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Viewpoint: Atmospheric CO₂, soil water, and shrub/grass ratios on rangelands

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Abstract

The abundance of woody plants on grasslands and savannas often is controlled by the availability of water and its location in soil. Water availability to plants is limited by precipitation, but the distribution of soil water and period over which it is available in these ecosystems are influenced by the transpiration rates of grasses. We discuss implications of recent and projected increases in atmospheric CO₂ concentration for transpiration, soil water availability, and the balance of grasses and shrubs. An increase in CO₂ concentration often reduces potential transpiration/leaf area by reducing stomatal conductance. On grasslands where effects of stomatal closure on transpiration are not negated by an increase in leaf temperature and leaf area, rising CO₂ concentration should slow the depletion of soil water by grasses and potentially favor shrubs and other species that might otherwise succumb to water stress. Predicted effects of CO₂ are supported by results from CO₂-enrichment studies in the field and are compatible with recent models of interactions between resource levels and vegetation pattern and structure.

Key Words: C₄ grasses, competition, rooting depth, stomatal conductance, transpiration

The importance of water availability to the geographic distribution of vegetation types (Whittaker 1975, Woodward 1987, Stephenson 1990) and their productivities is widely-recognized (Rosenzweig 1968, Webb et al. 1983, Sala et al. 1988). Soil water balance, thus, is a key component of current models to predict effects of climatic and atmospheric change on vegetation (Woodward 1993, Neilson and Marks 1994). On grasslands and savannas, where plant productivity is strongly coupled to precipitation (Webb et al. 1983, Sala et al. 1988, Pandey and Singh 1992), water availability in space and time exerts a dominant climatic control on the balance between grasses and woody species. In his study of southern African savannas, Tinley (1982) concluded that soil water availability was the most important factor controlling the relative abundances of grasses and trees or shrubs. Similar conclusions have been drawn in other tropical savannas

(Medina and Silva 1990) where most grasses possess the C₄ photosynthetic pathway. Water balance, however, also affects shrub/grass ratios in temperate and subtropical regions where the two growth forms coexist (Williams et al. 1987). These and other studies (e.g., Neilson 1986, Sala et al. 1992) suggest that relatively small changes in water balance may cause relatively large changes in the structure of grassland ecosystems.

Atmospheric CO₂ concentration has nearly doubled since the last Ice Age, 18,000 years ago (Delmas et al. 1980), and has increased from about 275 ppm (parts per million; Neftel et al. 1985, Raynaud and Barnola 1985) to the present concentration near 355 ppm during the last 200 years. It may rise to twice the current level during the next century (Trabalka et al. 1986). Stomatal conductance usually declines as atmospheric CO₂ concentration rises (Morison 1987). On grasslands, a decline in stomatal conductance that reduces transpiration rate will increase soil water availability during intervals between rainfall. Woody or other plants that were previously excluded by low water availability may be favored as a result.

We review effects of atmospheric CO₂ concentration on stomatal conductance and processes at the leaf, canopy, and higher scales that regulate the effect of stomatal closure on transpiration. We then discuss consequences of slower transpiration for soil water levels and the balance between grasses and shrubs on grasslands and savannas. Effects of climatic changes that may accompany rising CO₂ concentration on grassland vegetation are addressed elsewhere (Parton et al. 1994). Influences of fire, browsing, grazing, and edaphic factors, other than soil water, that affect woody abundance also are not reviewed (Belsky 1990, Archer 1994, Archer et al. 1995). C₄ species dominate many warm temperate and tropical grasslands and savannas. We, therefore, emphasize possible effects of CO₂ on C₄-dominated ecosystems like rangelands of the central and southern Great Plains and southwestern U.S. Consequences of rising CO₂ for transpiration and soil water balance on C₃-dominated grasslands are briefly discussed.

Interactions Between CO₂ Concentration and Transpiration

One of the more consistent, though not universal, effects of an increase in atmospheric CO₂ concentration is a decrease in leaf or stomatal conductance (Morison 1987, Field et al. 1995). Morison and Gifford (1984a) found that leaf conductance of 16, mostly

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C₃, agricultural and horticultural species declined a mean 36% when grown at double the present CO₂ concentration. Few studies report stomatal conductance or resistance of C₄ plants grown at different atmospheric CO₂ concentrations. In our review of the stomatal responses of C₄ plants to CO₂, conductance was reduced an average 34% across 16 observations and 29% across 12 species by an approximate doubling of the current CO₂ concentration (Table 1). Little is known of the stomatal responses of plants grown at lower-than-current CO₂ levels. Available evidence suggests, however, that stomatal conductance may be more sensitive to a given change in CO₂ over subambient than elevated concentrations (Fig. 1; Polley et al. 1996a).

It is important to recognize that conductance is typically measured on sunlit leaves near the tops of well-watered plants. Absolute differences in conductance between CO₂ treatments are usually reduced by water stress (Gifford and Morison 1985), low light levels such as those found within canopies (Knapp et al. 1994), and high leaf-to-air vapor pressure deficits (Morison and Gifford 1983, Bunce 1993).

A decrease in conductance tends to reduce transpiration and lessen the rate at which soil water is depleted in a given environment. For these changes to occur, however, effects of stomatal closure on transpiration must not be offset by an increase in leaf area or leaf temperature, or by feedbacks between transpiration and evaporative demand of the atmosphere.

Most C₃ plants grow and accumulate leaf area faster when atmospheric CO₂ concentration is increased (Poorter 1993), partly because higher CO₂ stimulates photosynthesis. This is particularly true when plants have adequate nutrition and are grown alone or in stands of low density (Bazzaz 1990). There are exceptions (Morgan et al. 1994), but photosynthesis, growth, and leaf area of C₄ plants are relatively unaffected by increases in CO₂ concentration when the soil is wet (Morison and Gifford 1984b, Curtis et al. 1989, 1990, Polley et al. 1994, Dippery et al. 1995, Polley et al. 1996a). Water conserved by closing stomates, how-

ever, may allow plants at high CO₂ concentration to continue growth longer into drought (Gifford and Morison 1985, Owensby et al. 1993b, Samarakoon and Gifford 1995). Higher CO₂ levels may also speed physiological recovery of some plants from drought (Knapp et al. 1993b).

Leaf growth and area in both C₃ and C₄ plants may be limited by resources other than water or CO₂. Low nitrogen availability frequently limits production on C₄ grasslands (Seastedt et al. 1991). The growth response of C₄-dominated tallgrass prairie to elevated CO₂ was limited by low nitrogen availability more during a dry year than during a relatively wet year (Owensby et al. 1994). Production of ungrazed tallgrasses may also be limited by light (Knapp et al. 1993a). These limitations may partially be offset if resource utilization efficiency rises as CO₂ concentration increases. Biomass production per unit of nitrogen increases as CO₂ concentration rises for both C₃ and C₄ species (Owensby et al. 1993a, Polley et al. 1994, Polley et al. 1995). Rising CO₂ increases the amount of carbon fixed per unit of absorbed light in C₃ (Long and Drake 1991), but not C₄ plants (Knapp et al. 1993b).

Other feedbacks may reduce effects of stomatal closure on transpiration. Leaf temperatures may increase when stomates close because less energy will be dissipated by transpiration (Morison and Gifford 1984a). The resulting increase in leaf-to-air vapor pressure gradient will lessen water savings from a decrease in conductance. Transpiration is also influenced by the temperature and humidity of air around and immediately above a plant canopy. When air in this canopy "boundary" layer does not mix with that higher in the atmosphere, its temperature and humidity become highly dependent on transpiration itself. Slower transpiration reduces humidity of the air in the boundary layer and increases the amount of energy that heats the air (Jarvis and McNaughton 1986, McNaughton and Jarvis 1991, de Bruin and Jacobs 1993). These changes, in turn, increase the evaporative demand of air and reduce water savings from stomatal closure. Stable boundary layers develop most frequently above well-

Table 1. The percentage change in stomatal conductance (gs) of well-watered C₄ plants caused by an approximate doubling of the current CO₂ concentration. Stomatal conductance was measured at or near the CO₂ level at which plants were grown. Conductance was reduced by a mean 34% across observations. CTC=closed-top chamber, OTC=open-top chamber, GC=growth chamber.

Species	Growth CO ₂ (ppm)	Growth Condition	Change in g _s (%)	Reference
<i>Andropogon gerardii</i>	337/658	CTC, Field	-42	Kirkham et al. 1991
<i>Andropogon gerardii</i>	354/716	CTC, Field	-36	Nie et al. 1992a
<i>Andropogon gerardii</i>	Ambient/2X Ambient	OTC, Field	-51	Knapp et al. 1993b
<i>Andropogon gerardii</i>	Ambient/2X Ambient	OTC, Field	-51	Knapp et al. 1994
<i>Andropogon gerardii</i>	Ambient/2X Ambient	OTC, Field	-51	Ham et al. 1995
<i>Andropogon glomeratus</i>	350/650	GC, Pot	+11	Bowman and Strain 1987
<i>Andropogon virginicus</i>	380/650	GC, Pot	-13	Wray and Strain 1986
<i>Amaranthus retroflexus</i> + <i>Setaria faberii</i>	350/700	GC, Pot	-55	Garbutt et al. 1990
<i>Atriplex canescens</i>	360/680	GC, Pot	-20	Polley et al. 1996a
<i>Echinochloa crus-galli</i>	350/675	GC, Pot	0	Potvin and Strain 1985
<i>Eleusine indica</i>	350/675	GC, Pot	0	Potvin and Strain 1985
<i>Eragrostis orcuttiana</i>	340/680	GC, Pot	-71	Smith et al. 1987
<i>Paspalum plicatulum</i>	340/590	GC, Pot	-37	Gifford and Morison 1985
<i>Schizachyrium scoparium</i>	360/680	GC, Pot	-58	Polley et al. 1996a
<i>Sorghum bicolor</i>	330/660	CTC, Field	-12	Chaudhuri et al. 1986
<i>Zea mays</i>	340/718	OTC, Pot	-51	Rogers et al. 1983

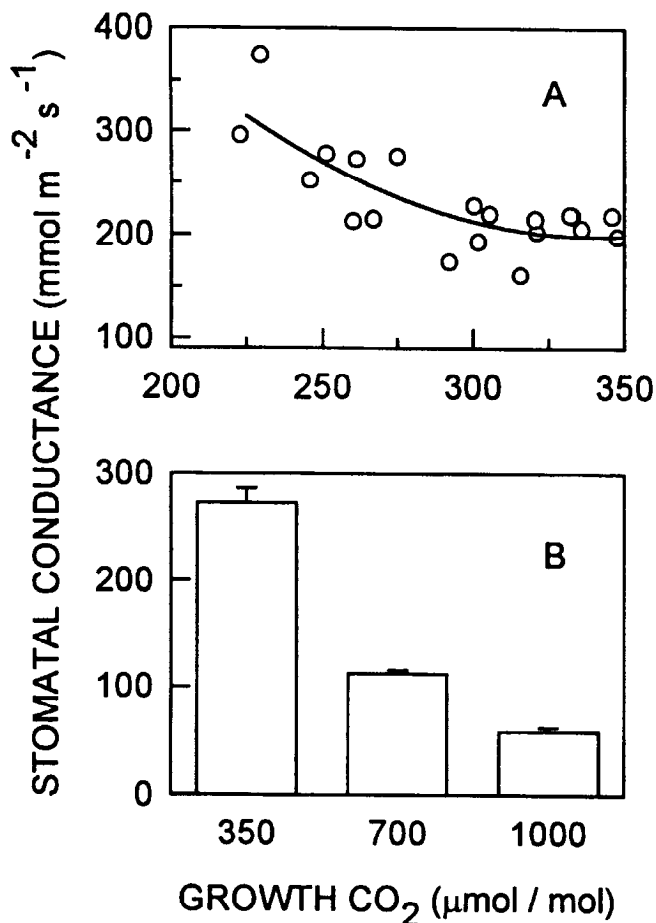


Fig. 1. Stomatal conductance of sunlit leaf blades of the C₄ grass *Schizachyrium scoparium* (little bluestem) as a function of the CO₂ concentration at which plants were grown. (A) The line is a regression through single measurements per plant with an infrared gas analyzer (Polley et al. 1994). (B) Vertical bars denote 1 standard error of the mean of 18 daily averages of leaf (blade) conductance. Conductance was measured during a separate experiment on 5 plants from each CO₂ treatment. Note that the scale of the y-axis differs in A and B.

watered agricultural crops with plant canopy conductances in excess of 20 mm sec⁻¹ (McNaughton and Jarvis 1991). Canopy conductances are smaller, and stomatal control of transpiration is greater, in most grasslands and other extensively-managed vegetation in arid and semi-arid regions (e.g., Valentini et al. 1995).

Atmospheric CO₂ and Evapotranspiration: Field Studies

Extensive data are now available from CO₂ enrichment studies on salt marsh in Maryland, USA (Drake 1992) and tallgrass prairie in Kansas, USA (Owensby et al. 1993b). These data can be used to evaluate impacts of elevated CO₂ on the water balance of C₄-dominated ecosystems. Doubling CO₂ caused little increase in leaf or canopy photosynthesis of C₄ grasses in either ecosystem, except during or shortly following drought (Ziska et al. 1990, Drake and Leadley 1991, Drake 1992, Kirkham et al. 1991, Nie et al. 1992a, 1992b, Knapp et al. 1993b), but reduced poten-

tial water loss by halving stomatal conductance (Kirkham et al. 1991, Knapp et al. 1994).

Water savings expected from the decline in conductance at elevated CO₂ concentration were partly offset in Kansas by higher leaf temperatures (Kirkham et al. 1991) and, in years with below normal precipitation, greater leaf area (Owensby et al. 1993b). In spite of these negative feedbacks on transpiration, water loss/soil surface area was significantly reduced by elevated CO₂ in both salt marsh and tallgrass prairie. Evapotranspiration was reduced even during drought periods when C₄ growth was stimulated by CO₂. Doubling CO₂ concentration reduced evapotranspiration from C₄ cord grass (*Spartina patens* (Ait.) Muhl.) communities in salt marsh by 28% to 29% in each of 2 years (Drake 1992). Kirkham et al. (1991) calculated that during a 1-month period in 1989, doubling atmospheric CO₂ concentrations reduced evapotranspiration 15% from C₄-dominated tallgrass prairie that was watered weekly to field capacity, and 7% when watered weekly to one-half of field capacity. Average rates of evapotranspiration per unit soil surface were reduced 18% under well-watered conditions and 8% when supplemental water was withheld the following year (Nie et al. 1992b). Similarly, daily evapotranspiration from tallgrass prairie near peak biomass was reduced 22% during a relatively wet year by doubling the current CO₂ concentration (Ham et al. 1995). As a result of the decline in evapotranspiration, soil water levels in tallgrass prairie were consistently higher at elevated CO₂ concentration (Kirkham et al. 1991), even during periods of relatively severe drought (Owensby et al. 1993b).

Similar changes in soil water balance are possible in C₃-dominated communities as CO₂ rises, if leaf growth is limited by nitrogen availability (Hatton et al. 1992, Polley et al. 1995), phenology, or other factors. Jackson et al. (1994) found that doubling the current CO₂ concentration on a C₃ grassland reduced stomatal conductance and transpiration of the dominant species, wild oat (*Avena barbata* Brot.), by about 50%. The decline in water use per unit leaf area at elevated CO₂ was not offset by an increase in leaf area, and soil water content increased 34% by season's end.

Field estimates of the amount of water that might be saved on more arid grasslands as CO₂ rises are not available. Rates of water loss will almost certainly depend on the size, intensity, and temporal pattern of precipitation events. Generally, however, effects of CO₂ concentration on soil water balance should be smaller in arid than in relatively mesic ecosystems (Table 2).

Table 2. Predicted effects of rising atmospheric CO₂ concentration on transpiration, soil water availability, and the balance of shrubs and grasses on arid and relatively mesic grasslands and savannas.

Parameter	Mesic Grassland	Arid Grassland
Transpiration/Leaf area	Reduced	Reduced
Leaf Area	Increased during dry periods	Increased
Total Transpiration	Reduced	Small or no reduction
Change in Soil Water Content		
Shallow	Increased	Little change
Deep	Potentially Increased	No change
Shrub/Grass Ratio of Vegetation	Increased (especially if most precipitation falls when plants are active)	Little change?

Most precipitation events in arid and semi-arid environments are small and a high proportion of water from small rainfall events is lost to evaporation (Noy-Meir 1973, Sala et al. 1992). Rising CO₂ concentration consistently increases growth and leaf expansion of C₄ grasses when water becomes limiting (Gifford and Morison 1985, Owensby et al. 1993b). Transpiration rates of C₄ species, therefore, may also decline less, as CO₂ rises, in arid than in more mesic ecosystems. Whether the smaller absolute effect of CO₂ on soil water balance in arid than in more mesic ecosystems will prove important to vegetation dynamics remains to be determined.

Potential Consequences of Lower Evapotranspiration to the Species Composition of Grasslands and Savannas

Grasses may prolong growth into periods without rainfall by reducing transpiration and effectively conserving soil water. There are at least 2 ways, however, in which water saved by grasses could benefit woody and other plants (Fig. 2). First, the water could be used by plants that share rooting space with grasses. Seedlings of shrubs and other plants depend at least initially on water in the rooting zone of grasses (Williams and Hobbs 1989, Harrington 1991, O'Connor 1995). Even large woody plants may compete directly with grasses for water and other resources (Carlson et al. 1990, Dugas and Mayeux 1991, Belsky 1994, Le Roux et al. 1995, Montaña et al. 1995). Secondly, water conservation by grasses could increase deep percolation of subsequent rainfall. Shrubs and other plants that root more deeply than grasses (Knoop and Walker 1985, Sala et al. 1989, Medina and

Silva 1990, Brown and Archer 1990, Sala et al. 1992, Axmann and Knapp 1993, Bragg et al. 1993, Nizinski et al. 1994) would be favored as a result. The depth to which precipitation moves depends partially on soil water content (Hanks and Ashcroft 1980). Deep percolation should increase, therefore, if the water content of upper soil layers remains higher for longer periods. Generally, this should occur more often in relatively-mesic than in arid grasslands.

Water at depth is recharged on some grasslands largely by rainfall during the dormant season of grasses (e.g., Cable 1969). In these ecosystems, changes in grass transpiration probably will not greatly affect growth of deeply-rooting shrubs. On many grasslands and savannas, however, shrubs depend on deep percolation of water during the period that grasses are growing (Knoop and Walker 1985), and could benefit from a positive feedback of rising CO₂ on soil water content.

The importance of the vertical distribution of soil water to shrub/grass ratios on savannas is well-recognized and has been conceptualized in a "two-layer" model of shrub/grass competition (Walter 1971, Walker et al. 1981, Walker and Noy-Meir 1982). Shallowly-rooting grasses are assumed to have primary access to, and to be superior competitors for, water in upper soil layers. The more deeply-rooting shrubs primarily access water below the roots of most grasses. The model does not consider influences of fire, browsing or grazing, and edaphic factors, other than soil moisture and soil texture, that could influence shrub/grass ratios (Belsky 1990, Archer 1994). It is, however, supported by studies in tropical savannas (Knoop and Walker 1985, Sala et al. 1989, Medina and Silva 1990), and is consistent with the observed influence of topography and drainage on woody cover (Tinley 1982, Coughenour and Ellis 1993).

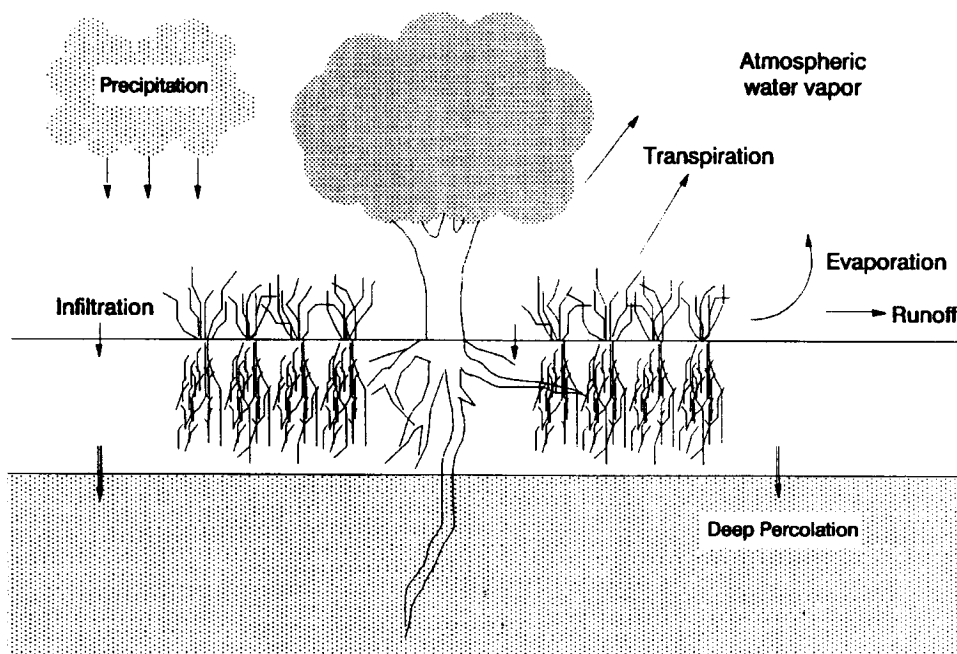


Fig. 2. Schematic diagram showing major pathways of water flux for grasslands and savannas. Rising atmospheric CO₂ concentration is predicted to reduce transpiration from shallowly-rooting grasses and other species, increase the duration of water in upper soil layers, and, in some ecosystems, increase percolation to soil layers occupied by deeply-rooting species like shrubs.

Results from a CO₂-enrichment study on tallgrass prairie in Kansas, USA are consistent with the prediction that some plants will benefit from changes in soil water balance at elevated CO₂. Although the mechanism has not been established, basal cover of forbs increased concurrently with soil water content following a doubling of the current CO₂ concentration (Owensby et al. 1993b). In the absence of fire or browsing, woody plants would likewise be expected to increase in size and abundance by exploiting the greater availability of soil water.

Woody ingress on grasslands may generate a series of positive feedbacks on ecosystem hydrology that reinforce the shift in growth form composition (Joffe and Rambal 1993). Grass production and transpiration often decline following woody invasion, resulting in higher soil water levels and, in some ecosystems, greater infiltration to soil depths where woody roots are concentrated (Knoop and Walker 1985, Sala et al. 1989). Heavy grazing or other factors that reduce leaf area and transpiration of grasses may also increase soil water content. Alternatively, water may move through woody roots from deep, moist soil to surface layers where it can be used by grasses (Richards and Caldwell 1987, Dawson 1993).

Relationship to Other Ecosystems and Other Hypotheses/Models

A progressive shift to taller plants as CO₂ concentration and average levels of soil water increase is compatible with predictions from the vegetation models of Tilman (1988) and Smith and Huston (1989). In both of these models, vegetation change through time or over spatial resource gradients is driven by the relationship between soil resource (water and nitrogen) availability and potential plant height. As soil water availability increases, competition for light favors an increase in the mean height at which leaf area is displayed (Smith and Huston 1989).

Vegetation dynamics on grasslands may, therefore, be increasingly driven by competition for light or other soil resources as soil water availability increases. Not all competitors of grasses will be favored. Perhaps only plants that can grow above the grass canopy, or that are competitive for the limited nitrogen on many grasslands, will benefit. Basal cover of *Poa pratensis* L. on tallgrass prairie declined at elevated CO₂, apparently because the short-statured grass was shaded by taller species or was limited by low nitrogen availability (Owensby et al. 1993b). Fertility and other soil characteristics are important determinants of shrub/grass ratios on some grasslands and savannas (Walker 1993). Saline or poorly-drained soils limit woody invasion (Belsky 1990), but soil fertility commonly determines the type (evergreen, sclerophyllous vs. deciduous, mesophyllous) of woody invader that is successful.

Variation in soil water content across landscapes also influences species composition on some grasslands and savannas (Coughenour and Ellis 1993, Walker 1993). Drainages, or sites that receive runoff, may have a greater abundance of shrubs than adjacent areas. It is, of course, difficult to predict effects of rising CO₂ on the spatial distribution of water on grasslands with complex terrain. Hydrologic simulations for a forested catchment, however, indicated that elevating CO₂ altered the spatial distribution of soil water by increasing the number of areas with moist soil (Hatton et al. 1992).

Water availability exerts an important control on the composition of vegetation on grasslands and savannas where evaporative demand often exceeds precipitation. Rising atmospheric CO₂ concentration increases plant production per unit of transpiration (Morison 1993, Polley et al. 1993), perhaps allowing plants to grow and reproduce on less water than was formerly required. These changes alone could alter species distributions and local abundances (Idso and Quinn 1983). On some grasslands and savannas, plant composition may also respond to indirect impacts of CO₂ on soil water balance. A CO₂-caused decrease in canopy transpiration rate should generally favor more mesophytic species by slowing soil water depletion and, in some ecosystems, may benefit more-deeply-rooting plants by increasing percolation. Effects of rising CO₂ on individual species, however, will remain difficult to predict. Species dynamics in any community depend on dispersal rates, seedling establishment, and other factors, including grazing and fire, that may vary independently of CO₂ concentration (Belsky 1990, Archer 1994, Archer et al. 1995, Polley et al. 1996b).

Effects of CO₂ concentration on soil water availability and vegetation dynamics in the future will also depend on accompanying changes in climate. Temperature-caused increases in evapotranspiration may offset predicted increases in precipitation in some regions (Neilson and Marks 1994) and reduce positive effects of higher CO₂ concentration on soil water balance. Given the sensitivity of species composition on grasslands to precipitation and soil water balance, interactions between climatic change and rising CO₂ concentration must be more clearly understood before we will be able to predict the future dynamics of vegetation in these ecosystems.

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