A Comparative Analysis of Hydrologic Responses of Tropical Deciduous and Temperate Deciduous Watershed Ecosystems to Climatic Change'

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Abstract--Lmg-term monitoring of ecological and hydrological processes is critical to understanding ecosystem function and responses to anthropogenic and natural disturbances. Much of the world's knowledge of ecosystem responses to disturbance comes from long-term studies on gaged watersheds. However, there are relatively few long-term sites due to the large cost and commitment required to establish and maintain them. Knowledge gamed from these sites is also important for predicting responses to future disturbances, such as climatic change, and these sites should be the focal point for the development and validation of predictive models. In this study, we apply a hydrologic model (PROSPER) using climate, vegetation, and soil parameters from watersheds in the mesic southeastern United States and in the dry tropical forests of western Mexico to assess the overall effects of climatic change (increased temperature and [CO_2]) on watershed hydrology. We found that evapotranspiration (ET) increased substantially in both ecosystem types, with increases ranging from 24 to 42%. These increases were directly attributable to changes in leaf energy balance and evaporative demand. Streamflow decreased more substantially, with virtually no streamflow under the greatest temperature increase scenario (+20%) at the site in western Mexico. Decreased stomata1 conductance was not sufficient to offset the effects of increased temperature.

Resumen—La hidrología de los ecosistemas forestales arbolados es un integrador clave de respuestas fimcionales al disturbio. El monitoreo a largo plazo de cuencas y clima proporciona la base para evaluar impactos potenciales de stresses, tales como el cambio climatico del clima, en la función del ecosistema. En este estudio, nosotros usamos un modelo enfocado a evaluar los impactos del cambio climático en evapotranspiración en dos ecosistemas contrastantes: coweeta hydrologic laboratory (usa) y la estación de biología de chamela (México). coweeta es un sitio de investigación ecológica a largo plazo (us-her) y es operada por el usda forest service research y chamela es una estación operada por la universidad nacional autónoma de México. Los dos consisten en una red de cuencas de monitoreo climatico a largo plazo.Coweeta se localiza en las montañas apalaches del oeste de Carolina, usa y se caracteriza por clima moderado húmedo (la temperatura media anual es de 12.6 °C y precipitación anual de 1786 mm). chamela se localiza en el estado de jalisco en la costa pacífica de México. La precipitación media anual es de 707 mm, con patrones estacionales pronunciados (80% de la precipitación cae entre Julio y Octubre), y la temperatura media anual es de 25 "C. Nosotros usamos el modelo hidrológico prosper para simular los impactos de cambio climatico (aumentó temperatura y [CO_2]) en las respuestas hidrológicas de estos ecosistemas para evaluar diferencias en la magnitud de la respuesta y para evaluar diferencias en las variables clave. Nosotros también demostramos la importancia del monitoreo a largo plazo para evaluar los patrones de respuesta y validar la construcción del modelo.

Watershed scale analyses of hydrologic responses to disturbances requires a commitment to long-term monitoring and an understanding of the basic principles regulating the flow of water through the soil-plant-atmosphere continuum. Detecting disturbance caused departures in hydrologic parameters such as streamflow, soil moisture, or evapotranspiration (ET) from "undisturbed" conditions requires knowing the inherent variation in watershed processes, which can only be determined from long-term measurement and analyses. However, establishment and maintenance of long-term hydrologic studies is expensive and hence, there are relatively few gaged watersheds with long-term records in North America. Where small catchment studies have been employed, considerable knowledge on basic hydrologic principles, hydrologic responses to forest management (Swank and Johnson 1994, Swank and Vose 1994), and hydrologic effects of long-term chronic atmospheric deposition (Swank and Vose 1997) has been obtained.

Knowledge gained from long-term watershed studies will also be critical for assessing (and detecting) the potential effects of future disturbances, such as climatic change, on watershed processes. Examination of climate-vegetation-hydrology responses from historical climatic data provides some insight into potential future responses to climatic change; however, conditions in the next century (i.e., elevated temperature and [CO_2]) are likely to exceed the range of variability exhibited in historical data. Hence, modeling hydrologic responses-especially if the model is physiologically based, validated, and parameterized on gaged watersheds-provides a useful tool to evaluate watershed scale responses to climatic change.

The hydrologic behavior of a watershed is determined by precipitation input, as modified by soil moisture storage and ET use. Changes in any of these determining factors will influence hydrologic behavior. Climatic change (i.e., increased [CO_2], increased air temperature) has the

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potential to directly alter ET via changes in leaf energy balance, evaporative demand, and stomata1 conductance. If substantial changes in ET occur as a result of climatic change, then watershed hydrologic behavior will also be altered with potential indirect effects on stream water, groundwater recharge, and soil moisture availability. These indirect responses could result into substantial effects on terrestrial and aquatic flora and fauna, and ecosystem processes such as nutrient and carbon cycling. Effects of climatic change on watershed hydrology has generally received less attention than potential effects on productivity. In part, this lack of attention might be due to a general consensus of increased water use efficiency (WUE) under elevated [CO_2] which is thought to offset drought effects (Norby and O'Neil 1991, Gunderson et al. 1993). However, most of these studies have not quantified the coincident effects of increased temperature on leaf energy balance and the potential feedbacks which might offset WUE gains. Similarly, most of these studies have been conducted under controlled greenhouse or garden conditions, and the soil-vegetation-atmospheric continuum has not been adequately represented.

The objective of our paper is to use a simulation model, PROSPER, to evaluate the effects of elevated air temperature (with and without changes in WUE) on key hydrologic parameters. Simulations were performed for two contrasting ecosystem types: the dry tropical forests of western Mexico and the mesic temperate deciduous forests of western North Carolina, USA. The primary purpose of this modeling exercise was not to provide exact predictions of watershed response, but rather to demonstrate the usefulness of a combined long-term measurement and modeling approach to understanding watershed processes in two contrasting ecosystems. Comparative studies are particularly useful for determining the robustness of model performance and for determining the general applicability of watershed ecosystem responses.

Description of PROSPER

We chose PROSPER to simulate hydrologic responses to climatic change because it has been validated and applied successfully in both conifer and hardwood forests in North America (Swift et al, 1975, Huff and Swank 1985, Vose and Swank 1992), and has performedwell in regional ET assessments (USDA 1980). PROSPER was developed from first principles of physiological, physical, and climatological processes regulating watershed hydrology and refined using data from long-term disturbed and undisturbed gaged watersheds at the Coweeta Hydrologic Laboratory (see site description section below) (Swift et al. 1975, Huff and Swank 1985). The combination of physical and biological controls on ET allows the model to be sensitive to changes in air temperature (via effects on energy balance and evaporative demand) and [CO,] (via effects on stomata1 conductance). PROSPER has been described in detail elsewhere (Goldstein and Mankin 1972, Huff and Swank 1985), thus, only a general description is provided here. PROSPER is a phenomenological, one-dimensional model that links the soil, vegetation, and atmosphere. Plant and soil characteristics are combined in an ET surface that is characterized by a surface resistance to water vapor loss. This resistance, which is analogous to the relationship between stomata1 resistance and leaf water potential, is a function of the water potential of the ET surface. Evapotranspiration is predicted by a combined energy balance-aerodynamic method that is a function of the surface resistance to vapor loss. PROSPER applies a water balance (through the use of electrical network equations) to the vegetation with the soil divided into layers. Hence, the flow of water within and between soil and plant is a function of soil conductivity, soil water potential, root characteristics for each soil layer, and surface water potential. Soil water flux during unsaturated soil conditions is governed by hydraulic conductivity, where hydraulic conductivity is estimated from the relationship between soil matric potential and moisture content using the procedure described in Luxmoore (1973). The version of PROSPER used in this study simulates ET and soil water redistribution between soil layers on a daily timestep.

PROSPER requires the following site-specific climatic data: solar radiation (daily total), precipitation (daily total), windspeed (daytime mean), air temperature (daytime mean), andvapor pressure (daytime mean). With the exception of precipitation, these data are used to compute evaporative demand in the energy balance-aerodynamic equation (Swift et al. 1975). In addition to climatic data, PROSPER requires several key soils andvegetation parameters (Table 1). Parameters shown in Table 1 represent "key" variables which substantially influence the simulation results. For the most part, these parameters were measured directly on the site; however, in some cases "best estimates" from the literature were utilized.

To evaluate the effects of climate change and elevated [CO_2] on hydrologic responses, we examined monthly and annual values of transpiration, ET, and drainage below the lowest soil layer. At Coweeta, drainage has been shown to be reflective of streamflow in all but the driest years (Vose and Swank 1992, Vose and Swank 1994), when drainage from soil water below the root zone is used to recharge a normally saturated deep soil layer. Shallow and coarse soils at Chamela would also suggests that drainage would be reflective of streamflow at Chamela.

Site Descriptions

Climate, soils, and vegetation data for the temperature deciduous forest were derived from a mixed hardwood forest (WS 2) at the United States Department of Agriculture, Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, located in the Blue Ridge Provence of the southern Appalachian Mountains of western North Carolina, USA. The Coweeta Hydrologic Laboratory has been in continuous operation since 1934 and has been a National Science Foundation Long-Term Ecological Research Site since 1980. The climate is classified as marine, humid temperate with water surplus in all seasons (Swift et al. 1988). The average annual precipitation varies from 1700 mm at the lower elevations to 2500 mm on the upper slopes. The mean monthly temperature ranges from 3.6 °C in January to 20.2 °C in July. Watershed 2 is 12 ha gaged watershed (weir elevation = 670 m), has a relief of 300 m, and has a south aspect. Soils are deep (6 m) ultisols and are

Table 1 .-Summary of key parameters required to run PROSPER.

Input parameter	Units	Coweeta,	Chamela
Canopy and aboveground			
Leaf Area Index	$m^2\ m^{-2}$	6.0	5.0.
Start leaf-out	Julian day	100	135
End leaf-out	Julian day	150	213
Start leaf-fall	Julian day	260	244
End leaf-fall	Julian Day	306	365
stomatal resistance (min)	s cm-'	2.5	2.0
'stomatal resistance (max)	s cm-'	50.0	50.0
Soils and belowground			
Thickness of each soil layer	cm	0-30;30-90;90-180	O-5050-1 00
Field capacity by layer	$cm^3\ cm^{-3}$	O-30 = 0.29	O-50 = 0.16
		30-90 = 0.30	50-100 = 0.15
		90-1 60 = 0.26	
Root surface area (%)	$m^2\ m^{-2}$	O-30 = 0.20 (75%)	O-50 = 0.10(85%)
		30-90 = 0.01 (25%)	50-100 = 0.06 (15%)

represented by typic hapludults and humic hapludults. Details of climate, vegetation, and soils are reported elsewhere (Swank and Crossley 1988).

Climate, vegetation, and soils data for the dry tropical forests were derived from a long-term ecosystem study initiated in 1981 at the Estacion de Biologia Chamela of the Universidad Nacional Autonoma de Mexico. Chamela is located in the state of Jalisco on the Pacific coast of Mexico. The climate of Chamela is influenced by tropical cyclones producing a highly variable annual rainfall regime (Garcia-Oliva et al. 1991). Mean precipitation is 707 mm (1977-1988) with more than a 500 mm difference between the wettest and driest year. Rainfall is strongly seasonal with 80% of the precipitation falling between July and October, with September being the wettest month. Temperature fluctuates little during the year and averages 25 °C. Data from watershed 1 (WS 1), a 15 ha gaged watershed ranging in elevation from 60 to 160 m, was primarily used to parameterize PROSPER. The predominant vegetation is the tropical deciduous forest type described by Rzedowski (1978), where leaf development and senescence patterns are controlled by rainfall. Soils are shallow (0.5 to 1 m) and predominantly sandy loams derived from rhyolite parent material. Details of the vegetation are reported in Maass et al. (1995) and Martinez-Yrizar et al. (1992) and details of the soils are reported in Maass et al. (1988).

Climate Change Scenarios

Estimates of changes in air temperature as a result of elevated [CO_2] vary considerably depending on the choice of global circulation model (GCM). For example, in the southern United States, air temperature responses range from +3 °C annually to +7 °C annually (McNulty et al. 1998). Estimates of changes in precipitation are more complex, with varying predictions in the timing of intra-annual rainfall patterns. In general, predicted changes in total annual precipitation are small (1 to 3%) (McNulty et al. 1998). We used actual climatic data for a “typical year” at our study sites, and altered air temperature by +10% and +20%, which resulted in increases in the range reported by GCM models (i.e., -2 to 7 °C). Because of the greater uncertainty and smaller magnitude of predicted precipitation response to elevated [CO_2], we made no changes to precipitation amount or intra-annual distribution.

There are vastly different reports in the literature about the impacts of elevated [CO_2] on stomata1 conductance and/or leaf level transpiration. Some of these differences are probably related to differences in species; however, varying results have also been reported within the same species. For example, Hennessey and Harinath (1998) report decreased stomata1 conductance in loblolly pine (*Pinus taeda*) at mid-level [CO_2] increases, while Teskey et al. (1998) reported no increases at any level of elevated [CO_2]. The vast majority of studies have reported either no change or a decrease in stomata1 conductance (Eamus and Jarvis 1989, Cuelemans and Mousseau 1994) which translates into decreased transpiration and increased water use efficiency (i.e., moles CO_2 assimilated per mole water transpired). To simulate the potential role of decreased stomata1 conductance on mitigating the effects of increased temperature, we decreased stomatal conductance by 2-fold in the +20% temperature simulations. Because PROSPER's model structure is based on an electrical resistance analogy, the stomata1 conductance response was accomplished by doubling stomata1 resistance.

Results and Discussion

Hydrology Under Ambient Climate

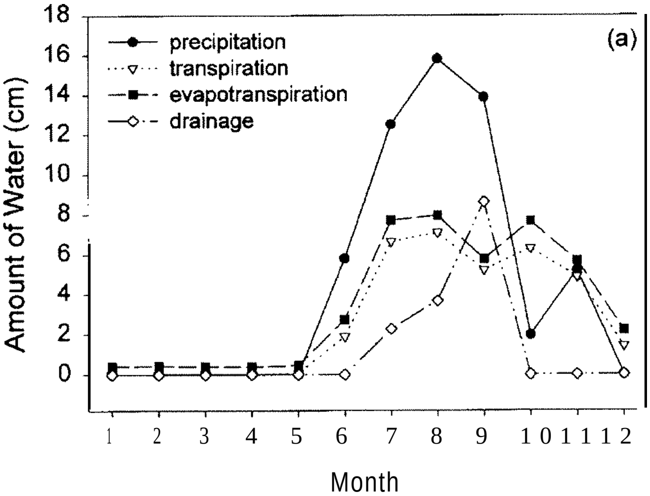
They were substantial differences in hydrologic processes between the Chamela and Coweeta watersheds under ambient climatic conditions. At annual scales, ET was considerably greater at Coweeta (103.9 cm $year^{-1}$) than at Chamela (41.3 cm year-') (Table 2); however, ET at Chamela was 75% of precipitation vs. 57% at Coweeta. Hence, evaporative demand was greater at Chamela, but limited by precipitation inputs. As indicated by ET-precipitation patterns at each site, drainage was considerably greater at Coweeta (80 cm $year^{-1}$) than at Chamela (9 cm year-'). These patterns and amounts are consistent with streamflow measure-

Table 2.—Predicted annual evapotranspiration and drainage under elevated air temperature and [CO,].

Climatic conditions	Coweeta ET	Coweeta Drainage	Chamela ET	Chamela Drainage
	cm/year			
ambient	103.9	79.6	41.3	10.2
+10% Temperature	134.2	49.6	51.2	1.6
+20% Temperature	148.7	35.4	53.8	0.2
+20% Temperature; 2 x resistance	134.2	49.2	49.1	3.4

ments at each site, which show perennial streamflow at Coweeta and ephemeral streamflow at Chamela.

Monthly patterns reflect differences in the seasonality of climatic driving variables (especially precipitation) and leaf area index development and senescence patterns (Fig. 1a,b).



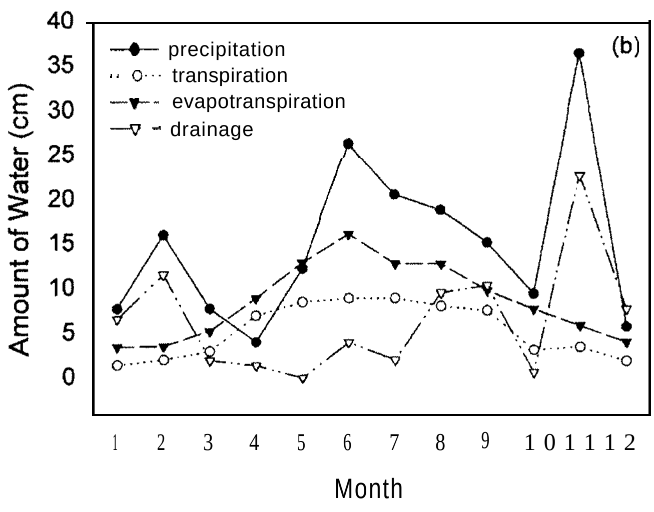


Figure 1.-Monthly precipitation, transpiration, evapotranspiration, and drainage under ambient climatic conditions for (a) Chamela and (b) Coweeta.

For example, precipitation patterns at Chamela resulted in no rainfall for a continuous six month period (December through May) (Fig. la). Beginning in June, rainfall stimulates leaf area growth at Chamela (Maass et al. 1995) and ET occurs. During June, rainfall inputs were not sufficient to produce drainage, as inputs were utilized in soil recharge and transpiration. Peak drainage occurredin September. In contrast, precipitation inputs at Coweeta were consistent, but variable throughout the year (Fig. lb). At Coweeta, leaf area development and senescence patterns are not a function of rainfall. Instead, these seasonal patterns are a function of photoperiod and temperature, which are relatively consistent from year-to-year. In contrast to patterns observed at Chamela, drainage occurred throughout the year, w peak values occurring during the leaf-off period (Novem through April).

Large differences in leaf area phenology, soils, and ambient climatic patterns between Chamela and Coweeta presents an interesting contrast on how these ecosystems might respond hydrologically to climatic change. A priori, we expected that the magnitude of response to increased temperature would be considerably larger at Coweeta because of a cooler environment and more available soil water (due to deeper soils and greater precipitation) relative to Chamela.

Hydrology Under Elevated Temperature

At an annual scale, effects of elevated temperature on ET were considerable for both Coweeta and Chamela (Table 2 and Fig. 2). For a 10% increase in air temperature, ET increased 29% and 24% above ambient for Coweeta and Chamela, respectively. The effect of a 20% increase in temperature was disproportionately greater at Coweeta, where ET increased 43% and Chamela ET increased 30%. A substantially reduced stomata1 conductance (2 x ambient stomata1 resistance), mitigated the effects of the 20% increase in air temperature to an effect comparable to a 10% air temperature increase (i.e., 29% and 19% increase in ET for Coweeta and Chamela, respectively) (Fig. 2).

Effects on drainage were proportionally more significant at Chamela than at Coweeta (Fig. 3). At 10% increased temperature, drainage at Chamela decreased 84% and was essentially eliminated (98% decrease) at +20% air temperature. At Coweeta, drainage decreased 38% and 58% at +10% and +20% air temperature, respectively. Like results observed with ET, decreased stomata1 conductance offset the responses to +20% air temperature to produce drainage

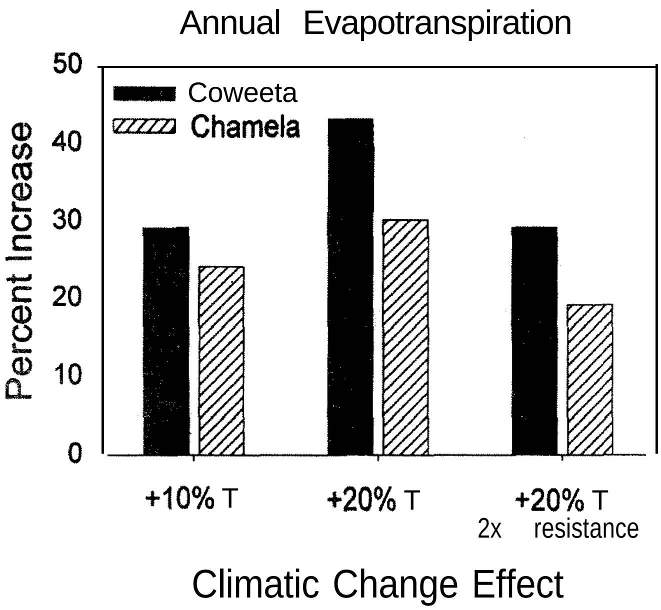


Figure P.-Percent increase (above ambient) in annual **evapotranspi-** ration under elevated temperature and [CO,].

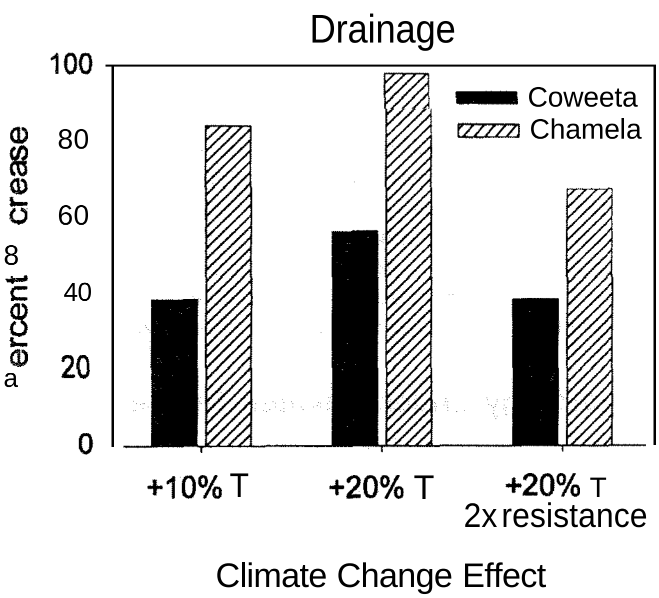


Figure L-Percent decrease in drainage (below ambient) in annual drainage under elevated temperature and [CO,].

responses comparable to (Coweeta) or lower than **(Chamela)** those observed with a **+10%** air temperature change.

Elevated temperature altered monthly ET and drainage patterns at both Chamela (Fig. **4a,b,c)** and Coweeta (Fig. **5a,b,c).** For example, at Chamela, peak drainage occurred in September under ambient climatic conditions (Fig. la), but shifted to August under **+20%** air temperature (Fig. 4b). Changes were even more significant at Coweeta, where elevated temperature **(+20%)** essentially eliminated drainage from April through October (Fig. 5b). **Over** the long-term, changes of this magnitude would severely alter the hydrologic behavior of streams, perhaps shifting from perennial to ephemeral streamflow patterns. Implications for aquatic species adapted to perennial streamflow would be severe.

Results of these simulations indicate that substantial changes in watershed hydrology are possible with climatic change. They also indicate that **while.decreased** stomata1 conductance (i.e., increased water use efficiency) might mitigate some of the effects of elevated temperature, substantial alterations in ET and drainage will still occur. Our results concur with those reported by Borchers and Nielson **(1998),** who used large scale models incorporating changes in species composition and WUE , to simulate a 20 to 40% decrease in runoff (drainage) in the southern United States as a result of climate change. In contrast, **McNulty** et al. (1998) used a combined productivity and hydrology model **(Pnet-IIS)** and predicted that reductions in leaf area (due to increased respiration costs) would offset increased evaporative demand, and runoff could increase 40 to 80% in the

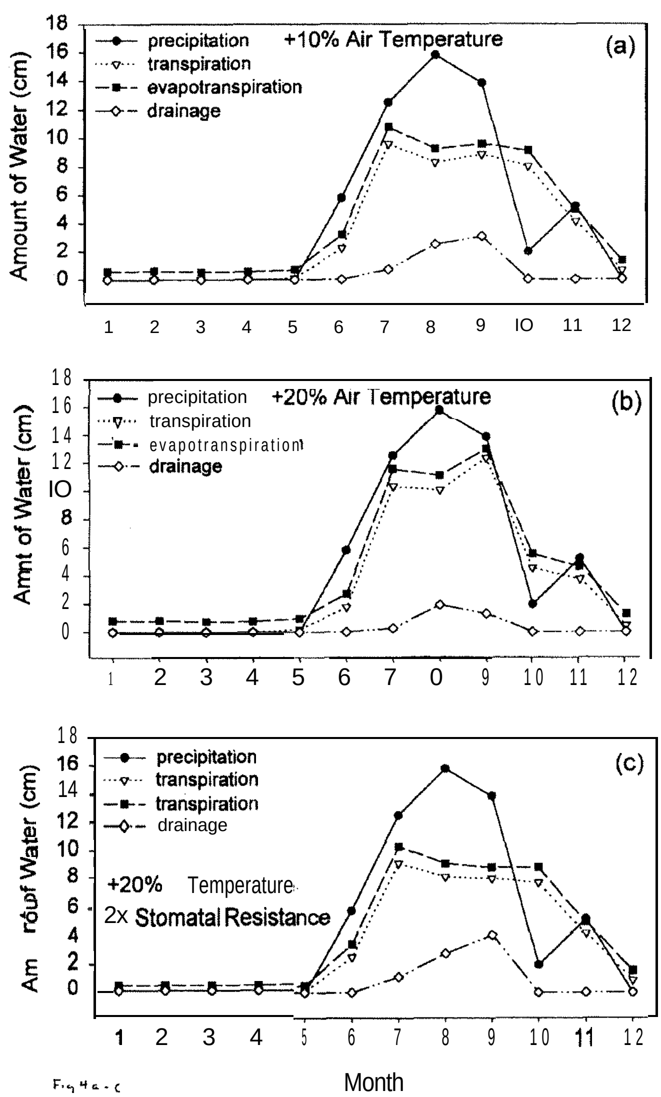


Figure **4.—Changes** in monthly patterns of hydrologic parameters for Chamela.

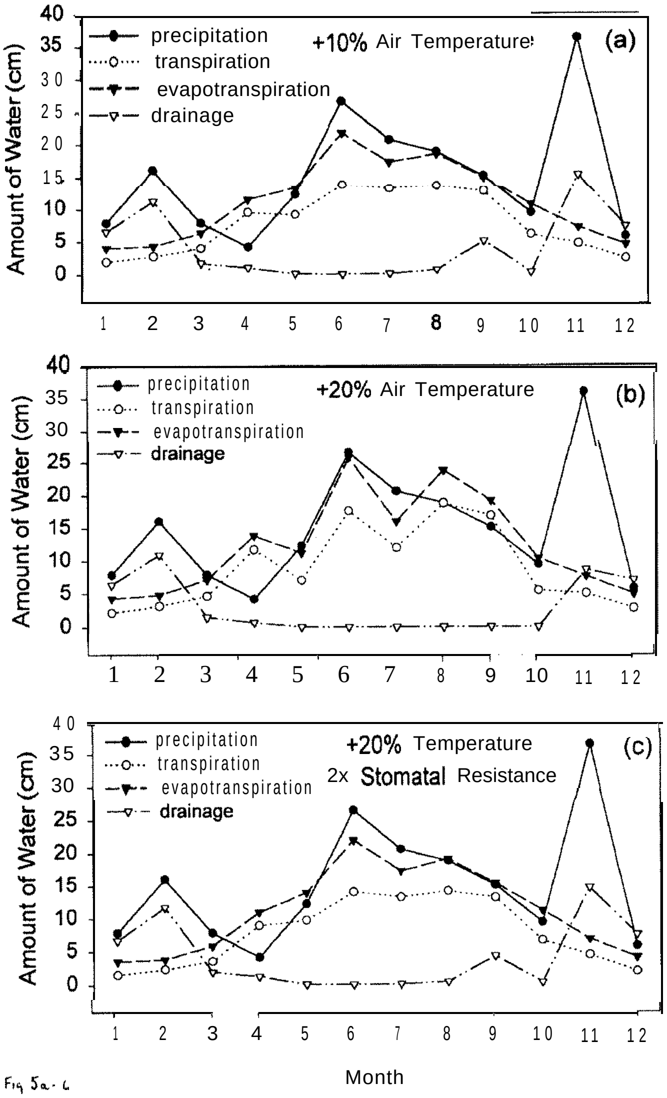


Figure 5.—Changes in monthly patterns of hydrologic parameters for Coweeta.

southern U.S. We did not consider the effects of increased temperature on leaf area or leaf area dynamics in our simulations because of considerable uncertainty about the role of respiration acclimation in mitigating the effects of increased temperature on leaf carbon balance (Amthor 1984). However, we know from sensitivity analyses of PROSPER and direct watershed-scale measurements (Swank et al. 1988) that changes in leaf area could have a substantial effect on our simulation results and this represents a considerable uncertainty in the results we obtained. Similarly, due to our short simulation interval (annual), we did not address the issue of changes in species composition. However, we suspect that changes in species composition alone would not substantially change the results we observed-the 2x change in stomata1 conductance is comparable to the range in variability among likely replacement species.

Conclusions

While the results we obtained suggest major changes in ET and streamflow under future climatic regimes, several aspects of our approach merit caution in evaluating the results we obtained. First, [CO_2] increases and resultant changes in temperature and physiological processes are likely to occur incrementally over the next 50-60 years. Changes in species composition and/or acclimation to the changing climate may have an impact on how ecosystems respond. Second, our one-year simulations provide only a snapshot of potential responses. Long-term exposure to significantly elevated temperature and [CO_2] may eventually result in quite different results than we predicted. Finally, we also intend to run simulations over the range of precipitation patterns observed at both sites to understand the interactions between potential effects of temperature and elevated [CO_2] and precipitation amount. Quite different patterns of response might be expected under extremely dry or wet years.

One of the strengths of this analysis is the linkage of detailed long-term measurements with model development, parameterization, and validation. Previous applications of PROSPER at Coweeta have shown excellent correspondence between predicted and measured ET and streamflow. Good performance under ambient conditions strengthens confidence in extrapolations both to altered climatic regimes and to other sites. Data and knowledge from long-term watershed studies provide critical sites for model development and evaluation before widespread application across ecosystems and regions. We are taking a very similar approach to understanding hydrologic processes and driving variables at Chamela (i.e, long-term gaged watersheds) and the model will also be validated at Chamela in the near future.

Acknowledgments

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