Chapter 6

Global change and the linkages between physiological ecology and ecosystem ecology

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A physiological basis for many ecosystem-scale patterns

Plant physiological ecology has focused historically on describing the basis of adaptation between organisms and their environment (Mooney & Chabot 1985; Mooney *et al.* 1987; Larcher 1995; Lambers *et al.* 1998). While the roots of physiological ecology are in both plant physiology and plant geography, the last several decades have seen the emergence of strong linkages between physiological ecology and ecosystem ecology, and also in the globalization of ecological thought (Mooney & Drake 1986; Ehleringer & Field 1993; Mooney 1998; Mooney *et al.* 1999; Mooney & Hobbs 2000).

Not all of the controls over processes at the physiological scale are directly relevant to processes at the ecosystem scale. Whereas the fluxes of water and CO_2 between the ecosystem and the atmosphere are often predictable knowing many of the basic physiological controls over leaf-level gas exchange (Canadell *et al.* 2000), this need not be the case for all metabolic processes. Aggregation properties at higher levels can result in additional controls over fluxes that are sometimes not predictable without also knowing how elements aggregate into a forest stand or entire ecosystem (Ehleringer & Field 1993). Yet frequently by identifying the mechanistic basis of plant performance, we can gain insight into controls and components of fluxes in ecosystems, the invasibility of species into ecosystems, sensitivity of individual species and plant communities to changes in resource availability, and biotic interactions among different species.

Changes are taking place in our environment and across the face of this planet. Global changes are occurring in many ways: atmosphere, land-use, and now also climate (IPCC 1996; Mooney *et al.* 1999; Huang *et al.* 2000). Consider these undebatable changes which have accelerated since the early 1950s: human population increase, conversion of lands into cultivation, fertilizer production, atmospheric greenhouse gases, and species extinctions. Humans are dominating and changing this planet in a way that no organism has since the first microbes began to produce

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oxygen 2–3 billion years ago. The consequences of these global changes are realized as loss of habitat, changes in species abundances and distributions, biological invasions, and the changes in dynamics and functioning of ecosystems. While it is easy to identify man as the driver for these changes, it is frequently less easy to predict exactly how plants, populations, and ecological systems will respond. Understanding the physiology and biochemistry of plants, however, does serve as a basis for scaling responses from tissue to whole organism to ecosystem scales (Ehleringer & Field 1993). Similarly, top-down approaches are useful in constraining our interpretations.

This chapter focuses on three global-change examples of how an understanding of physiological processes has led to new insights into controls over the functioning of terrestrial ecosystems. We focus on examples where physiological properties of the individual organisms contribute to the functioning of the ecosystem in direct ways. In the first example, a *palaeoecological* study, we examine how shifts in atmospheric CO_2 through history have influenced the abundances of different photosynthetic pathways, leading to changes in the animal species occurring across these landscapes. The second example, a *current-ecological* study, describes how measurements of the carbon isotope ratio of plant tissue and atmospheric CO_2 are used to study metabolic properties and partition CO_2 exchange processes within ecosystems and between the ocean and terrestrial ecosystems. The temporal and spatial integration that is provided by measurements of stable isotope ratios helps to improve understanding of controls on ecosystem function. In the last, a *future-climate change* example, we explore the physiological basis for the sensitivity of arid-land ecosystems to anticipated changes in the distribution of monsoonal precipitation. Here we explore the consequences of morphological and physiological differences in rooting patterns to water uptake at the ecosystem level.

Atmospheric CO_2 and C_3–C_4 ecosystems

The functioning of ecosystems in the geological past probably overlaps considerably with how they function today, except where climatic and atmospheric conditions today contrast with conditions in the past. Understanding the past and how ecosystems have changed through time may provide clues to the future. Atmospheric CO_2 is a global parameter that has varied in the past and has had an impact on the world's ecosystems. The rise in atmospheric CO_2 today is a direct consequence of fossil fuel consumption, cement production, and forest burning associated with land-use changes. Humans have played a significant role in increasing atmospheric CO_2 since the dawn of the Industrial Revolution. Over the past 420 000 years, atmospheric CO_2 had varied between approximately 180 and 280 p.p.m. (Petit *et al.* 1999). Humans and many other species evolved in a low-CO_2 world. Yet today the Earth's atmosphere is changing rapidly. Human activities now exert a significant impact on the atmosphere and thereby also on the Earth's climate system (Vitousek *et al.* 1997). With today's CO_2 levels more than 30% greater than values three centuries ago, global warming has received the greatest

attention. Yet there are other direct effects of elevated CO_2 on ecosystems, not the least of which is that physiological processes, such as photosynthesis and photo-respiration; the rates of these processes vary directly with atmospheric CO_2 levels.

At the biochemical level, ribulose 1,5-bisphosphate carboxylase-oxygenase (rubisco) catalyses the reduction of CO_2 with ribulose bisphosphate to form two molecules of phosphoglyceric acid, a three-carbon molecule. This initial photosynthetic reaction forms the basis of C_3 photosynthesis and the eventual production of sugars and other carbohydrates. However, rubisco also has an oxygenase activity in which O_2 is substituted for CO_2, leading to the formation of one molecule each of phosphoglyceric acid and phosphoglycolate. An eventual product of this oxygenase activity is CO_2, which leads to the oxygenase activity being referred to as photorespiration. In spite of the high selectivity for CO_2 by rubisco, oxygenase activity increases as the CO_2/O_2 ratio decreases. Oxygenase activity also increases faster with temperature increase than does carboxylase activity. As a consequence photorespiratory rates increase as atmospheric CO_2 decreases and/or habitat temperatures increase.

An evolutionary solution to the dilemma of increased photorespiration is C_4 photosynthesis, a modification in which the C_3-photosynthesis cycle is now restricted to specific cells within the leaf interior (often bundle-sheath cells). These bundle-sheath cells are now physically surrounded by mesophyll cells with high phosphoenolpyruvate (PEP)-carboxylase activity. PEP carboxylase combines PEP and CO_2 to form oxaloacetate, a four-carbon molecule, as the initial photosynthetic product. Since PEP carboxylase activity is so much higher than Rubisco activity, the $[CO_2]$ environment of Rubisco in C_4 plants is high, resulting in a high CO_2/O_2 ratio and the virtual elimination of photorespiration. The $[CO_2]$ inside C_4 leaves at the site of Rubisco activity is thought to be in excess of 2000 p.p.m. (Sage & Monson 1999), which makes the CO_2 concentration similar to what C_3 plants would have experienced back in the Cretaceous! Yet the C_4 cycle is more energetically expensive, because it requires additional adenosine triphosphate (ATP) to regenerate PEP from pyruvate in order to maintain the cycle. Modelling results indicate that the intrinsic differences in the C_3/C_4 photosynthetic pathways have implications that scale to the ecosystem level, influencing the relative distributions of C_3 and C_4 plants, and also influencing the mammalian herbivores that feed on these plants.

Ehleringer *et al.* (1997) modelled the trade-offs between photorespiratory carbon losses in C_3 photosynthesis vs. increased energetic costs in C_4 plants as a function of the environmental $[CO_2]$ and temperature conditions. That analysis, known as the quantum-yield model, predicted clear boundaries in the environmental conditions favouring the presence of C_3 vs. C_4 photosynthesis (Fig. 6.1). Atmospheric CO_2 concentration is predicted to have a strong influence on the relative competitive abilities of C_4 plants. For the modern atmosphere of about 365 p.p.m. CO_2 the C_3/C_4 crossover temperature for conditions favourable to C_4 photosynthesis was about 22–24°C. This predicted C_3/C_4 crossover is consistent with the global distributions of grasses and sedges today (Ehleringer *et al.* 1997; Epstein
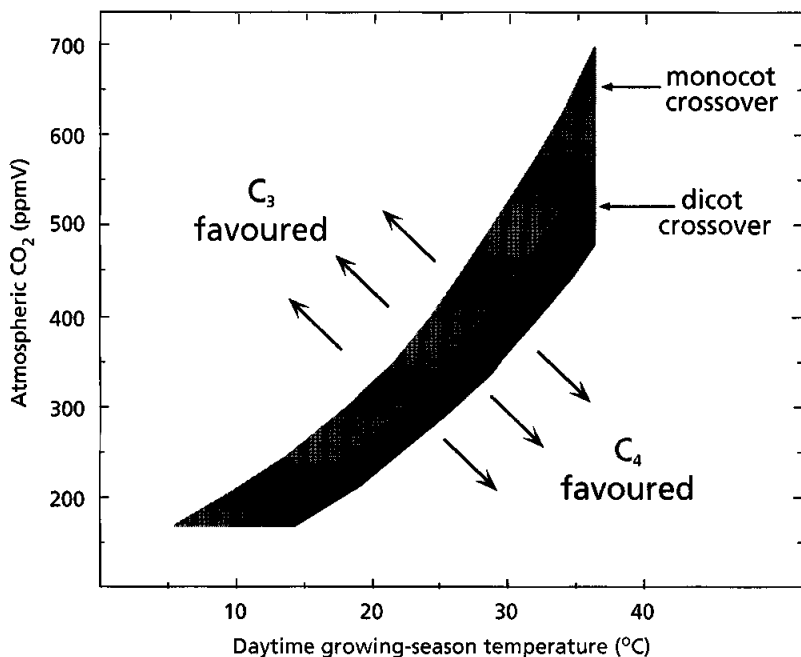
Figure 6.1 The combinations of atmospheric CO_2 and growing season temperatures that favour C_3 plants vs. C_4 plants. The light grey region represents the transition zone for C_3/C_4 monocot species and black region represent the transition zone for C_3/C_4 dicots. (Model is based on Ehleringer *et al.* 1997.)

et al. 1997; Tieszen *et al.* 1997; Sage & Monson 1999). A more detailed discussion of the evolution of C_4 photosynthesis is found in Sage and Monson (1999).

At lower CO_2 concentrations, such as were present during full glacial conditions, the crossover temperature is much lower (about 15°C). The emerging palaeo-ecological literature is revealing that C_4-dominated ecosystems were much more expansive during the glacial periods than today (Ficken *et al.* 1998; Street-Perrott *et al.* 1998; Huang *et al.* 1999). On the other hand, the quantum-yield model predicts that when CO_2 concentrations exceed about 500 p.p.m. the window of favourable temperatures for C_4 photosynthesis is set very high (at about 40°C), implying that few environments of Earth would favour C_4 photosynthesis. Therefore, this modelling exercise suggests that the 'C_4-world' is possible only when atmospheric CO_2 concentrations are low.

Carbon isotope ratios can be used as indicators of the relative abundances of C_3 vs. C_4 vegetation types through geological time (Cerling & Quade 1990; Cerling *et al.* 1997). The difference in the initial carboxylation reaction of C_3 and C_4 photosynthesis results in a large difference in their $^{13}C/^{12}C$ ratios (Farquhar *et al.* 1989). C_3 plants have carbon isotope ratios ranging from about −22 to −30‰

(though rarely as low as −35‰), whereas C_4 plants have carbon isotope ratios ranging from −11 to −15‰. Carbon isotope values form the main basis by which we can understand the spread of C_4 ecosystems in the geological record. Pollen morphology is not distinct enough to distinguish between C_3 and C_4 grasses, so pollen records cannot be used to determine the relative abundance of C_4 grasses in fossil floral records. In addition, because grasses are generally found in regions that are highly oxidizing, the fossil record of grasses is extremely poor. However, animal tissues preserve information about diet choices, and so the distinction between C_3 browsers and C_4 grazers is recorded in the fossil record in the form of tooth enamel, a bioapatite phase that is very resistant to recrystallization during diagenesis. Tooth enamel is enriched by about 14‰ compared to diet, so that C_3 hyper-browsers have carbon isotope ratios about −12‰ whereas C_4 hyper-grazers have carbon isotope ratios values about 0‰ (Cerling & Harris 1999). The high dietary selectively of grazers enhances the C_4 signal. However, some animals (including grazers) eat mixtures of C_3 and C_4 plants, resulting in intermediate $\delta^{13}C$ values.

Figure 6.2 shows the isotopic distinction between C_3 and C_4 plants, indicating that modern mammals consume either mostly C_3 or C_4 plants in their diets, and that before 8 million years ago there were no mammals with a C_4-dominated diet. Therefore, before 8 million years ago the global vegetation was dominated by C_3 photosynthesis (Cerling et al. 1997). By 6 million years ago, however, mammals with C_4-dominated diets are found in Asia, Africa, North America and South America. Equids dispersed from North America into the Old World by 10.5 million years ago and have C_3-dominated diets in North America, Asia and Africa until 8 million years ago. By 6 million years ago, however, they changed to a C_4-dominated diet in Pakistan, Africa and southern North America (Fig. 6.3). Equids in Europe and northern North America maintained a C_3-dominated diet, presumably C_3 grasses. The period at the end of the Miocene was one of global faunal change, with major faunal turnover in many parts of the world (Fig. 6.4). In many regions this time had been interpreted to be a major change in flora from a forested or closed habitat to a more open habitat. We now know it to be the time when C_4 grasses first underwent global expansion and established the significant presence of C_4 photosynthesis in low to intermediate latitudes, where they currently make up 30% or more of the net primary productivity.

The C_3/C_4 quantum-yield crossover model has important implications for evolution during the last several million years. Major changes occurred in the evolution of mammals, especially grazing mammals coincident with the expansion of C_4 ecosystems. Humans evolved in this low-CO_2 world and there are indications that a C_4 diet was associated with an ancestral hominid (Sponheimer & Lee-Thorp 1999). At present, we can document that for the last 400 000 years, the Earth has been alternately in Glacial or Interglacial conditions, with characteristic CO_2 concentrations of approximately 180 and 280 p.p.m., respectively (Petit et al. 1999). Today, humankind's thirst for cheap energy has resulted in fossil fuel burning which has increased atmospheric CO_2 to levels that should influence the competitive interactions between C_3 and C_4 grasses. If the predictions of the quantum-yield model
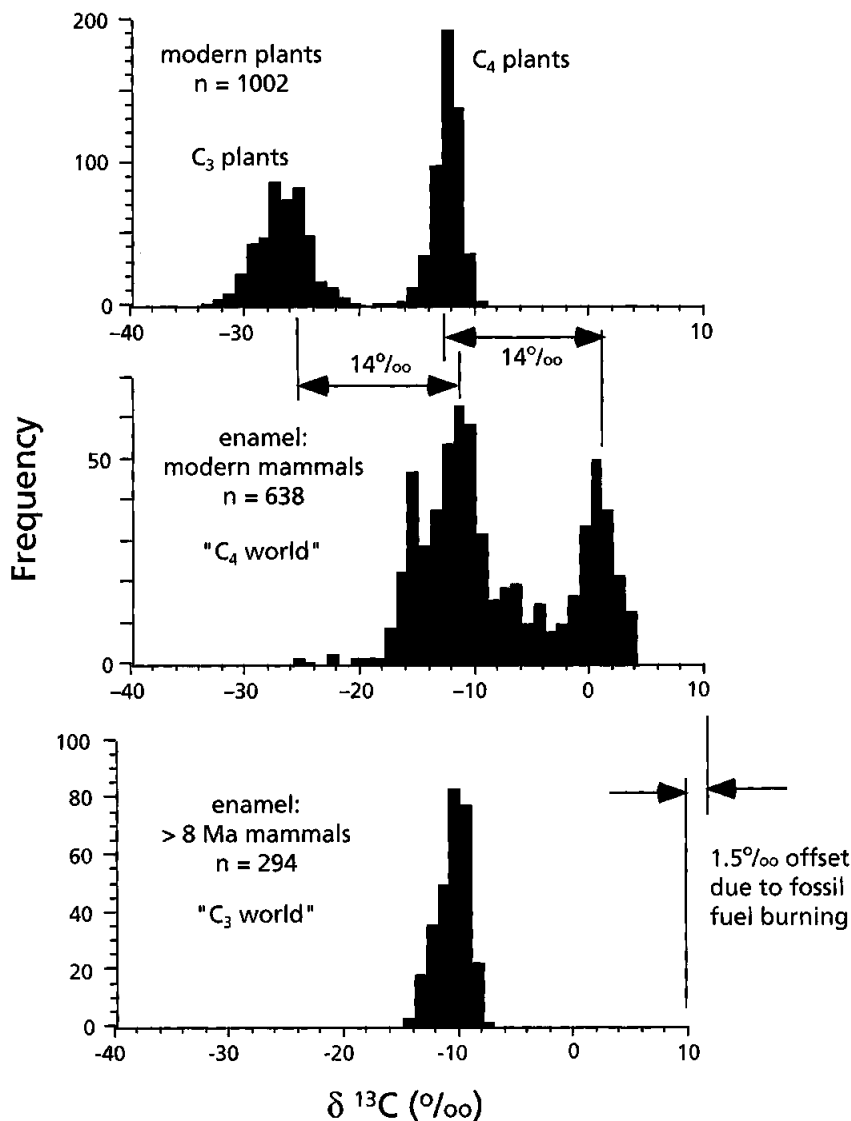
Figure 6.2 Frequency histograms of the $\delta^{13}C$ values of modern C_3 and C_4 plants (a), the tooth enamel of modern mammals (b), and the histogram of enamel from fossil tooth enamel for mammals that are older than 8 million years (c). (Adapted with permission from Cerling *et al.* 1997.)

hold up and stand the test of time, this physiological hypothesis predicts that C_4 taxa in a high-CO_2 world should eventually exhibit a decreased competitive ability relative to C_3 taxa in those areas where both photosynthetic types coexist today. Paired species comparisons may not always reflect a simple, uniform CO_2-
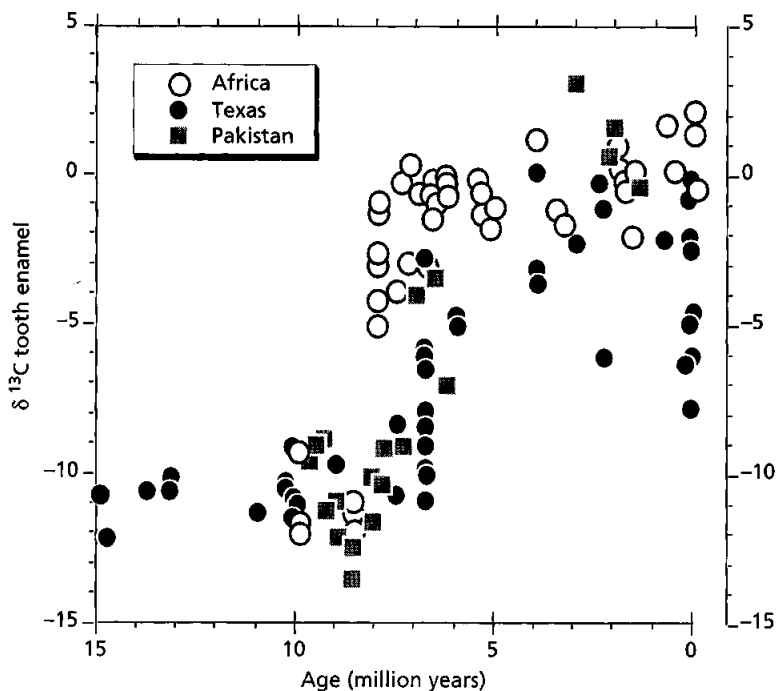
Figure 6.3 The $\delta^{13}C$ values of tooth enamel from fossil equids that grazed in grasslands in Kenya, Texas, and Pakistan between 15 million years ago and the present. (Adapted with permission from Cerling & Quade 1990.)

dependent competitive transition, because other physiological or phenological factors may come into play (Wand *et al.* 1999). Yet if overall the hypothesis is correct, then it is likely that both invertebrate and vertebrate herbivorous taxa in low-latitude regions will be exposed to new diets in the next century that will result in different digestibilities and therefore also influence the competitive ability of the fauna in these ecosystems.

Carbon isotopes in ecosystem and global carbon cycle studies

Linkages between ecophysiology and ecosystem ecology are important for understanding many of the global changes taking place today. Currently there are uncertainties about some specifics of the global carbon budget and the role that terrestrial ecosystems play in that budget (Fan *et al.* 1998; Lloyd 1999; Battle *et al.* 2000; Schimel *et al.* 2000). Atmospheric studies have been very important in illustrating the need to better understand the processes that control CO_2 exchange in terrestrial ecosystems. High-precision measurements of the concentration and stable isotope ratios of atmospheric CO_2, in combination with atmospheric
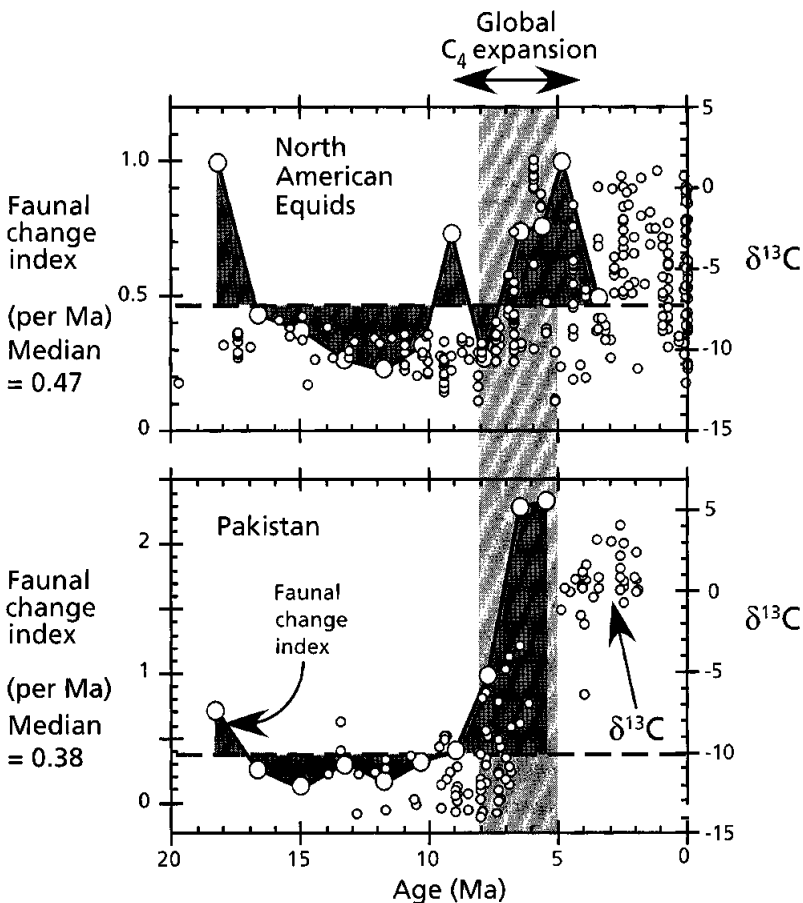
Figure 6.4 Changes in the faunal index for groups of mammalian grazers from North America and Pakistan between 20 million years ago and present.

transport models, have been used to infer CO_2 uptake and release on a global basis (Ciais *et al.* 1995; Battle *et al.* 2000). For example, there is a strong north–south gradient in the concentration of atmospheric CO_2, with higher concentrations observed in the northern hemisphere (Trolier *et al.* 1996; Fung *et al.* 1997). However, the difference in CO_2 concentration between northern and southern hemispheres is smaller than predicted, based on well-known emissions of fossil fuels. These CO_2-concentration data have been used to infer that there is a strong sink for CO_2 in northern temperate regions. In addition, atmospheric CO_2 in the northern hemisphere has higher amounts of ^{13}C than would be predicted based on fossil fuel emissions and observed CO_2 concentration measurements (Fung *et al.* 1997). These carbon-isotope data have been used to infer that the sink in the northern hemisphere is primarily associated with carbon uptake in terrestrial ecosystems (Battle *et al.* 2000). This argument is based on the fact that C_3 plants (the dominant plant type in northern temperate terrestrial ecosystems) preferentially take up ^{12}C during photosynthesis and discriminate against CO_2 containing ^{13}C (Farquhar *et al.* 1989). As a result, ^{13}C reaches higher levels in the atmosphere as it is left behind during net carbon uptake in terrestrial ecosystems. In contrast, net uptake of CO_2 from the atmosphere by the oceans does not result in any significant discrimination against ^{13}C (Ciais *et al.* 1995; Fung *et al.* 1997). Other recent analyses of atmospheric CO_2 concentration and isotopic measurements have shown large year-to-year changes in the net uptake of carbon by the terrestrial biosphere (Ciais *et al.* 1995; Francey *et al.* 1995; Battle *et al.* 2000). Some of these changes are probably associated with El Niño and other large-scale climate anomalies (Braswell *et al.* 1997). However, the mechanisms responsible for net carbon sequestration in terrestrial ecosystems and the exact spatial location of the ecosystems contributing most to the global terrestrial sink remain controversial (Lloyd 1999). Evidence also exists for changes in the seasonality of carbon exchange in terrestrial ecosystems. It appears that spring occurs earlier now in the northern hemisphere, based on changes in the timing and amplitude of the seasonal cycle of atmospheric CO_2 and on satellite observations (Keeling *et al.* 1996; Myneni *et al.* 1997; Randerson *et al.* 1998). All these results and interpretations about important changes in the global carbon cycle have come from atmospheric studies. Yet the basis of this response is physiological and ecological. We need further ecosystem studies to better understand the processes contributing to carbon uptake and release in terrestrial ecosystems. A major research challenge is to more accurately define the mechanisms and location of terrestrial sinks for atmospheric CO_2, and how these sinks will respond to changes in climate, land use and management practices.

The study of stable isotope fractionation during carbon cycling in terrestrial ecosystems provides a useful way to make the link between physiological and ecological processes on the ground and the atmospheric measurements described above (Flanagan & Ehleringer 1998; Bowling *et al.* 1999; Ehleringer *et al.* 2000). In C_3 plants there are two primary processes that cause carbon isotope ratios to change during photosynthesis, diffusional fractionation and enzymatic fractionation by rubisco. The carbon isotope ratio of plant organic material depends on the

relative influence of diffusional and enzymatic fractionation which is controlled by the ratio of leaf intercellular CO_2 (c_i) and atmospheric CO_2 (c_a). This c_i/c_a ratio is important because it is a function of photosynthetic capacity and stomatal conductance. Changes in c_i/c_a and leaf carbon isotope ratio are a function of changes in either photosynthetic capacity or stomatal conductance or both (Farquhar et al. 1989).

Therefore, in addition to indicating photosynthetic pathway, carbon isotope discrimination against ^{13}C provides much information about the physiological and ecological functioning of plants in ecosystems. The carbon isotope ratio of C_3 plant tissue provides an assimilation-weighted average of c_i/c_a, a parameter that will vary as changes in environmental conditions induce variation in photosynthesis rate and stomatal conductance. Information about processes integrated over the life of the leaf are recorded by the ^{13}C content of leaf tissues and this allows subtle ecological differences in water-use efficiency and light-use efficiency to be distinguished within and among species in an ecosystem (Pearcy & Pfitsch 1991; Ehleringer et al. 1993; Berry et al. 1997; Buchmann et al. 1997a,b). Ehleringer (1994) and Brooks et al. (1997a) have illustrated distinct differences in ^{13}C among life forms or functional groups in different ecosystems. Variation in plant ^{13}C values appears to be related to plant water- and light-use strategies and to longevity of leaves in different plant functional groups. The carbon isotope ratio of plants averaged over the community can reflect environmental variation among different plant communities along rainfall, light or other environmental gradients (Ehleringer & Cooper 1988; Stewart et al. 1995). Ecosystem processes, such as the proportion of respired CO_2 that is re-fixed by photosynthesis before leaving a forest canopy, can also be studied using measurements of leaf carbon isotope ratio (Brooks et al. 1997b; Buchmann et al. 1997b, 1998).

The power of the stable isotope measurements on plant leaf tissues is that we can obtain time-integrated data on plant metabolism, and this is difficult or impossible to do with other physiological approaches because of limitation in equipment measurement resolution, or because of the time requirement for manually collecting many physiological measurements. In addition to the temporal integration of metabolic activities, stable isotope measurements of atmospheric CO_2 can be used to provide spatial integration of physiological information. At the ecosystem level, carbon isotope discrimination that occurs during net ecosystem carbon uptake should reflect the photosynthesis-weighted average of discrimination in all photosynthetically active plants in the ecosystem. Because there is no fractionation during mitochondrial respiration, the carbon isotope ratio of respired CO_2 reflects the composition of the substrate used for respiration. The isotope ratio of respired CO_2 can be measured at a range of spatial scales from individual ecosystem components (e.g. soil or leaf) to the entire ecosystem, to the landscape level using Keeling plot analyses (Flanagan & Ehleringer 1998).

Measurements of the isotope ratio of respired CO_2 reflect the spatially and temporally integrated ^{13}C content of organic matter within an ecosystem. A Keeling-plot analysis provides one means of quantifying the carbon isotope ratio of CO_2

leaving different terrestrial ecosystems (Fig. 6.5). The Keeling plot is basically the analysis of a mixing of two pools of CO_2. In effect, at any point in time the bulk atmosphere is considered to have a single fixed CO_2 concentration with a specific $\delta^{13}C$ value. Respiration from the plant, animal and microbial components increases the CO_2 concentration of this bulk air and alters its $\delta^{13}C$ value. The Keeling plot is a representation of this mixing process, obtained by sampling the air within canopies during periods of respiration. The intercept of a Keeling plot ($\delta^{13}C$ of CO_2 vs. $1/CO_2$) is the flux-weighted mean $\delta^{13}C$ value of the source (i.e. plants, animals and microbes). The basis for differences in the Keeling-plot intercepts is not only differences in the proportions of C_3 and C_4 photosynthesis, but also differences in physiological constraints associated with C_3 photosynthesis (Farquhar et al. 1989).
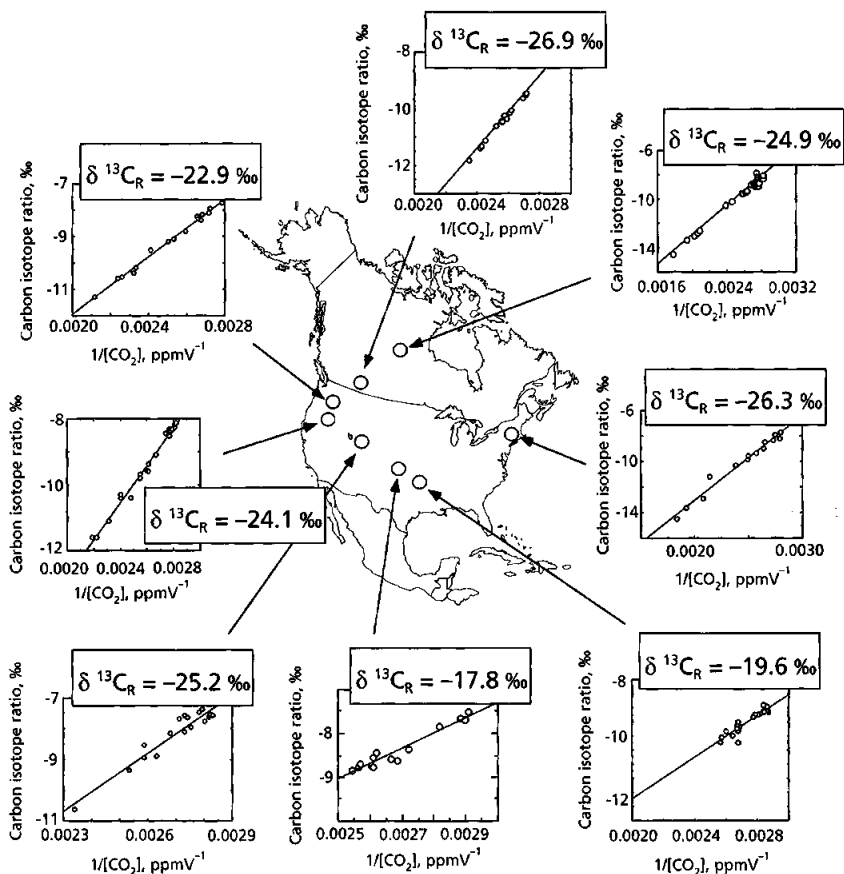

Figure 6.5 Variations in the carbon isotope ratio of CO_2 of ecosystem respiration (derived from Keeling plots) for different ecosystems across North America. (Data are from Ehleringer & Cook 1998; Flanagan et al. 1996; J. Berry, J. Ehleringer & L. Flanagan, unpublished.)

Ehleringer and Cook (1998) have used isotopic approaches to characterize how CO_2 respired from ecosystems along a precipitation gradient changes between wet and dry periods (Fig. 6.6). These data reveal shifts to lighter ^{13}C values of respired CO_2 as water stress is relieved. This same physiological pattern is commonly seen at the leaf level as stomata open to allow greater gas exchange under higher plant water potentials (Farquhar $et\ al.$ 1989; Ehleringer $et\ al.$ 1993).

There is much interest in making whole-ecosystem measurements of carbon isotope discrimination for several important reasons. First, knowledge of average photosynthetic discrimination at the global level, weighted by ecosystem type and productivity, is an important input to studies that partition the net uptake of anthropogenic CO_2 emissions between the ocean and terrestrial biosphere (Fung $et\ al.$ 1997). Secondly, whole-ecosystem discrimination measurements could provide information about the canopy weighted value of c_i/c_a, and therefore the spatially integrated water-use efficiency of the canopy. Thirdly, in ecosystems with significant proportions of C_3 and C_4 plants, measurements of whole-ecosystem
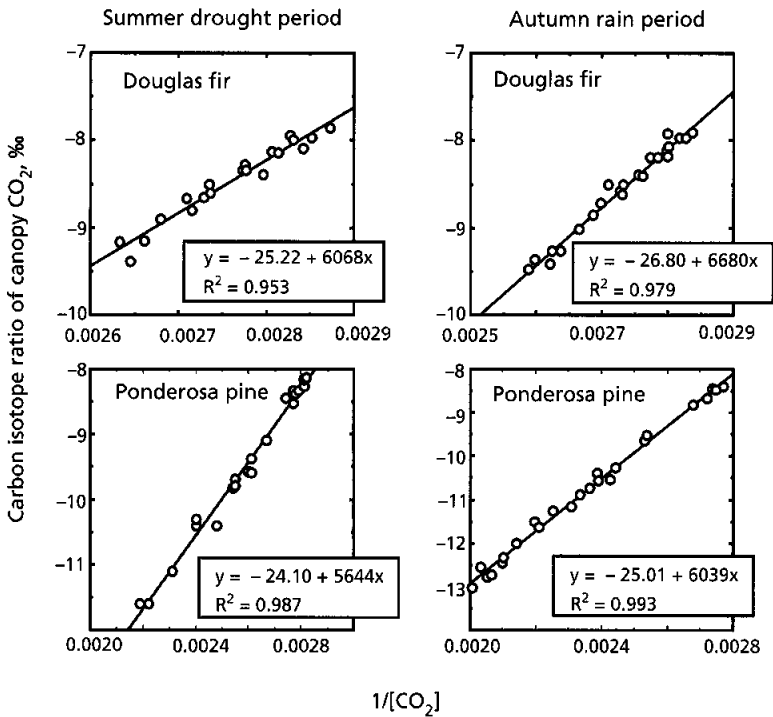

Figure 6.6 Variations in the carbon isotope ratio of CO_2 of ecosystem respiration (derived from Keeling plots) for Douglas fir and ponderosa pine ecosystems in central Oregon during the summer drought period and later in the autumn after rains have commenced. (Modified with permission from Ehleringer & Cook 1998.)

discrimination can be used to partition the contribution of the different photosynthetic pathways to total ecosystem productivity (Miranda *et al.* 1997). Fourthly, simultaneous measurements of ecosystem CO_2 fluxes using eddy covariance and isotope fluxes can allow the partitioning of net ecosystem CO_2 exchange into the component fluxes, gross photosynthesis and total ecosystem respiration (Yakir & Wang 1996; Bowling *et al.* 2001; Yakir & Sternberg 2000). We provide below further discussion and examples of a few of these important applications of ecosystem-level carbon isotope discrimination.

Many atmospheric inversion studies use a global average value of 18‰ for the carbon isotope discrimination that occurs during net uptake of CO_2 by terrestrial photosynthesis (Ciais *et al.* 1995; Battle *et al.* 2000). Fung *et al.* (1997) have shown how sensitive the results of the terrestrial–ocean partitioning exercise can be to variation in the terrestrial photosynthetic discrimination parameter. We know from empirical and modelling studies that carbon isotope values should vary greatly among ecosystems (e.g. Fig. 6.5), with significant change along latitudinal and altitudinal gradients (Körner *et al.* 1988, 1991; Lloyd & Farquhar 1994; Ciais *et al.* 1995; Fung *et al.* 1997). However, there are few measurements of isotope discrimination occurring in association with ecosystem CO_2 flux studies (Lloyd *et al.* 1996; Flanagan *et al.* 1996, 1997; Yakir & Wang 1996; Bakwin *et al.* 1998). This physiologically based, ecosystem information is needed in order to test global model discrimination calculations and improve confidence in the terrestrial–ocean ecosystem partitioning studies.

Ecosystem carbon budgets are controlled by the balance between carbon uptake during photosynthesis and carbon loss during respiration. Net CO_2 exchange of an ecosystem can now be measured with eddy covariance techniques (Baldocchi *et al.* 1988; Wofsy *et al.* 1993; Aubinet *et al.* 2000). However, a relatively small change in either photosynthesis or respiration can influence whether an ecosystem is a net source or sink for CO_2 (Goulden *et al.* 1998; Valentini *et al.* 2000). We would like to have direct, separate information on the rate of ecosystem photosynthesis and respiration, because the environmental controls on the two processes are quite different. In eddy covariance studies, total ecosystem respiration rate is often calculated from the net CO_2 exchange measurements made at night when photosynthesis is not active. However, this procedure is subject to a variety of important errors and often underestimates total ecosystem respiration rates (Goulden *et al.* 1996; Lee 1998; Aubinet *et al.* 2000).

An alternative approach makes use of stable isotope measurements to partition net ecosystem CO_2 exchange into its component fluxes (Bowling *et al.* 2001). In this approach simultaneous measurements of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 are made while eddy covariance techniques are used to measure net ecosystem CO_2 exchange. Figure 6.7 shows an example of the results of flux partitioning using stable isotopes, for an active corn crop during August. The calculated rate of total ecosystem respiration at the start of the light period is much higher than would have been estimated from the night-time eddy covariance measurements made
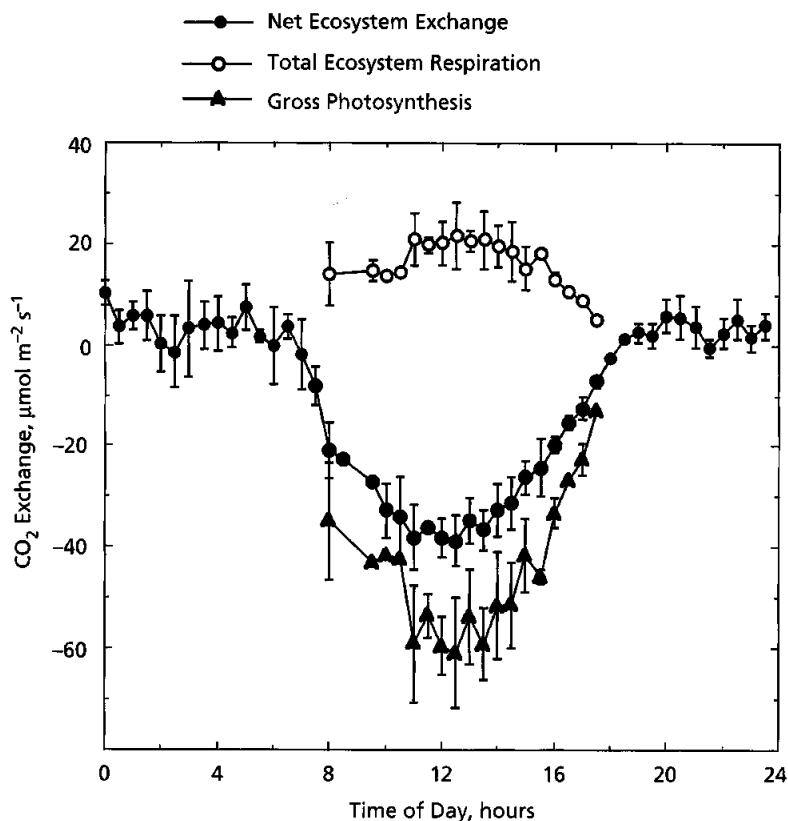
Figure 6.7 Partitioning of net ecosystem CO_2 exchange in a corn field into net photosynthesis and ecosystem respiration components, based on the approaches developed by Bowling *et al.* (2001). (From L.B. Flanagan, unpublished.)

under low turbulence. This stable isotope approach shows good promise for providing more mechanistic insights into the processes that control the carbon budget of an entire ecosystem.

A novel approach proposed by M.H. Conte and J.C. Weber (unpublished) for temporally and spatially integrating measurements of ecosystem carbon isotope discrimination is the isotopic analysis of plant leaf waxes collected in aerosol samples. A variety of wax compounds are produced to provide a protective covering on the surface of plant leaves. These waxes can be removed from the plant by physical disturbance (wind) and transported in the atmosphere as micron-sized particles. The carbon isotope composition of the leaf wax is dependent on fractionation during photosynthesis and secondary fractionation that occurs during the synthesis of the wax (wax and lipid molecules are generally depleted in ^{13}C relative to bulk plant tissue, Farquhar *et al.* 1989). Changes in the isotopic composition of

the wax should reflect variation in photosynthetic discrimination against ^{13}C near the time of wax synthesis. Therefore, it is likely that the leaf-wax carbon isotope ratio will record daily to weekly changes in photosynthetic discrimination and can be used to study seasonal variation in ecosystem metabolism. M.H. Conte and J.C. Weber (unpublished) have shown strong (5–6‰) seasonal variation in the carbon isotope ratio of leaf waxes purified from aerosol samples collected in Bermuda. The Bermuda aerosol samples primarily reflect material produced and released from vegetation on the North American continent, and so represent a continental scale integration of ecosystem discrimination. This novel technique shows great promise for future analyses of ecosystem metabolism at a range of temporal and spatial scales. The interpretation of the data is based on physiological principles, yet the implications of these results are at the landscape and continental scales.

Precipitation dynamics and the functioning of an arid-land ecosystem

In response to global changes occurring today, species composition and the patterns of the cycling of carbon and other nutrients may be altered in the future. Here there are strong linkages between ecophysiology and ecosystem ecology. Arid-land ecosystems respond strongly to the patterns in which resources are supplied, most importantly the variability and timing of rainfall events (Noy-Meir 1973; Ehleringer et al. 1998). This dependency implies a strong relationship between physiological status and ecosystem productivity. In fact, primary productivity at the ecosystem scale is a strong linear function of cumulative precipitation (Le Houérou 1984; Noy-Meir 1985; Gutierrez & Whitford 1987; Gutierrez et al. 1988; Sala et al. 1988; Ludwig et al. 1989; Ehleringer et al. 1998), although the efficiency of production tends to be lower for summer-rain events than for winter-growth periods. Relevant to this, Reynolds et al. (1999) showed that interannual variation in summer precipitation in a desert ecosystem of western North America had less impact on the productivity of some desert perennials than changes in the amounts of winter precipitation. However, other woody and herbaceous species appear more sensitive to shifts in summer precipitation, with the northern distributions of many perennial species tied to the limits of summer monsoonal moisture inputs (Shreve & Wiggins 1964; Ehleringer & Phillips 1996). Arid-land ecosystems of south-western North American experience high year-to-year variability in precipitation, with El Niño and La Niña events representing two extremes of a moisture-input scale. These extreme-year types can have significant and persistent effects. For example, Brown et al. (1997) have attributed the recent expansion of woody perennials in the central Sonoran Desert to a series of unusually wet winters.

Throughout many North American deserts, precipitation distribution is biseasonal with the fraction of summer/winter precipitation following latitudinal gradients (Fig. 6.8). Winter precipitation falls at a time when the activity of many perennials is minimal or restricted by cold temperatures. Thus, wintertime moisture tends to percolate to deeper soil layers, with moisture from summer thunderstorms, in contrast, penetrating only the upper soil layers (Fig. 6.9). In effect, this
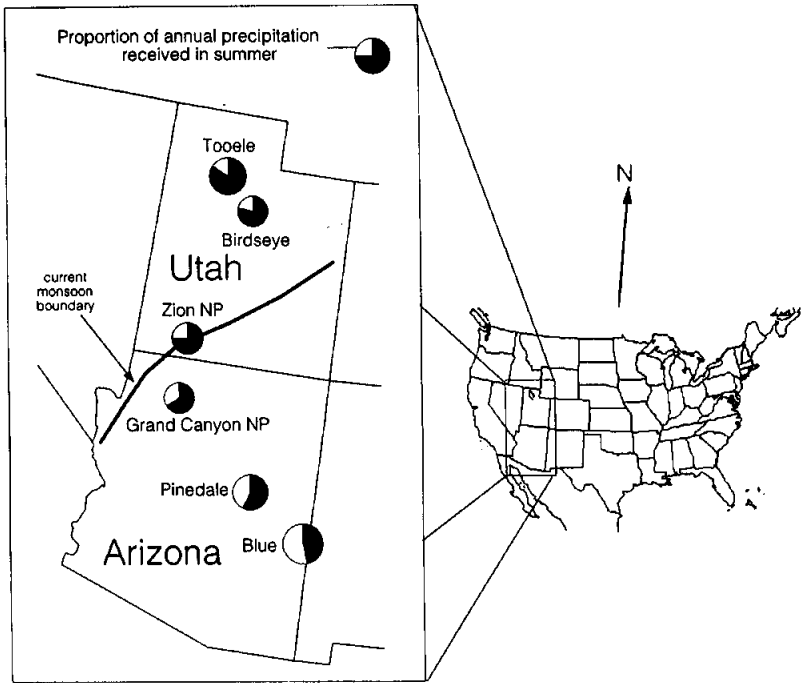
Figure 6.8 Changes in the fraction of total annual precipitation that falls in the summer along a geographical gradient in western North America. All sites average approximately 400 mm annual precipitation and are occupied by a *Juniperus–Pinus–Quercus* woodland. NP, National Park. (Modified with permission from Williams & Ehleringer 2000.)
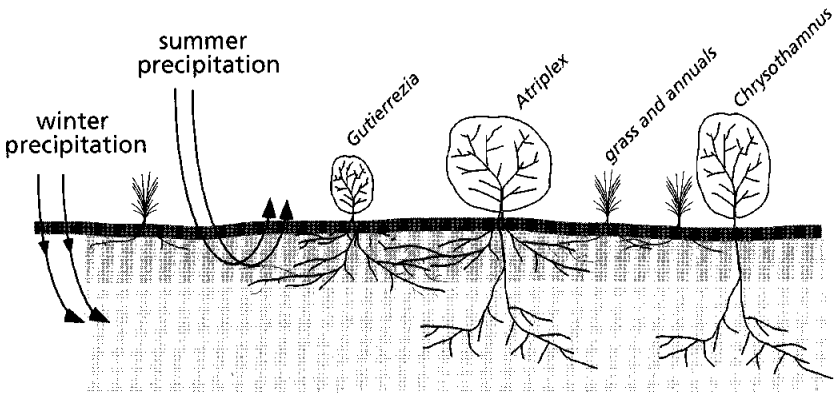

Figure 6.9 In arid-land ecosystems of western North America, moisture from winter-precipitation events tends to percolate into deeper soil layers, whereas moisture from summer-precipitation events tends to penetrate only into the upper soil layers. The bimodal precipitation patterns tends to create two distinct soil layers, each charged primarily by different precipitation regimes.

phenomenon creates a two-layer moisture distribution and forms the basis for distinguishing water relations responses among different species within the vegetation (Ehleringer *et al.* 1999). Some plant species are able to access soil moisture from both surface and deep soil layers (Ehleringer *et al.* 1991). Yet Shreve and Wiggins (1964) noted that in warmer arid-land sites, this bimodal precipitation pattern was associated with distinct and non-overlapping annual and herbaceous floras. At a larger scale, the northern distributions of many arid-land woody taxa are correlated with these summer precipitation limits. For example, the distribution of the turbinella live oak (*Quercus turbinella*) stops abruptly at the monsoon boundary, with this species occurring only in those habitats with summer rain. In contrast, the distribution of *Quercus gambelii* spans the monsoon boundary. Isotopic studies using naturally occurring differences in the abundances of deuterium or ^{18}O in winter- vs. summer-derived precipitation reveal a significant use of surface moisture by *Q. turbinella*, whereas *Q. gambelii* appears not to derive significant proportions of its water from moisture in upper soil layers (Phillips & Ehleringer 1995; Ehleringer & Phillips 1996). Similar northern distribution limits and summer-moisture dependencies appear to contribute to the sharp distribution boundaries of the alligator juniper *Juniperus deppeana* and pinyon pine *Pinus edulis* (Williams & Ehleringer 2000), whereas distributions of the related taxa *J. osteosperma* and *P. monophylla* appear not to be limited by summer-precipitation boundaries.

Because of the constraints water has on the gas-exchange activities of arid-land plants, changes in water availability may play a much more prominent role in the functioning of arid-land ecosystems in the near future than other global changes, such as increasing atmospheric CO_2 or increased dry nitrogen deposition (Ehleringer *et al.* 1999). Elevated CO_2 is expected to have an indirect effect and increase water-use efficiency (Field *et al.* 1997), but extensive evaluations of this hypothesis are not yet available. Ehleringer *et al.* (1999) showed that it was only during strong El Niño years that summer moisture inputs significantly impacted arid regions north of the normal monsoon boundary. Climate × change scenarios predict both warming and shifts in the monsoon boundary. Williams and Ehleringer (2000) observed that the responsiveness of trees to summer moisture input appeared related to the average monsoonal precipitation input in a threshold-type pattern (Fig. 6.10). In more northerly sites, trees did not utilize summer-derived moisture in the upper soil layer, whereas in southerly sites, where summer moisture inputs were greater, plants tend to utilize summer rains. In part, this difference between northern and southern populations may be due to differences in the intensity of individual rain events, but it is also likely that populations adjust their rooting habit to make better use of an increasingly reliable water source in the shallow soil. Herbaceous perennials should be even better adapted to exploit near-surface soil resources and should, in general, have a competitive advantage over most of the woody perennials on the wet end of the monsoonal gradient.
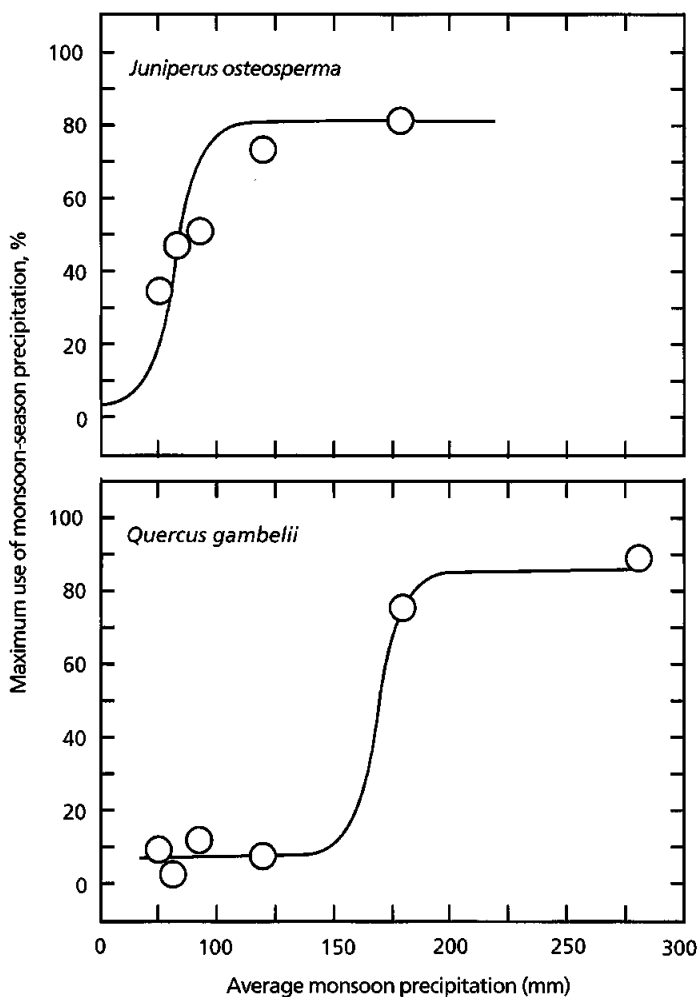
Figure 6.10 The maximum use of moisture derived by summer precipitation events by juniper and oak in arid woodland along the geographical gradient shown in Fig. 6.8. (Modified with permission from Williams & Ehleringer 2000.)

Most precipitation events in the arid lands are typically less than 10 mm (Ehleringer 1994), although during El Niño years the precipitation event size is larger (Cayan & Webb 1992). One adaptation to arid-land conditions is often thought to be the capacity to utilize small precipitation events before the water is lost through surface evaporation (Sala & Lauenroth 1982). Yet isotopic water-source observations indicate niche differentiation with respect to soil moisture use in arid-land and semiarid woodland ecosystems (Ehleringer *et al.* 1991; Flanagan *et al.* 1992; Donovan & Ehleringer 1994; Phillips & Ehleringer 1995). Not

all species respond equally to summer moisture inputs, suggesting that some vegetation elements will be more sensitive to shifts in the ratio of winter- vs. summer-precipitation inputs. When large precipitation events (≥ 25 mm) which occur on average only once a summer were applied to trees in the arid woodlands or to shrubs in the desert regions of the Intermountain West, there was often a limited response by many of these species to utilize summer rain (Lin *et al.* 1996; Williams & Ehleringer 2000). While annuals and grass species located within the current monsoon boundary tend to fully respond to summer-rain events, woody species respond in a much more limited fashion. Given the strong general relationships between precipitation input and productivity, it is possible that there are ecotypic differences among woody plants in their relative capacities of roots to utilize surface moisture. Shifts in the amount of summer-rain input, whether through climate cycles or through global climate shifts, are likely to influence the productivities of different life form elements in arid-land ecosystems. The sensitivity of vegetation structure in these ecosystems is likely to be a function of how rapidly the changes occur in climate relative to the genetic changes.

We are beginning to understand trade-offs associated with pulse utilization and pulse frequency (Schwinning & Ehleringer 2001). As an extreme example, allocation of a large fraction of root biomass to shallow layers increases the capacity to take up water during a pulse, yet also lowers the rate of water uptake between pulses, when moisture is available only in deeper soil layers. Similarly, a high leaf-to-stem ratio enables rapid water uptake during a pulse, but increases the risk of hydraulic failure between pulses (Sperry *et al.* 1998; Sperry 2000). Conversely, a low leaf-to-stem ratio reduces potential transpiration but enables plants to maintain a more moderate water status throughout the drought period. The key to avoidance of low water potentials that may induce hydraulic failure is to reduce transpirational surface area. The costs and benefits of specific allocation strategies vary with the intensity and the duration of pulses, with pulse frequency and with the availability of alternative water sources, such as water stored in deeper soil layers left over from winter precipitation. While our understanding of these physiological trade-offs is incomplete, it is clear that physiological properties and morphological traits do shape the nature of plant responses to moisture input at the whole-plant and ecosystem scales. Consequently, it may be possible to predict the directions of vegetation shifts within arid-land ecosystems if we can better understand how drought cycles and monsoon patterns will shift in an elevated-CO_2 world.

Summary

Physiological ecology has a rich tradition investigating mechanisms of adaptation between organisms and their environment. Increasingly, our understanding of plant physiological ecology has proved valuable for addressing larger-scale questions related to ecosystem dynamics and biosphere–atmosphere fluxes. Nowhere is

this linkage more apparent than in global change studies, where the focus is on determining how ecosystems are responding to atmospheric, hydrologic and land-use changes. The examples discussed in this chapter demonstrate the natural melding of physiological ecology and ecosystem ecology: a *palaeoecological example*—C_3/C_4 photosynthesis in response to atmospheric CO_2 and its impacts on productivity and animal diversity; a *current-ecological* example—stable isotope ratios in CO_2 fluxes between the biosphere and the atmosphere that allow determination of carbon sources and sinks in different ecosystems and under land-use change activities; and a *future-climate change* example—water-resource partitioning, competition and ecosystem dynamics in arid ecosystems in response to monsoon-boundary shifts.

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