19. Modern and Future Semi-Arid and Arid Ecosystems

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19.1 Introduction

Arid and semi-arid ecosystems are diverse biotic assemblages with wide variations in topographic, climatic, edaphic, geologic, and biological conditions. These ecosystems include dry and humid grasslands in all latitudes and altitudes, scrub, tropical and subtropical savannas, dry forest, and coastal ecosystems. Such regions comprise up to 40% of the world's land surface and by some estimates account for up to 30% of global terrestrial net primary productivity. Semi-arid grasslands cover approximately 33 million km^2 (25% of the land surface) on all continents except Antarctica. Savanna ecosystems cover an estimated 25 million km^2 in Africa, South America, Asia, and Australia. With several exceptions in the Mediterranean ecosystem, these arid and semi-arid regions are not species rich, but endemism tends to be very high. Functional diversity, however, may be rather high (Smith, Monson, and Anderson 1997), as many species have evolved strategies for growth and survival under extreme environmental conditions, including high and low temperature, low and episodic precipitation, and periodic protracted drought. Annual rainfall averages up to 350 mm and 700 mm for arid and semi-arid systems, respectively. It has been suggested that these systems are likely to be among the most responsive to changes in atmospheric CO_2 (Strain and Bazzaz 1983; Smith et al. 2000).

Semi-arid and arid ecosystems should respond favorably to rising CO_2 since plant function is primarily limited by water availability (Mooney et al. 1991).

This projection derives from the often-measured ability of elevated CO_2 to reduce water stress in many plants (Strain 1992). Additionally, the effects of elevated CO_2 on photosynthesis and stomatal conductance are such that the photosynthesis/transpiration ratio in arid systems should be relatively higher than in more mesic systems (Knapp et al. 1996), directly impacting carbon gain and whole-system water loss and likely enhancing the plant community productivity (Melillo et al. 1993). Rising CO_2 may also affect vegetation composition, promoting plant survival through drought by reducing water stress in adult plants and by establishing seedlings (Smith, Monson, and Anderson 1997). The most significant long-term response to elevated CO_2 may be the manifestation of interactions with additional global change factors that could significantly influence vegetation change and aggregated shifts in other biogeochemical cycles important for ecosystem function. In this regard, how nitrogen and water availability co-vary and influence a CO_2 response in arid ecosystems may be critical to understand (Smith, Monson, and Anderson 1997; Ehleringer 2001).

19.2 Effects of Atmospheric CO_2 Across Multiple Scales of Organization

19.2.1 Physiological Responses of Plants from Arid and Semi-Arid Ecosystems

19.2.1.1 Photosynthetic Gas Exchange and Down-Regulation

A rise in CO_2 often increases net rates of photosynthesis in many C_3 plants Under a doubling of CO_2, assimilation rates may increase by as much as 75% depending on the environmental conditions and plant growth form. Warmer temperatures can additionally stimulate photosynthesis responses (Berry and Björkman 1980; Sage and Sharkey 1987). C_3 photosynthesis is a CO_2-unsaturated biochemical reaction, and higher rates of net photosynthesis occur under elevated CO_2 as a result of increased substrate availability at the site of carboxylation and reduced competitive inhibition by photorespiration activity, increasing the efficiency of ribulose-1,5-biphosphate carboxylase/oxygenase, or, Rubisco (Bowes 1991, 1993). This mechanism does not result in increased photosynthetic performance in C_4 plants because C_4 plants already achieve high CO_2 concentrations around the chloroplasts (Ghannoum et al. 2000).

Long-term exposure to elevated CO_2 can result in a range of responses, including the maintenance of increased rates of photosynthesis (Arp 1991; Körner and Miglietta 1994; Hamerlynck et al. 2000a,b; Huxman and Smith 2001), the down-regulation of photosynthesis (DeLucia, Sasek, and Strain 1985; Tissue and Oechel 1987; Sage, Sharkey, and Seemann 1989; Oechel et al. 1995), or nonsignificant responses (Jackson et al. 1995; Huxman and Smith 2001). In the case where increased photosynthesis under elevated CO_2 occurs initially, concomitant increases in leaf carbohydrate concentrations can result in a negative feedback on photosynthetic capacity (Tissue, Thomas, and Strain 1993). Referred to as photosynthetic down-regulation, this may represent a homeostatic adjustment that aligns whole-plant processes and carbon gain rates to within some bounds important for coordinated function. In semi-arid systems, photosynthetic down-regulation does not appear to be a major limitation to plant carbon gain, as it has been observed for well-watered plants only under conditions that were not favorable for whole-plant growth (Huxman et al. 1998c; Naumburg et al. 2003). Indeed, many plants in semi-arid ecosystems show increases in net photosynthetic rates and carbon gain under elevated CO_2 even in the presence of down-regulation activity (Cure and Acock 1986; Oechel et al. 1995; Curtis and Wang 1998). This is most likely as a result of plant carbon-sink strength remaining strong when resources are available for plant growth and when stomata are open. The result is that during periods with high resource availability, elevated CO_2 results in greater leaf-level photosynthesis in many arid plants (Hamerlynck et al. 2000a; Huxman and Smith 2001; Hamerlynck et al. 2002; Naumburg et al. 2003).

19.2.1.2 Plant Water Use, Stomatal Conductance, and Transpiration

Stomatal conductance reflects a balance that plants maintain in order to maximize carbon gain while minimizing water loss (Cowan and Farquhar 1977). This is true also for plants growing in semi-arid environments that may have been selected to maximize water-use efficiency in the context of other limiting resources (Bloom, Chapin, and Mooney 1985). Increases in atmospheric CO_2 concentrations cause stomatal closure (Linsbauer 1917), which results in decreased transpiration (Ketellapper 1963). The role of CO_2 in regulating stomatal conductance (g_l) has been well studied, with C_3 and C_4 herbaceous species showing, on average, a 40% decrease in conductance in response to a doubling of ambient CO_2 concentration (Morison 1985). In a tall-grass prairie, stomatal conductance in the dominant C_4 species decreased by 21% in a dry year and by 59% in a wet year (Knapp, Hamerlynck, and Owensby 1993). In Mediterranean grassland, elevated CO_2 led to a 45% decrease in stomatal conductance in mid-season. This decrease in stomatal conductance under elevated CO_2 can result from either decreases in stomatal aperture or decreases in stomatal density (Clifford et al. 1995; Webb et al. 1996; Beerling, McElwain, and Osborne 1998). Continuous, long-term exposure to elevated CO_2 does not appear to dampen this response as has been shown for plants growing near natural CO_2 springs where for generations plants have been exposed to an elevated CO_2 environment (Betterini, Vaccari, and Miglietta 1998). Thus, rising atmospheric CO_2 allows the potential for plants in arid ecosystems to meet the growth demand for carbon substrate with less water lost through transpiration.

Decreases in leaf-level conductance in response to exposure to elevated CO_2 have been observed in numerous studies in semi-arid ecosystems (Jackson et al. 1994; Oechel et al. 1995; Bremer, Ham, and Owensby 1996; Nijs et al. 1997; Huxman and Smith 2001). This response to elevated CO_2 allows plants to increase water use efficiency (WUE), which is the mass of carbon fixed per mass of water transpired. Herbaceous plants often show the largest decreases in stomatal conductance and increases in WUE, while woody species tend to show smaller or nonsignificant responses (Curtis and Wang 1998; Saxe and Heath 1998; Ellsworth 1999). In the most arid ecosystems, the decreases in stomatal conductances by plants have been seen primarily during periods of high resource availability when photosynthetic and transpiration fluxes are greatest (Pataki et al. 2000; Nowak et al. 2001).

While it has been frequently reported that elevated CO_2 can compensate for the expected decrease in carbon gain elicited by water deficits (Tyree and Alexander 1993), the mechanisms responsible extend beyond simple increases in leaf-level water-use efficiency (Chaves and Pereira 1992; Tyree and Alexander 1993) and include a range of functionally co-related traits (Table 19.1). Increases in leaf-level water-use efficiency under elevated CO_2 conditions are a partial result of photosynthetic stimulation, which leads to greater carbon gain per unit water loss (Tyree and Alexander 1993).

Changes in root characteristics also play an important role in increased leaf-level water-use efficiency under elevated CO_2 at the whole-plant under water-limiting conditions when exposed to elevated CO_2 may be related to selective carbon allocation toward roots (i.e., higher root/shoot ratio), which may be beneficial in the survival of water-limited plants through enhanced balance between water uptake and canopy transpiration (Bazzaz 1990; Chaves and Pereira 1992). Exposure of plants to elevated CO_2 and water limitation has been shown to alter the capacities of roots to transport water through their xylem conduits. In soy-

Table 19.1. The interaction between elevated CO_2 and drought on several inter-related physiological processes and plant organs for sunflower (*Helianthus annuus*) grown in glasshouse conditions (data from Huxman 1999). It should be noted that any single character change associated with growth at elevated CO_2 does not completely predict the "drought-alleviation" in biomass production exhibited by this species.

	Treatment			
	Ambient CO_2		Elevated CO_2	
Character	well-watered	droughted	well-watered	droughted
Root/Shoot biomass ratio $g\ g^{-1}$	0.45+.0.5	0.48+0.02	0.42+.0.4	0.41+0.03
Root/Shoot area ratio $cm^2\ cm^{-2}$	1.91+0.35	2.01+0.12	2.38+0.30	3.15+.024
Assimilation rate $\mu mol\ m^{-2}s^{-1}$	10.7+0.79	9.57+2.8	19.4+2.27	10.76+1.93
Stomatal conductance $mmol\ m^{-2}s^{-1}$	130+14	103+28	174+28	48+27
Water-use efficiency $\mu mol\ CO_2\ mmol^{-1}\ H_2O$	4.43+0.44	4.52+066	7.06+1.18	9.84+0.20
Root hydraulic conductivity $m\ s^{-1}\ MPa^{-1}\ X\ 10^{-8}$	7.27+1.3	3.54+.054	4.25+1.27	4.67+0.30

bean, root hydraulic conductance decreased 26% at elevated CO_2 (Bunce 1996) and in sunflower whole root system hydraulic conductivity decreased by nearly 50% (Huxman, Smith, and Neuman 1999) compared to ambient-CO_2-grown plants. We are still in our infancy in understanding the influences of elevated CO_2 on different physiological processes, plant organs, and their inter-relationships. Yet from the information available today there is a clear suggestion that multiple mechanisms exist to affect continued plant growth under water-limited systems.

19.2.2 Community Responses of Water Limited Ecosystems to Rising Atmospheric CO_2

Changes in individual plant performance should impact competitive hierarchies and the representation of different species in terrestrial communities at elevated CO_2 (Bazzaz 1990). This assumption is supported by the strong, species-specific effects of elevated CO_2 seen in nearly all ecosystems studied to date. Elevated CO_2 is expected to have a differential impact on C_3 versus C_4 plants as was discussed by Ehleringer in Chapter 10. Studies have shown that higher concentrations of CO_2 might favor plants that fix carbon via the C_3 photosynthesis over C_4 photosynthetic pathways, altering the current pattern of C_4 dominance in many semi-arid ecosystems (Ehleringer, Cerling, and Helliker 1997). Additionally, there is the potential that elevated CO_2 will foster non-native species invasions, especially in conditions where plant growth rates are CO_2 dependent (Dukes and Field 2000). In recent studies, growth rate differences at elevated CO_2 between native and non-native species have been detected that are consistent with the expectation that native species will be out-competed by non-native species in a higher CO_2 environment (Poorter and Navas 2003). However, many of these ideas have been based on the assumption that changes in total biomass production scale directly to changes in fecundity. How seed production and future-offspring growth potential are influenced by elevated CO_2 is not well known (Huxman et al. 1998a; Huxman and Smith 2001; Jablonski, Wang, and Curtis 2002). Will elevated CO_2 alter species composition in plant communities, and, if so, what is the potential for changes in ecosystem functioning? For Ward's discussion of some of the possible fecundity adjustments that can take place as plants adjust to a different CO_2 regime, see Chapter 11.

19.2.2.1 Functional Type Response in Xeric Ecosystems

Existing plant distributions are likely to be impacted by temperature changes, an indirect effect of elevated CO_2. One common life form that is likely to be impacted is the succulent species, the distribution of which tends to be sensitive to thermal regimes. Freezing conditions, even for a brief period, tend to cause extensive mortality among some succulent species. Based on the expected shifts in temperature conditions, the distribution of many succulent species, such as *Yucca brevifolia*, is expected to expand considerably (Dole, Loik, and Sloan 2003).

Arid and semi-arid ecosystems are floristically rich assemblages in contrast to other temperate-region ecosystem types (Beatley 1974; Cody 1986; Smith, Monson, and Anderson 1997). While arid lands themselves do not necessarily have high species diversity per unit area, they represent landscapes diverse in plant functional types. This pattern is in contrast to many other ecosystems, such as temperate grasslands and forests, which have high biological diversity with relatively low functional diversity (Tilman et al. 1997). Applying a "functional type" approach to the question of how vegetation assemblages may respond to rising CO_2 seems applicable. Two approaches can be employed when placing plants into functional groups and attempting to understand how different physiological and life history properties relate to distribution. First, characteristics that are likely to be influenced by climate change can be used to form the functional groups. Examples might include photosynthetic pathway or growth potential (Poorter and Navas 2003). Second, we might focus on those characteristics that are important for current species distribution, which may better help us understand current constraints on distribution patterns. In fact, combining these approaches may provide significant power in the prediction of future plant distributions.

For many ecosystems in the arid southwestern North America, there are significant patterns between climate and the distribution of general life history strategy (e.g., perennial versus annual). It has been suggested that the distribution of perennial plants is related to seedling survival in the abiotic environment near the soil surface (Smith and Nowak 1990). The high rates of seedling mortality are mostly the result of adverse environmental conditions (Fenner 1985; Franklin et al. 1992). How elevated CO_2 influences seedling survival is generally unknown, but the available evidence suggests that elevated CO_2 can offset plant responses to environmental stress during early life stages (Huxman et al. 1998a; Housman et al. 2003) and can increase the likelihood of the establishment of long-lived perennials.

For annual plants and some fast-growing perennials, the ability to produce a substantial seed crop is critical for long-term persistence (Mulroy and Rundel 1977). Annual plants have often been categorized as "stress avoiders" as a result of their life history strategy of being present only in the form of seeds during periods of extended stress. Evaluations of the reproductive characteristics of annual plants in arid ecosystems suggest that seed production in these groups may be affected by growth at elevated CO_2 (Smith et al. 2000). Size of seed crops of desert plants is often a linear function of plant size (Ehleringer 1985), and elevated CO_2 typically increases both plant growth rate and plant size after a period of exposure (Poorter and Navas 2003). Plant size and nutrient status are commonly influenced by plant growth under elevated CO_2 (Bazzaz, Coleman, and Morse 1990; Bazzaz 1997), and it would not be unexpected that a change in reproductive characteristics, such as shifts in seed quality, would also occur in the future (Huxman et al. 1998a).

19.2.2.2 C_3 Versus C_4 Photosynthetic Pathway Dominance

Photosynthetic rates and light-use (quantum yield) efficiencies and growth of C_3 species increase with elevated CO_2 (Carlson and Bazzaz 1980; Cure and Acock 1986; Wand et al. 1999). While not all C_4 species show a significant, positive photosynthetic response, growth in many C_4 species is indirectly stimulated by elevated CO_2 as a consequence of new leaf area production and changes in whole-plant water status (Woodward, Thompson, and McKee 1991; Polley, Johnson, and Derner 2002). Across a range of taxa, C_4 plants do not appear to increase growth rate at elevated CO_2 to the same extent as C_3 plants (Poorter, Roumet, and Campbell 1996; Poorter and Navas 2003). As discussed in Chapter 10, quantum yield and photorespiration rates in C_3 leaves are sensitive both to changes in atmospheric CO_2 and to changes in temperature. Rising CO_2 coupled with moderate increases in temperatures are thus expected to provide a relatively greater enhancement for C_3 plants as compared to C_4 plants (Long 1991). In a future high CO_2 world, C_3 species may not exhibit the energetic tradeoff associated with increasing temperature that has allowed for the proliferation of C_4 species in the low CO_2 world that plants have experienced for the last several million years (Hatch 1992). Thus, in conditions typical of many arid and semiarid ecosystems, the relative competitive ability of C_4 plants might be diminished (see Chapters 9 and 10).

Leaf-level photosynthesis measurements in mixed C_3/C_4 communities often show a greater proportional response of photosynthesis or stomatal conductance by C_3 species as compared to C_4 species at elevated CO_2 (Owensby et al. 1993; Owensby et al. 1999; Morgan et al. 2001; Polley, Johnson, and Derner 2002). However, fractional productivity or representation in the community does not always reflect a similar pattern. This is most likely due to the effects that elevated CO_2 has on whole-system water budgets (Owensby et al. 1993; Polley, Johnson, and Derner 2002) and the energetic implications of increases in whole-system productivity. In a tallgrass prairie, production by C_4 grasses increased considerably at elevated CO_2, while production from C_3 species did not change (Owensby et al. 1993; Owensby et al. 1999). In the shortgrass steppe, proportional production of C_3 and C_4 species did not change at elevated CO_2 because of indirect feedbacks associated with the availability of soil water (Morgan et al. 2001). When constrained to comparisons within the grass morphological form, C_3 and C_4 species have similar growth responsiveness to elevated CO_2 (Wand et al. 1999) but show variation in the form of that response (e.g., increases in vegetative vs. clonal growth). The C_3 species that have increased in abundance at elevated CO_2 in CO_2-exposure experiments involving mixed communities have been the herbaceous and woody C_3 life forms rather than grasses, which could be a simple reflection of grasses being shaded and out-competed by taller life forms. This may be the most consistent trend in the C_3 versus C_4 literature and suggests that when systems are comprised of plants where there is covariation between life form and photosynthetic pathway, shifts in the abundance of C_3

and C_4 species may be expected. Interactions with other global change factors may be especially important for understanding the relative performance and abundance of C_4 and C_3 plants in arid regions at elevated CO_2. Relaxation of the cold season temperature constraint by general atmospheric warming may extend the C_4 growing season. Greater primary production at elevated CO_2 combined with increased growing season precipitation may alter fire disturbance characteristics in arid land, differentially affecting C_3 and C_4 species (Sage 1996). Nitrogen deposition may result in a homogeneous landscape, favoring grassland physiognomies over shrublands (Reynolds, Hilbert, and Kemp 1993). The frequency and intensity of episodic drought may alter the relative performance of C_3 and C_4 species in nonintuitive manners (Ward et al. 1999). Additional traits, such as seed quality, may differentially affect species that "escape" drought in a different life history stage (Huxman et al. 1998a). Thus, the issue of C_3 versus C_4 responsiveness in water-limited ecosystems is quite complex and requires an understanding of interactions among factors. For these functional types, the ecological outcome of elevated CO_2 may be strongly influenced by temperature, precipitation, and disturbance scenarios in arid lands. In this regard, there is not likely to be a single expected outcome from these multifactor interactions.

19.2.2.3 Woody Plant Encroachment, Invasive Species, and Rising CO_2

How elevated CO_2 may influence shifts in plant community composition through changes in woody-plant encroachment and non-native species introductions may substantially alter the structure/function properties of semi-arid and arid ecosystems. Invasion by non-native species has the ability to shift patterns of nutrient availability (Evans et al. 2001) and disturbance (D'Antonio and Vitousek 1992) such that further dominance by the non-native is facilitated. The representation of woody versus nonwoody plants in the flora of water-limited regions is important for local, regional, and global biogeochemical and hydrological processes (Reynolds, Virginia, and Schlesinger 1997; Jackson et al. 2002). As a result, water-limited regions are classified based on total cover and functional diversity, which is related primarily to the presence of woody plant species (Smith, Monson, and Anderson 1997). In contracted desert regions, perennial cover is sparse, low in–stature, and restricted to washes and runon areas. True deserts are dominated by shrubs and dwarf shrubs with $<10\%$ total perennial cover. Semidesert shrublands (steppes) have approximately 10% to 30% perennial cover. Shrublands dominated by large shrubs (0.5–2 m high) have approximately 30% perennial cover. Perennial grasses dominate grasslands with fairly continuous cover. The relative change in the total abundance of woody species has, therefore, a large impact on the properties of the material and energy exchange patterns in the whole system.

Rising CO_2 may affect several plant and system characteristics that would favor increased woody plant species encroachment or the maintenance and increased vigor of currently established woody plant species. Rising CO_2 may differentially affect C_3 woody plant seedlings as compared to C_4 grasses, facilitating shrub establishment (Polley, Johnson, and Tischler 2003). Reduced transpiration rates from grasses may provide greater water recharge to depth and may facilitate coexistence of the two growth forms (Polley et al. 1997). Additionally, increased carbon balance during and following disturbances such as fire may facilitate woody plant dominance in a number of systems. Bond and Midgely (2000) suggest that woody plant seedlings will be able to reach heights critical for escaping the detrimental impacts of periodic fire, typical of many semi-arid savannas, much quicker as a result of increased growth rates and carbon balance associated with rising CO_2 (Fig. 19.1).

A similar argument for growth-rate induced changes in species composition has been made for non-native species success with rising CO_2 (Smith, Strain, and Sharkey 1987; Huxman, Hamerlynck, and Smith 1999; Ziska 2003). Rising CO_2 may allow fast-growing plant species to accumulate biomass at proportionally greater rates than slower-growing plant species (Poorter and Navas 2003). This would allow these fast-growing species to reach important life history stages (such as reproduction) quickly, increasing their competitive abilities and probabilities of success in novel habitats on a model that is conceptually similar to the shrub encroachment pattern (Fig. 19.1). Such life history shifts, as a result of changes in growth rate, are likely critical for understanding non-native species dynamics with global change (Dukes and Mooney 1999; Dukes and Field 2000). Empirical data for both changes in woody-plant encroachment and non-native species success are lacking but critical for understanding the structure of semi-

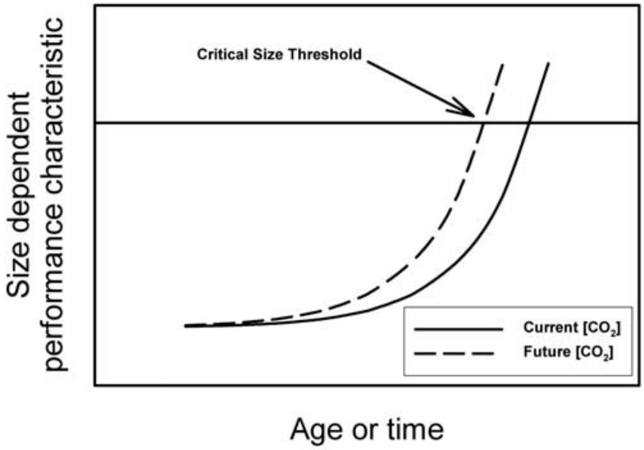

Figure 19.1. The relationship between size-related growth characteristics and age or time for two different conditions; ambient (solid line) and elevated CO_2 (dashed line). The horizontal line represents a threshold for important life history events or escape from the destructive nature of disturbance (adapted from Bond and Midgely 2000), which occurs at an earlier time or age in elevated CO_2 grown plants.

arid and arid ecosystems in a future high-CO_2 world. How interactions between woody species and non-native invasions (typically grasses) may play out for native species composition, productivity, and disturbance regimes is unknown but is likely to have impacts on ecological processes in arid lands.

Across a gradient of water limitation, disturbance by fire has differential probabilities associated with fuel load (flammable biomass), which is directly proportional to total production and the fraction of shrub and tree to grass life forms upon the landscape (Trabaud, Christensen, and Gill 1993). Woody plant encroachment and non-native species invasion in semi-arid and arid ecosystems may increase the probability and recurrence of fire (Torn and Fried 1992; Mayeux, Johnson, and Polley 1994). Shifts in species composition toward more fast-growing grass life forms may result in lower ignition requirements yet greater water balance in whole-plants and ecosystems may increase ignition heat requirements (Sage 1996). The ability for plants to quickly return significant biomass to the landscape following a disturbance event may reduce the time between events. In water-limited ecosystems where fire has a large impact on ecosystem structure and function, changes in fire frequency and intensity are very important. However, for more xeric ecosystems, where fire has not been present in recent history, it could now significantly alter the vegetative characteristics of the landscape such as species composition. How fire may alter the responsiveness of water-limited ecosystems to rising CO_2 and other global change factors is unknown, but an important implication of shifts in species composition (Smith and Huxman 2001).

19.2.3 Ecosystem Responses to Rising Atmospheric CO_2

19.2.3.1 Ecosystem Carbon and Nitrogen Cycling

Numerous papers describe plant or ecosystem responses to elevated CO_2 (Körner 2000), but the evidence of generally stimulatory responses from studies with individual plants (Kimball 1983) is mixed at the ecosystem scale, including examples of substantial net primary production increases as well as modest responses or no change (Mooney et al. 1999). In semi-arid ecosystems, aboveground biomass generally increases under elevated CO_2, but this response is highly site-dependent and variable within systems across years (see Mooney et al. 1999 for a detailed review). Belowground biomass appears to increase in conjunction with aboveground biomass, but data are limited and highly variable (Canadell et al. 1996). The response of grassland net primary production to elevated CO_2 is greatest when water is limiting (Volk, Niklaus, and Körner 2000), suggesting that indirect increases in water availability are more important than are the direct impact on rates of carbon fixation. Additionally, at the extreme end of xeric conditions, dry years and wet years have the opposite response, where CO_2 enhancements in production are seen only during extremely wet years (Smith et al. 2000).

Focusing on net primary production provides information only about the flow of carbon in and out of plants. For a comprehensive ecosystem-level understanding of carbon cycling dynamics in response to elevated CO_2, an evaluation of net ecosystem production, or net primary production minus carbon losses, is necessary. Net ecosystem production incorporates autotrophic activity along with heterotrophic use of carbon energy sources that represents an actual measure of total carbon flux from an ecosystem. This can be estimated from measurements of net ecosystem exchange of CO_2 by large-scale material and energy flux measurements. These summed for a year provide a more robust estimate of net ecosystem production. A number of studies have attempted to estimate ecosystem C uptake under elevated CO_2 using net ecosystem CO_2 exchange measurements (Nie et al. 1992; Oechel et al. 1994; Fredeen and Field 1995; Ham et al. 1995; Kimball et al. 1995; Drake et al. 1996; Stocker, Leadley, and Körner 1997; Diemer and Körner 1998; Fredeen, Koch, and Field 1998). Such studies frequently report increases in net ecosystem C uptake under elevated CO_2. However, very few studies have been conducted in arid or semi-arid ecosystems, and few have conducted measurements over a period of time that would be required to understand lag and interactive effects in whole-ecosystem variables. Furthermore, the majority of these studies have measured net ecosystem exchange using open dynamic chambers (but see Oechel et al. 1994), a technique subject to pressure anomalies that can lead to substantial overestimates of ecosystem C uptake (Lund et al. 1999).

In arid and semi-arid ecosystems, the dynamics of carbon and nitrogen cycling are closely regulated and coupled to inputs of precipitation (Schlesinger 1997). It may be expected that elevated CO_2 influences patterns of nitrogen cycling, and this effect occurs through linkages to changes in ecosystem carbon status. Elevated CO_2 could decrease nitrogen availability through production of litter with high C:N ratios and increases in labile carbon in the soil via root exudation. Each of these result in the immobilization of nitrogen (Hungate et al. 1999). Some experiments have documented the reduction in tissue N concentration as plants increase production without increased N demand, but data on this from water-limited regions is lacking. There is little evidence for decreases in decomposition rates, and therefore in N availability, as a result of changes in litter quality with elevated CO_2. Considering the differential environmental control over decomposition in arid lands, any change in nitrogen cycling that involves decomposition as a mechanism may be speculative.

A more plausible effect that elevated CO_2 may have on nitrogen cycling would occur through changes in soil moisture resulting from reduced evapotranspiration. Increases in soil moisture could stimulate microbial activity and lead to increase nitrogen mineralization when carbon sources are not limiting (Hungate et al. 1997). Elevated CO_2 may also stimulate N mineralization in the following ways: through increased in-root exudation of highly labile C compounds combined with this soil water mechanism (Hungate et al. 1997), or through increased carbon supply to nitrogen-fixing bacterial symbionts. However, large shifts in the magnitude of nitrogen available in arid-land ecosystems may not be expected from rising CO_2, as linkages between production and nitrogen cycling may maintain the systems within certain bounds defined by the relationship between evapotranspiration and ecosystem leaf area (Hungate et al. 1999). Only with very large shifts in biomass on a landscape or shifts in system water balance should large effects on nitrogen cycling be expected. This could occur if it were mediated through shifts in the composition of vegetation specifically involving a change in dominant life form that affected the magnitude and characteristics of evapotranspiration.

19.2.3.2 Ecosystem Water Budgets

Soil Moisture and Water Availability. In arid and semi-arid plant communities, decreases in stomatal conductance can facilitate a higher efficiency of water use at the ecosystem level and increases in the availability of soil water (Fig. 19.2, Field, Jackson, and Mooney 1995). Many studies conducted in water-limited systems have shown that, especially in dry years, elevated CO_2 decreases ecosystem evaportranspiration so that water-use efficiency is enhanced (Fredeen and Field 1995; Ham et al. 1995; Field et al. 1997; Grunzweig and Körner 2001). In arid and semi-arid systems, this indirect impact of elevated CO_2 can enhance whole-system productivity, depending on the timing and magnitude of the availability of the additional soil water resource (Lockwood 1999). The degree of system aridity may also be important, as increased growth and leaf area production may offset decreases in stomatal conductance at the whole-plant scale (Pataki et al. 2000).

If decreased leaf-level transpiration does lead to decreased evapotranspiration

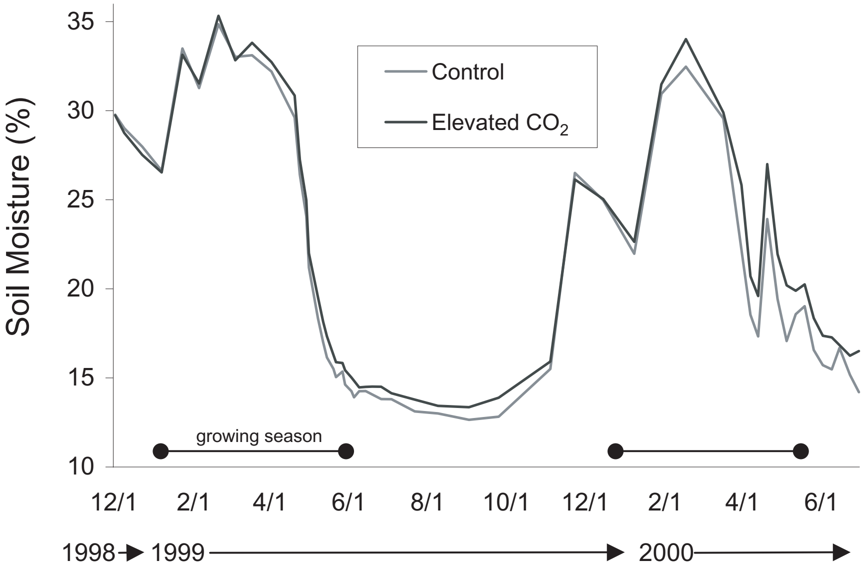

Figure 19.2. Soil moisture increases in late growing season in response to elevated CO_2.

under elevated CO_2, the effects on ecosystem primary production could be profound in water-limited ecosystems. A number of studies in semi-arid ecosystems have reported an increase in soil water content and leaf-water potential under elevated CO_2 (Jackson et al. 1994; Bremer, Ham, and Owensby 1996; Field et al. 1997; Niklaus, Spinnler, and Körner 1998; Owensby et al. 1999). Soil water content has been shown to remain high under elevated CO_2 conditions relative to control plots by as much as 18% in the tallgrass prairie (Owensby et al. 1999) and by 22% in a calcareous grassland (Niklaus, Spinnler, and Körner 1998). A similar pattern has also been reported for shortgrass steppe ecosystems (Morgan et al. 2001), but in the driest ecosystem, no significant differences in soil water content between elevated CO_2 and control plots has been detected in a Mohave Desert ecosystem (S. Smith, unpublished data).

Runoff and Deep Drainage. In many ecosystems, the effects on persistent residual soil moisture also have potential consequences for runoff, deep drainage, and nutrient leaching. Studies addressing the effects of elevated CO_2 on groundwater recharge and subsurface flow (collectively called drainage), runoff, and stream flow have largely been limited to modeling analyses (Aston 1984; Idso and Brazel 1984; Hatton et al. 1992; Jackson et al. 1998) and container experiments (Casella, Soussana, and Loiseau 1996). Modeling analyses predict an increase in both drainage and streamflow, but none of these studies have been adequately constrained by experimental data. In one of the few studies to make direct measurements, Casella, Soussana, and Loiseau (1996) found a 9% increase in drainage for perennial ryegrass swards grown in containers under elevated CO_2. In a modeling study constrained by experimental data, Lund (2001) also showed that elevated CO_2 increased annual drainage by 7% in a Mediterranean grassland. In general, increases in drainage will be greatest when large differences in evapotranspiration coincide with heavy precipitation to create a large pool of stored soil water that is not immediately lost to the atmosphere (Huxman et al. in review).

In semi-arid ecosystems where the leaf to air vapor pressure gradient is large, decreases in stomatal conductance under elevated CO_2 are associated with decreases in leaf-level transpiration (Pataki et al. 2000). Decreases in leaf-level transpiration can influence ecosystem-level evapotranspiration but only if canopy leaf area index does not increase proportionally. Several studies of semi-arid systems have examined the influence of elevated atmospheric concentrations of CO_2 on canopy transpiration and soil evaporation and have shown that decreased leaf-level transpiration can result in a 10% to 25% decrease in evapotranspiration (Nie et al. 1992; Ham et al. 1995; Stocker, Leadley, and Körner 1997). The relative reduction in evapotranspiration under elevated CO_2 is often less than the relative decrease in leaf-level transpiration for three reasons. First, soil evaporation and canopy interception of precipitation are not under stomatal control; yet these two factors are a significant proportion of ET in semi-arid systems (Huxman et al. in review). Second, evaporation from the soil may increase with an increase in soil water content as a result of decreased transpiration and increased soil hydraulic conductance. Third, a decrease in total leaf-level transpiration can be offset by a CO_2-driven increase in overall leaf area index, or, LAI (Gifford 1988; Nie et al. 1992; Schapendonk et al. 1997).

19.3 Plant and Ecosystem Responses to CO_2 in the Context of Multiple Global Change Factors

At this stage in our understanding, most of the experimental research on plant and ecosystem responses to global change in semi-arid and arid ecosystems have addressed responses to single global change factors, with relatively few studies exploring responses to two or more interacting treatments (Oechel et al. 1995; Oren et al. 2001). Yet with the information available from more mesic ecosystems, we can speculate on how future arid and semi-arid ecosystems might respond to those global factors that change indirectly as a consequence of a change in atmospheric CO_2.

19.3.1 Temperature

Concurrent with the predicted increase in CO_2, changes in the mean temperature of Earth's atmosphere of 1.5°C to 4°C are distinctly possible (Watson et al. 1990). This change in heat load on the planet may consist of both increases in mean growth temperatures and changes in the number and frequency of high temperature events (Wagner 1996)—both of which are important for understanding the overall impacts of climate change (Woodward and Williams 1987; Peters and Lovejoy 1992; Loik and Harte 1996; Roden and Ball 1996). While plant responses to a change in mean growing season temperature are much better understood, responses to high temperature extreme events that could interact with changes in CO_2 concentrations are less well known (Roden and Ball 1996; Sage 1996).

Rising CO_2 concentrations affect the processing of light energy through photochemical membranes (Sharkey 1985; Sage 1994), resulting in either a greater load of electron transport (Long 1991) or a decreased photochemical efficiency, leading to an increased susceptibility of photoinhibition (Roden and Ball 1996). In addition, stomatal conductance can decrease in elevated CO_2 (Knapp et al. 1996), potentially reducing the ability of the plant to reduce heat load (Sage 1996). Each of these factors suggest that while plants may perform greater at slightly higher growth temperature and elevated CO_2, the reduced ability to dissipate heat through nonphotochemical mechanisms may be exacerbated by the interaction between elevated CO_2 and an extreme temperature event. Results of studies evaluating these patterns are inconclusive but are important to continue, considering that species distributions in arid regions are limited by the ability of seedlings to survive the abiotic environment near the soil surface (Fenner 1985; Smith and Nowak 1990; Franklin et al. 1992). What little work has been done suggests that plants with high growth rates, or plants that experience temperature extremes concurrent with their growth season, may actually experience an increase in ability to tolerate high temperatures when exposed to elevated CO_2 (Huxman et al. 1998b; Taub, Seemann, and Coleman 2000). However, there is considerable variation in this response and the response to low temperature extremes, which suggests the potential for complex shifts in species boundaries in arid regions (Hamerlynck et al. 2000a; Loik et al. 2000; Dole, Loik, and Sloan 2003).

19.3.2 Precipitation

Anthropogenic emissions of greenhouse gases are expected to substantially influence hydrologic cycling, altering global and regional precipitation regimes (Houghton et al. 2001). We might see these alterations either through changes in the seasonality of precipitation (winter vs. summer) or in total precipitation amounts. Shifts in precipitation amounts in arid-land ecosystems have the potential to far exceed the impact of rising $[CO_2]$ and temperature on terrestrial ecosystems, since primary productivity in arid and semi-arid regions is often a linear function of total precipitation. General Circulation Models (GCMs) predict mean increases in global precipitation of up to 7% during this century (Houghton et al. 2001). Precipitation intensity and the frequency of extreme events are predicted to increase throughout the globe, raising the potential for episodic events that might have long-term consequences to ecosystems (Easterling et al. 2000). Yet at this point, the scenarios for specific geographic regions remain ambiguous, with unresolved discrepancies between the outputs of different models (Weltzin et al. 2003).

For arid and semi-arid regions, the availability of water more than any other factor dominates recruitment, growth and reproduction, nutrient cycling, and net ecosystem productivity (Smith et al. 1997; Neilson and Drapek 1998; Weltzin and McPherson 2000). For example, predicted increases in summer precipitation might contribute to a substantial "greening" across wide areas of the arid Southwest, primarily by increasing the density and relative production of C_4 grasses (Neilson and Drapek 1998). It was initially suggested that under relatively high water availability, plants from arid and semi-arid regions would show a photosynthetic down-regulation and thereby limit the potential CO_2 stimulatory effect (Oechel et al. 1995; Huxman et al. 1998c). This is apparently not the case in the arid Mohave Desert ecosystem, where without water availability, elevated CO_2 has no effect because of the absence of plant activity (Smith et al. 2000). As a result, an enhancement in year-to-year variability in production, beyond the extreme values already seen, could result from the coupling of CO_2 effects on semi-arid and arid ecosystems and enhanced variability in year-to-year rainfall.

19.3.3 Interactions among Multiple Climate Change Factors

A few ecosystem studies address effects of elevated CO_2 in combination with other global changes at the ecosystem scale. Oechel et al. (1994) found that warming could extend the time over which elevated CO_2 stimulated net primary production in arctic tundra. Oren et al. (2001) observed a parallel result with N addition in a pine plantation. Reich et al. (2001) report increased sensitivity of net primary production to elevated CO_2 with added nitrogen but only when species diversity is high. Several studies from agricultural ecosystems also have shown that enhanced nitrogen availability can lead to larger increases in net primary production in response to elevated CO_2 (Idso and Idso 1994). In each of these studies involving nitrogen-limited ecosystems, the sensitivity of net primary production to elevated CO_2 increased with the addition of nitrogen or, in the tundra example, with a treatment that indirectly increased nitrogen availability.

Several modeling studies have addressed ecosystem responses to multifactor global changes (Schimel et al. 2000; McGuire et al. 2001), but the theoretical foundation for predicting ecosystem responses to simultaneous changes in multiple factors, including elevated concentration of CO_2 and temperature and alterations in the timing and rates of precipitation, N deposition, and species movements, is incomplete. For some processes (e.g., photosynthesis), well-tested mechanistic models support the simulation and interpretation of multifactor responses (Farquhar, von Caemmerer, and Berry 1980). For many others, however, including biomass allocation, the timing of seasonal activity, the competitive balance between C_3 and C_4 plants, and other species changes, the empirical data are too sparse to support credible models or to allow comprehensive hypothesis tests.

Both empirical and modeling studies highlight potential contrasts between responses to single global changes versus multiple, interacting global changes. Stimulation of plant growth by elevated CO_2, for example, may be strongest when water is limiting (Owensby et al. 1999), when nutrients are abundant (Kimball and Mauney 1993), or when plant species diversity is high (Reich et al. 2001). Ecosystem responses to future global changes depend strongly on the interactions. A more plausible explanation of ecosystem responses to realistic global changes depends on a thorough understanding of responses to multiple, simultaneous changes.

The results from the Jasper Ridge Global Change Experiment, which manipulated atmospheric CO_2, temperature, precipitation, and N deposition in a full-factorial manipulation in Mediterranean annual grassland, suggest a fundamentally different kind of ecosystem response than would be expected from the combination of responses to a single manipulated factor. Over the first two years of the manipulations and across all of the treatment combinations (Fig. 19.3), elevated CO_2 had no significant effect on net primary production. In the third year, 2001, the mean net primary production for all treatment combinations with elevated CO_2 was 988 ± 52 g m^{-2} versus 1089 ± 54 g m^{-2} for all treatment combinations with ambient CO_2 (Shaw et al. 2002). Indeed, in all treatment combinations involving elevated CO_2, elevated CO_2 suppressed the allocation of carbon to the roots, decreasing the positive effects of increased

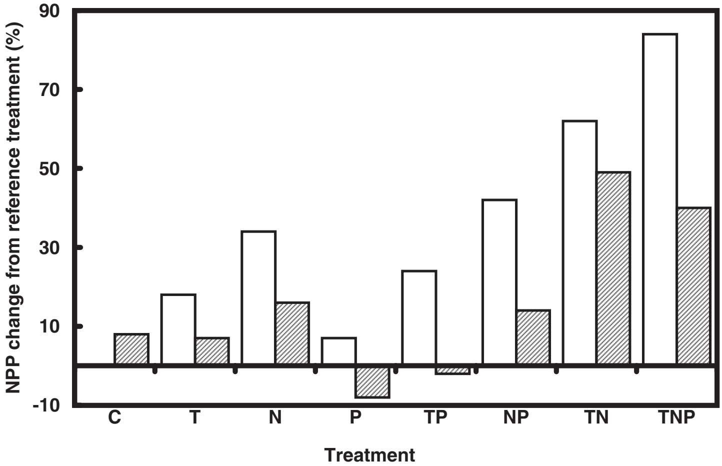

Figure 19.3. Percent changes in net primary production for each treatment, relative to corresponding reference. For each treatment combination, the reference is defined as all ambient CO_2 plots in which the variable(s) that defines each treatment combination is also at ambient (from Shaw et. al 2002). amb, ambient; C, elevated CO_2; N, N deposition; T, increased temperature; P, increased precipitation. For treatments T, N, and P, n=24 plots. For treatment TP, NP, and TN, n=12. For treatments C and TNP, n=6. For example, the open bar for the increased temperature pair (T) is calculated using all treatments with increased temperature but no elevated CO_2 (n=24). The gray bar in the same pair (T) is calculated using all treatments with increased temperature and elevated CO_2 (n=24).

temperature, precipitation, and N deposition on net primary production (Shaw et al. 2002).

19.4 Summary

We have a good understanding of ecological importance of CO_2 effects on growth, survival, and reproduction in plants from water-limited regions. We know that increases in water use-efficiency occur as a result of multiple character changes in many plants and that in some systems, these changes in water use can impact whole-system water balance. We additionally know that during periods that are not limited by other important resources, elevated CO_2 can lead to greater productivity on a landscape for water-limited systems. However, despite considerable effort being directed toward understanding plant and ecosystem responses to elevated CO_2 in semi-arid and arid ecosystems, we have limited knowledge of the expected pattern beyond the same range of biomes with experimental systems. This stands in contrast to the importance of these biome types in their rank cover of the globe. The fraction of the human population that is directly affected by processes such as desertification, decreased productivity of rangelands, and water yield of semi-arid landscapes is substantial, and greater attention to these systems is certainly warranted. Additionally, there is little understanding of how important modifiers of the CO_2 response may shape these future landscapes (Smith, Jordon, and Hamerlynck 1999). For example, in the southwestern United States shifts in the relative frequency of winter-versus-summer rainfall have been predicted, with either greater summer or winter precipitation possible. It has also been suggested that the magnitude of rainfall may shift along with interannual variability. Each of these climatic factors has been said to be critically important in shaping the structure and function of the arid regions, perhaps to a greater degree than rising CO_2.

Several concepts emerge relative to how elevated CO_2 will impact structure, composition, and process in water-limited systems. The covariation in life form with photosynthetic pathway may result in shifts in the relative abundances of C_3 versus C_4 taxa. Within semi-arid and arid ecosystems, the responses to elevated CO_2 may be a function of the magnitude and interannual variablility of precipitation (Fig 19.4). In semi-arid ecosystems, CO_2 effects in relatively wet years can result in limited overall impacts on the ecosystem. However, in extremely arid systems, the greatest effect occurs in wetter years (Smith et al. 2000). As a result, increasing CO_2 may have two general effects across a range of water-limited ecosystems: (1) *reducing* year-to-year variation in production for relatively mesic systems by disproportionately increasing production in dry rather than wet years, and (2) *increasing* year-to-year variation in more xeric systems, where production

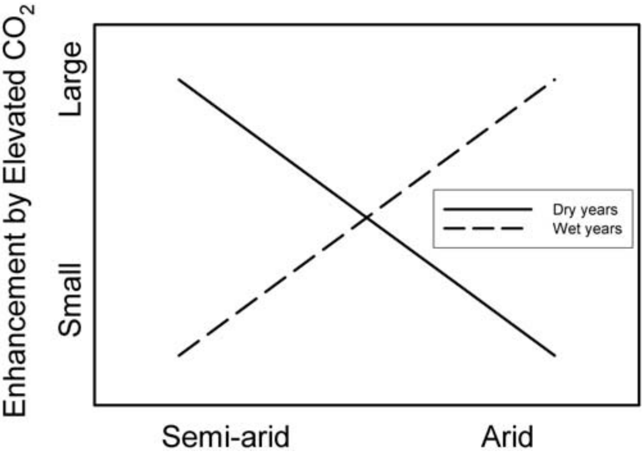

Figure 19.4. The conceptualized effects of elevated CO_2 on plant and ecosystem function across a gradient of water availability for semi-arid and arid ecosystem types. The dashed line represents relatively wet years (annual hydrologic year precipitation), and the solid line is for relatively dry years.

is greatly enhanced in wet years and not affected in dry years. That is, the characteristics of water limitation may diminish in relatively mesic ecosystems and become more pronounced in relatively xeric ecosystems. It is possible that elevated CO_2 may make some water-limited regions more arid rather than less.

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