was less runoff and soils were much drier with wheat/fallow than with potential steppe vegetation on hillslope 140. Because irrigation maintained soil moisture, runoff and volumetric soil water content were much higher in the irrigated crops of hillslope 40 than in the steppe. Runoff from irrigated crops was high and continuous from the onset of irrigation until harvest. Evaporation did not differ between steppe and wheat–fallow vegetation in hillslope 140, but was three times greater in hillslope 40, where water was augmented by unlimited irrigation to crops (Fig. 4c).

Annual net carbon production increased by a factor of four, from 262 to 1134 g $C \cdot m^{-2} \cdot yr^{-1}$, and the amount of water transpired increased by a factor of four, from 102 to 437 mm/yr, when steppe was converted to irrigated crops in hillslope 40 (Fig. 4d, e). The mixed wet crop and steppe type accumulated 1134 g C/m^2 compared with 262 g C/m^2 for the steppe-only potential vegetation in hillslope 40. Conversion of shortgrass steppe to mixed steppe and dryland crops in hillslope 140 also resulted in net C gain of 218 g C/m^2, an increase of 85%. Photosynthesis and respiration changes were negligible between current and potential vegetation for the mountain hillslope 111, where land cover changes were minimal.

Soil water was lower in the dry crop vegetation relative to steppe, due to greater ET losses in the croplands. Soil water content in the dry crops rarely exceeded 20%, and was between 10 and 15% through the growing season. Soil water was 12% greater throughout the year for the steppe (Fig. 4b). While steppe grasses were never stressed by low predawn water potentials, the wheat–fallow vegetation was subjected to values of −1.8 to −2.0 MPa late in the growing season (Fig. 4f).

Land use change from steppe to croplands caused an increase in early-season photosynthesis and transpiration. Rates of net photosynthesis increased earlier and decreased earlier in the mixed dry crop and steppe land cover than for steppe in hillslope 140. For hillslope 40, rates for net photosynthesis began to increase earlier in the mixed wet crop and steppe current land cover than in the steppe potential land cover.

Discussion

Comparison of RHESSys results with measured values

The simulation results for annual above- and belowground net primary productivity agreed well with measured values for the different vegetation types (Table 6). The RHESSys output for tundra was 269 g $C \cdot m^{-2} \cdot yr^{-1}$ (108 g C aboveground if one assumes that belowground productivity is 150% that reported for aboveground productivity) (Webber and May 1977). This fell within the reported ranges of measured aboveground production of 40–140 g $C \cdot m^{-2} \cdot yr^{-1}$ (Webber and May 1977, Bowman et al. 1993, Walker et al. 1994). Coniferous forest productivity, simulated at 326 g $C \cdot m^{-2} \cdot yr^{-1}$, fell within the 137–344 g $C \cdot m^{-2}\ yr^{-1}$ range of above- and belowground productivity measured by Arthur and Fahey (1992). Our simulated grassland above- and belowground result, 411 g $C \cdot m^{-2} \cdot yr^{-1}$, or ~164 g aboveground $C \cdot m^{-2} \cdot yr^{-1}$, was slightly higher than the range of 100–150 g $C \cdot m^{-2} \cdot yr^{-1}$ reported for aboveground productivity by Sala et al. (1988). Crop comparisons are not presented, because while crop yield is readily available, total aboveground production for crops is rarely measured.

Although we made no attempt to develop a hydrologic budget with our simulations, our modeled water parameters were within the same order of magnitude as the measured values presented by Dennehy et al. (1993; Table 6). The simulated precipitation for 1992, 2.54×10^{10} m^3/yr, was close to the long-term mean

TABLE 6. Simulated and measured values for productivity and hydrologic parameters for the South Platte Basin.

Parameters	Simulated values	Observed values
Net primary production (g $C \cdot m^{-2} \cdot yr^{-1}$)		
Tundra, aboveground	108	40–140 (Webber and May 1977, Bowman et al. 1993, Walker et al. 1994)
Coniferous, above- and belowground	326	137–344 (Arthur and Fahey 1992)
Shortgrass, aboveground	164	100–150 (Sala et al. 1988)
Hydrologic inputs (m^3/yr)		
Precipitation	$25\,432 \times 10^6$	$24\,680 \times 10^6$ (Dennehy et al. 1993)
Trans-basin diversions	not simulated	494×10^6 (Dennehy et al. 1993)
Hydrologic outputs (m^3/yr)		
Evaporation	$14\,688 \times 10^6$	
Transpiration	$11\,220 \times 10^6$	
Sublimation	401×10^6	
Evapotranspiration (nonirrigated)		$21\,842 \times 10^6$ (Dennehy et al. 1993)
Consumptive water use		2382×10^6 (Dennehy et al. 1993)
Reservoir and stream		494×10^6 (Dennehy et al. 1993)
Sum evaporation, transpiration, and sublimation	$26\,309 \times 10^6$	$24\,718 \times 10^6$
Discharge	6162×10^6	485×10^6 (Dennehy et al. 1993)

precipitation of 2.47×10^{10} m^3/yr. The combined simulated flux of moisture to the atmosphere, evaporation, transpiration, and sublimation was 2.66×10^{10} m^3/yr, compared with the estimated 2.47×10^{10} m^3/yr of Dennehy et al. (1993). Discharge values were not as well matched with the measured values, probably because we made no attempt to match the amount of water we used to irrigate the wet crops with actual values.

The conversion of 21 000 km^2 steppe and 2300 km^2 coniferous vegetation to dry and irrigated cropland resulted in 80% more primary production for the South Platte Basin (Table 3). In contrast, a −2°C cooling increased basin production by only 3%, and a +4°C warming decreased basin productivity by 16% (Table 4). Clearly, land use has a greater influence on regional carbon stocks than does warming or cooling. In this, our findings corroborate those of Burke, Schimel, and Parton and their colleagues (Parton et al. 1987, Schimel et al. 1990, Burke et al. 1991).

Basin-wide evaporative losses increased by 31% as a result of land use change, compared with a decrease of 15% from cooling and an increase of 28% for warming. Climate warming, therefore, was as important to the regional evaporative flux as land use change. Transpiration increased by 84% as a result of land use change, whereas there was very little basin-wide response to cooling and warming, with changes of −9% and +3%, respectively. The increase in the transpiration flux reflects the marked increase in the LAI of lands planted to crops.

Basin-wide estimates are somewhat misleading, since very different dynamics were displayed by the individual vegetation types. Crops receiving irrigation water lost far more to the atmosphere via transpiration and evaporation than did wheat–fallow and steppe. This illustrates that land use change was important, but perhaps more important was the availability of irrigation water. The total annual water lost to the atmosphere from steppe or dry crops was 350 and 366 mm, respectively. These values are very close to the long-term precipitation mean of 334 mm for the plains part of the South Platte Basin. In contrast, the wet crops lost 969 mm water via evaporation and transpiration, clearly a result of additional water supplies.

The irrigated croplands also lost a large amount of water via discharge, as was seen for hillslope 40 in Fig. 4a. Runoff from the irrigated land was >700 mm, compared with 59 mm from this hillslope with shortgrass steppe. We have no way of verifying actual loss from this hillslope, but there is anecdotal evidence to suggest that the large discharge is not unreasonable. Irrigation accounts for 93%, or 2215×10^6 m^3/d, of consumptive water use of South Platte Basin water, and irrigation return flows are 4610 m^3/d (Dennehy et al. 1993). In the mid-1800s, surface flow in the South Platte River disappeared each summer for the last 200 km of river before its confluence with the North Platte. Since 1910 the river has remained perennial due to irrigation development and irrigation return flows (NRC 1992).

Annual evaporation decreased by 13% in both steppe and dry crops with cooling, and increased by 20% with warming (Table 4). Losses via transpiration were similar for steppe; less water was transpired with cooling and more was transpired with warming. Transpiration from dry crops, on the other hand, decreased only slightly (2%) with cooling, and decreased substantially (15%) with warming. The mean annual soil water content for dry cropland from hillslope 140 was 28% with current climate. Annual soil water dropped to 9% with 4°C warming, partly due to a longer growing season of 149 d with warmer climate, compared with 106 d under the current climate scenario. Measured ranges for soil moisture for north-central Colorado are 20–30% moisture at field capacity, and 8–10% at wilting

point (Lapitan and Parton 1996). Decreased transpiration and a longer growing season were thus the result of inadequate soil moisture and high vapor pressure deficits for plant growth, a conclusion that is corroborated by a loss of 27% productivity in dry croplands and increased evaporation under the warming scenario.

Temperature change resulted in significant alterations in hydrologic and other ecosystem properties. Tundra, especially in the spring, exhibited a strong response to temperature. May is a critical time for tundra vegetation, and there was a strong decline in production (83%) from 23 to 4 g $C \cdot m^{-2} \cdot mo^{-1}$ when the current temperatures were cooled. There was an even stronger increase, 104% more plant productivity, or 47 g $C \cdot m^{-2} \cdot mo^{-1}$, with warming. Water losses via transpiration and evaporation were equally responsive to temperature changes, also primarily in the spring, although the absolute volumes of water were not great. May transpiration losses increased 223% over the control, to reach nearly 10 mm, and evaporation increased by 36% to 19 mm. In contrast to the plains vegetation, water was not limiting to productivity or evaporative water loss. Under the current climate scenario, 173 mm was evaporated or transpired annually to the atmosphere from tundra, far lower than measured mean annual precipitation of 1099 from Loch Vale Watershed.

The coniferous vegetation type was a broad collection of forest vegetation ranging from open ponderosa pine savanna below 2800 m elevation and on south-facing slopes, through dense "dog-hair" stands of lodgepole pine between 2500 and 2900 m, to mesic Englemann spruce and subalpine fir on north-facing slopes and above 2900 m (Stohlgren and Bachand 1997). Soil depths for forest hillslopes were variable, ranging from an estimated 15 cm depth to over 60 cm, contributing to the complex response predicted from such different areas. Responses to climate variation differ among species and with soil depth, so our lumped approach should be taken only as a general guide of forest behavior. For example, low elevations underwent water stress at the same time that high elevations were saturated with snowmelt water. Overall, plant productivity declined with both warming and cooling scenarios, but for different reasons. Low-elevation forest soils dried to below wilting point earlier with warming, preventing photosynthesis. The onset of the growing season was delayed with cooling by ~11 d. Transpiration and evaporation declined with cooling and increased with warming. The combined annual water lost through evaporation and transpiration (317 mm) is slightly less than the measured mean annual precipitation of 432 mm at Estes Park. With warming, evaporative and transpiration losses increased to 392 mm for the entire forest vegetation band, so it is likely that at the lowest elevations PET exceeded ET, creating water stress. Field capacity for forest soil moisture has been reported as 30%, and wilting point as 20% (Sanford et al. 1991). The annual mean soil water holding content for hillslope 111 was 28% under the control climate, and declined to 24% with warming. Again, however, our results did not take into account the extreme spatial variability of the coniferous vegetation type.

Our warming and cooling experiments did not include any influence of increasing CO_2. There is some evidence that the changes in plant and community dynamics brought about by elevated CO_2 will be complex. Polley et al. (1996) discuss possible encroachment of woody plants onto grasslands because elevated CO_2 often increases nitrogen use efficiency and growth of woody and other C_3 plants, and increases tolerance of C_3 plants to heat and drought. Short-term experiments have shown that rising levels of CO_2 shift the competitive balance to favor C_3 over C_4 plants, but it is not yet known whether this is true over the long term (Morse and Bazzaz 1994, Polley et al. 1996). Elevated CO_2 increases water use efficiency; in water-limited environments this should increase primary production (Polley et al. 1996). Over the long term, we expect no net change in water flux for the South Platte Basin, however, because the increased soil moisture brought about by elevated CO_2 will be offset by the increased leaf area (Ojima et al. 1993). Our results are similar to RHESSys simulations of wetter regions of North America, where fertilization with CO_2 increased respiration significantly, but did not have a great effect on water fluxes or net photosynthesis (Band et al. 1996).

Response to regional land use change combined with global change will be more complex than we have portrayed. Land cover change exerted a large influence on annual plant productivity and water fluxes when grasslands were converted to crops, while the effect of temperature change on productivity and water fluxes was stronger in the mountain vegetation. This point emphasizes the importance of topographic and climatic complexity to understanding regional responses (Lammers et al., 1997). Recent records suggest that cooling is occurring in the mountains coincident with warming on the plains (Williams et al. 1996, Chase et al. 1998, Stohlgren et al. 1998). Our results should be used more as an heuristic tool, therefore, than as interpretation of future responses.

Implications for feedbacks to atmosphere and regional climate

There is a large and well-established body of literature describing the effects of humans on local, regional, and global environments (see, for example, Goudie 1990, Turner et al. 1990). There is no question that human activity has altered landscapes through deforestation, grazing, and agriculture, for thousands of years (McDowell et al. 1990). There is increasing evidence that, in addition to altering processes occurring at the land surface, irrigated agriculture can alter regional climate. Studies of the U.S. southern Great Plains have documented increases in the severity and

frequency of summer storms and decreases in summer temperatures accompanying irrigation (Beebe 1974, Barnston and Schickedanz 1984, Rabin and Martin 1996). Pielke et al. (1997) have suggested that the cumulative effects of regional land use changes on climate may amount to a global-scale force in climate change.

Land surface energy fluxes are influenced by albedo, surface roughness, and especially moisture flux (Copeland et al. 1996). Water vapor is globally the most significant greenhouse gas, and may also be a major influence on regional climate dynamics (Chase et al. 1996). Our simulations suggest that 420 mm of water from the South Platte Basin is transmitted to the atmosphere from agricultural lands (sum of annual transpiration and evaporation from Table 4), up from a simulated 306 mm from pre-settlement vegetation. Our results strongly suggest that more moisture is evaporated and transpired and for a longer period during the growing season in dry and especially irrigated croplands. Mesoscale model results describe the physics by which the added moisture influences the climate through increasing convective instability enhancing local circulations (Anthes 1984, Segal et al. 1989, Lee 1992, Seth and Giorgi 1996, Chase et al. 1998). Chase et al. (1998), in simulations of the South Platte Basin climate with the Regional Atmospheric Modeling System (RAMS), have shown that land use change from native grasses to agriculture and urbanization could produce a regional cooling effect throughout the entire basin, including mountainous zones. Records of climate, river discharge, and seedling migration to lower elevations corroborate such a regional cooling (Williams et al. 1996, Stohlgren et al. 1998).

It is abundantly clear that water use change, more than land use change, is driving the responses observed in our simulations. Much of this water is not locally obtained. Native water does not drive land use or climate change in the South Platte Basin. "The West is defined . . . by inadequate rainfall. We can't create water, or increase the supply. We can only hold back and redistribute what there is," wrote Wallace Stegner (1987:6). Irrigation in the western United States leads to significant seasonal and spatial redistribution of water, and this influences the flux of water vapor into the atmosphere. Water for irrigation, and increasingly, for urban growth, is redirected from the South Platte headwaters and from the Colorado and Arkansas river basins (NRC 1992). The South Platte Basin water transfers are among the largest in the country, and support highly productive farming in eastern Colorado (NRC 1992). Much has been written about the consequences, ecological, as well as economic and social, of large western interbasin water transfers, including those that supply the growers and residents of the South Platte Basin. Water transfers always have repercussions; while they benefit those communities that receive and can profit by additional water, dewatered communities suffer. Ecological repercussions are complex. High-elevation and western-slope aquatic and riparian communities have suffered from inadequate volumes, while irrigation return flows have changed the South Platte from seasonally dry to perennial (NRC 1992). The results from our RHESSys simulations suggest yet one more environmental change caused by water redistribution: transpiration losses of water sufficient to change the regional climate.

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