Ecosystems (1998) 1: 416–426

ECOSYSTEMS

Ecology of Soil Erosion in Ecosystems

David Pimentel* and Nadia Kounang

College of Agriculture and Life Sciences, Cornell University, 5126 Comstock Hall, Ithaca, New York 14853-0901, USA

ABSTRACT

Each year, about 75 billion tons of soil are eroded from the world's terrestrial ecosystems. Most agricultural land in the world is losing soil at rates ranging from 13 tons/ha/year to 40 tons/ha/year. Because soil is formed very slowly, this means that soil is being lost 13–40 times faster than the rate of renewal and sustainability. Rain and wind energy are the two prime causes of erosion from tilled or bare land. Erosion occurs when the soil lacks protective vegetative cover. Soil erosion reduces the productivity of the land by loss of water, soil organic matter, nutrients, biota, and depth of soil. The greatest threat to providing food for a rapidly growing human population is soil erosion. Abandoned, eroded agricultural land is replaced by clearing forested ecosystems.

Key words: soil; erosion; food; agriculture; nutrients; water.

INTRODUCTION

Soil erosion from land areas is widespread and adversely affects all natural and human-managed ecosystems, including agriculture and forestry. For that reason, soil erosion ranks as one of the most serious environmental problems in the world. Its effects are pervasive, and its damages are long lasting (Pimentel and others 1995a).

Although soil erosion has occurred throughout history, it has intensified as expanding human populations, coupled with their diverse activities, intrude farther into natural ecosystems. Erosion degrades soil quality in natural, agricultural, and forest ecosystems, thereby reducing the productivity of the land. As a result, the diversity of plants, animals, and microbes is diminished. Ultimately, the stability of entire ecosystems is threatened (Pimentel and others 1995a). To offset the damages that erosion inflicts on crops, large quantities of fertilizers and pesticides, plus irrigation, are intensively used. Not only are these inputs fossil-energy dependent, but they also harm human health and pollute the environment (Pimentel and others 1995a).

When agricultural land is eroded and can no longer be made productive, it is abandoned. To compensate for the loss, forests are cleared to provide needed agricultural land (Myers 1989). Indeed, erosion is the major cause of the deforestation now taking place throughout the world.

This article reviews the global dimensions of soil erosion and the impact erosion has on both natural and managed ecosystems.

MEASURING SOIL EROSION

Although soil erosion has been taking place slowly in natural ecosystems throughout geologic time, its cumulative impact over billions of years is significant. Worldwide, erosion rates range from a low of 0.001–2 tons/hectare/year (t/ha/yr) on relatively flat land with grass and/or forest cover to rates ranging from 1 to 5 t/ha/yr on mountainous regions with normal vegetative cover. Even low rates of erosion sustained over billions of years result in the displacement of soil. Often eroded soil accumulates in valleys, forming vast alluvial plains. Over a period of 100 years at an erosion rate of 2 t/ha/yr on 10 ha, erosion deposits soil equivalent to about 1 ha of land with a soil depth of 15 cm. The large deltas of the

---

Received 17 February 1998; accepted 26 May 1998.

*Corresponding author; e-mail: dp18@cornell.edu

world, such as the Nile and the Mississippi, are the result of many centuries of erosion.

On sloping agricultural land under tropical rainfall, as much as 400 t/ha/yr of soil is lost (Pimentel unpublished report, 1990). Under arid conditions with relatively strong winds, as much as 5600 t/ha/yr of soil has been reported lost (Gupta and Raina 1996).

The large amounts of soil that are eroded from the land end up in streams, lakes, and other ecosystems. The US Department of Agriculture (USDA 1989) reports that 60% of the water-eroded soil ends up in streams. Further evidence that large amounts of water-eroded soil end up in streams and rivers is the fact that approximately 2 billion tons/year of soil are transported down the Yellow River in China into the gulf (Follett and Stewart 1985; Lal and Stewart 1990; McLaughlin 1993; Zhang and others 1997).

According to some investigators, approximately 75 billion tons of fertile soil are lost annually from the world's agricultural systems (Myers 1993), whereas other investigators have estimated that only 24 billion tons of soil are lost each year (Crosson 1997). In fact, the 75 billion tons is a conservative value. Soil scientists Lal and Stuart (1990) and Wen (1997) report that 6.6 billion tons of soil per year are lost in India and 5.5 billion tons are lost annually in China. Based on the fact that these two countries occupy about 13% of the world's total land area, the estimated 75 billion tons of soil lost per year worldwide is entirely logical. The amount of soil lost in the United States is more than 4 billion tons per year. In addition, serious soil erosion takes place in other regions of the world (Pimentel 1993; Oldeman 1997).

CAUSES OF EROSION

Erosion occurs when soil is exposed to water or wind energy. Raindrops hit exposed soil with great energy and launch soil particles along with the water into the air. Raindrop splash and resulting sheet erosion remove a thin film of soil from the land surface. Sheet erosion is the dominant form of erosion (Allison 1973; Foster and others 1985). The impacts of both are intensified on sloping land, where more than half of the soil contained in the splashes is carried downhill to valleys and waterways (Pimentel and others 1995a).

Wind energy dislodges soil particles and carries them off the land. Airborne soil particles are often transported thousands of miles. For instance, soil particles eroded from African ecosystems have been identified as far west as Brazil and Florida (Simons 1992), whereas Chinese soil eroded during spring plowing has been found deposited in Hawaii (Parrington and others 1983).

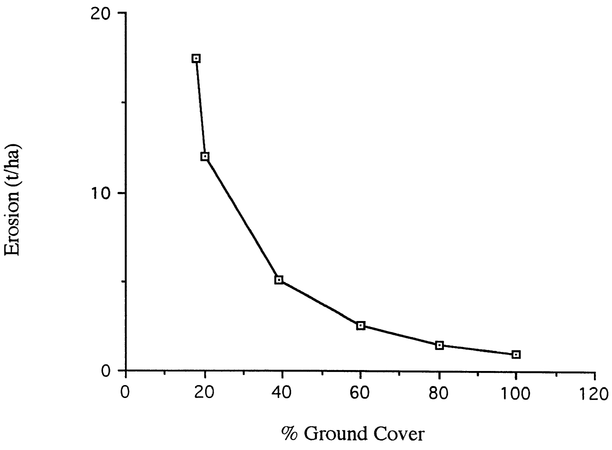

Figure 1. Soil erosion rates related to percentage of ground cover in Utah and Montana. After Trimbel and Mendel (1995).

Land areas covered by plant biomass, living or dead, are protected and experience reduced soil erosion because raindrop and wind energy is dissipated by the biomass layer. In Missouri, for example, barren land lost soil 123 times faster than did land covered with sod, which lost soil at less than 0.1 t/ha/yr (US Forest Service 1936). In Utah and Montana, as the amount of ground cover decreased from 100% to less than 1%, erosion rates increased approximately 200 times (Trimble and Mendel 1995) (Figure 1).

Loss of vegetative cover is especially widespread in developing countries because population densities are high, agricultural practices frequently are inadequate, and cooking and heating often depend on the use of crop residues for fuel. For example, about 60% of crop residues in China and 90% in Bangladesh are stripped from the land and burned for fuel (Wen 1993). In areas where fuelwood and other biomass are scarce, even the roots of grasses and shrubs are collected and burned (McLaughlin 1991). Such practices leave the soil barren and fully exposed to rain and wind energy.

Erosion rates on sloping lands are exceedingly high. Erosion rates are high especially on marginal and steep lands that are being converted from forests to agricultural use to replace the already eroded, unproductive cropland (Lal and Stewart 1990). In Nigeria, for instance, cassava fields on steep slopes (approximately 12% slope) lost 221 t/ha/yr, compared with a loss of 3 t/ha/yr on relatively flat land (less than 1% slope) (Aina and others 1977). Similarly, in the Philippines, where more than 58% of the land has a slope of greater than 11%, and in Jamaica, where 52% of the land has a slope greater than 20%, soil erosion rates are as high as 400 t/ha/yr (Lal and Stewart 1990).

In forested areas, a minimum of 60% forest cover of the landscape is necessary to prevent soil erosion (Singh and Kaur 1989). The significance of this problem is illustrated in the Himalayan regions of India where the lower mountain areas are heavily forested. As the human population has increased there, extensive deforestation has followed. Now only 35% of that region is covered with forests and frequent landslides and soil erosion are common problems. Hawley and Dymond (1988) reported that 100% tree cover reduced storm damage and landslides at least 70%.

The structure of the soil itself influences the ease with which it can be eroded. Soils with medium to fine texture, low organic matter content, and weak structural development are most easily eroded. Typically, these soils have low infiltration rates and, therefore, are subject to high rates of water runoff with the eroded soil being carried away in the water flow (Foster and others 1985).

Although world agricultural production accounts for about three-quarters of the soil erosion worldwide, erosion also occurs in other human-modified ecosystems (El-Swaify and others 1985; Lal and Stewart 1990). The construction of roadways, parking lots, and buildings are examples of this problem. Although the rate of erosion from construction sites may range from 20 to 500 t/ha/yr, erosion associated with construction is relatively brief, generally lasting only while the construction disturbs the land surface. Once the disturbed land surface is seeded to grass or vegetation regrows naturally, erosion decreases (International Erosion Control Association 1991).

Natural areas also suffer erosion; this is especially evident along stream banks. There erosion occurs naturally from the powerful action of moving water. On steep slopes (30% or more), a stream cut through adjacent land can cause significant loss of soil (Alonso and Combs 1989). Even on relatively flat land with a 2% slope, stream banks are eroded easily, especially during heavy rains and flooding. The presence of cattle in and around streams further increases stream-bank erosion. For example, in Wisconsin, a stream area inhabited by cattle lost about 60 tons of soil along each kilometer of stream length per year (Trimble 1994; Trimble and Mendel 1995).

As expected, erosion accompanies landslides and earthquakes (Bruijnzeel 1990). Overall, the erosion impact from earthquakes is comparatively minimal because these events are relatively rare worldwide. In contrast, for landslides—which are more frequent than earthquakes—the damage is more widespread. Landslides are usually associated with diverse human activities, such as the construction of roads and buildings and the removal of forests.

SOIL LOSS IN AGRICULTURAL LANDS

Cropland

Nearly one-half of the earth's land surface is devoted to agriculture; of this, about one-third is planted to crops and two-thirds to pasture land (USDA 1993). Of the two, cropland is more highly susceptible to erosion because it is tilled repeatedly. This practice exposes the soil to wind and water erosion. In addition, cropland often is left bare between plantings for several months of the year. Erosion on agricultural land is intense and estimated to be 75 times greater than that occurring in natural forest areas (Myers 1993).

On croplands, it is common to find that up to 100–200 t/ha/yr of soil have been eroded either by rainfall or wind or by a combination (Maass and Garcia-Oliva 1990). In extreme circumstances, erosion may exceed 450 t/ha/yr (Hurni 1985; Lal and Stewart 1990; Troeh and others 1991; Huang 1996).

Currently, about 80% of the world's agricultural land suffers moderate to severe erosion, while only 10% experiences relatively slight erosion (Pimentel 1993; Speth 1994; Lal 1994). Worldwide, erosion on cropland averages about 30 t/ha/yr and ranges from 0.5 to 400 t/ha/yr (Pimentel and others 1995a). As a result of erosion, during the last 40 years, about 30% of the world's arable land has become unproductive and, therefore, has been abandoned for agricultural use [World Resources Institute (WRI) 1994]. The nearly 1.5 billion ha of arable land that are now under cultivation for crop production are about equal in area to the amount of arable land (2 billion ha) that has been abandoned by humans since farming began (Lal 1990, 1994). The abandoned land, once biologically and economically productive, now produces little biomass and has lost most of its initial biodiversity of plants and animals (Pimentel and others 1992; Heywood 1995).

The lowest erosion rates on cropland average about 13 t/ha/yr and occur in the United States and Europe (Barrow 1991; USDA 1994). However, these relatively low rates of erosion greatly exceed the average rate of natural soil formation, which ranges from 0.5 to 1 t/ha/yr (Troeh and Thompson 1993; Lal 1994; Pimentel and others 1995a). More than 90% of US cropland now is losing soil faster than the sustainable, replacement rate (Hudson 1982; Lal 1984).

Even so, in the United States, erosion is severe in some of the most productive agricultural ecosystems. For instance, one-half of the fertile topsoil of Iowa has been lost during the last 150 years of farming because of erosion (Risser 1981; Klee 1991). Unfortunately, high rates of erosion (about 30 t/ha/yr) continue there because of the rolling hills and type of agriculture practiced (USDA 1989). Similarly, 40% of the rich soil of the Palouse region in the northwestern United States has been lost during the past 100 years of cultivation. Intensive agriculture is employed in both of these regions and monocultural plantings are common. Also, in many areas, fields are left unplanted during the late fall and winter months, exposing the soil to erosion.

Worldwide, soil erosion rates are highest in agroecosystems located in Asia, Africa, and South America, averaging 30–40 t/ha/yr. In developing countries, soil erosion is particularly severe on small farms because they often occupy marginal lands where the soil quality is poor and the topography steep and hilly. In addition, the poor farmers raise row crops such as corn, which are highly susceptible to erosion (Southgate and Whitaker 1992). For example, in the Sierra region of Ecuador, 60% of the cropland was recently abandoned because erosion and inappropriate agricultural practices that left the land exposed to water and wind erosion caused severe soil degradation (Southgate and Whitaker 1992). Similar problems are evident in the Amazonian region of South America, especially where large forested areas are being cleared to provide more land for crops and livestock.

Pasture Land

In contrast to the average soil loss of 13 t/ha/yr from US cropland, pastures lose about 6 t/ha/yr (USDA 1994). However, erosion rates intensify whenever overgrazing occurs. This now is occurring on more than half of the world's pasture land (WRI 1994). In many developing countries, heavy grazing by sheep and goats has removed most of the vegetative cover, exposing the soil to erosion. Even in the United States, about 54% of the pasture lands, including those on federal lands, is now overgrazed and has become subject to high erosion rates (Hood and Morgan 1972; Byington 1986).

Forest Land

In stable forest ecosystems, where soil is protected by vegetation, erosion rates are relatively low, ranging from only 0.004 to 0.05 t/ha/yr (Bennett 1939; Roose 1988; Lal 1994). Tree leaves and branches intercept and diminish rain and wind energy, while the leaves and branches cover the soil under the trees to protect the soil further. However, this changes dramatically when forests are cleared for crop production or pasture. For example, in Ecuador, the Ministry of Agriculture and Livestock reported that 84% of the soils in the hilly, forested northeastern part of the country should never have been cleared for pastures because of the high erodibility of the soils, their limited fertility, and overall poor soil type (Southgate and Whitaker 1992).

EFFECTS OF EROSION ON PRODUCTIVITY

Erosion reduces the overall productivity of terrestrial ecosystems in several ways. First, in order of importance, erosion increases water runoff, thereby decreasing water infiltration and the water-storage capacity of the soil (Troeh and others 1991; Pimentel and others 1995a). Also, organic matter and essential plant nutrients are lost in the erosion process and soil depth is reduced. These changes reduce biodiversity in the soil (Troeh and others 1991; Pimentel and others 1995a). Because these factors interact with one another, it is almost impossible to separate the specific impacts of one factor from another. For example, the loss of soil organic matter increases water runoff, which reduces water-storage capacity. This diminishes nutrient levels in the soil and also reduces the natural biota biomass and the biodiversity of the entire ecosystem.

Overall, the cumulative effects of erosion directly diminish plant productivity. For example, erosion reduced corn productivity by 12%–21% in Kentucky, 0–24% in Illinois and Indiana, 25%–65% in the southern Piedmont of Georgia, and 21% in Michigan (Frye and others 1982; Olson and Nizeyimana 1988; Mokma and Sietz 1992). In the Philippines over the past 15 years, erosion caused declines in corn production by as much as 80% (Dregne 1992). Such major reductions in food-crop yields are particularly serious at a time in history when the growing human population continues to require increased quantities of food and more than 2 billion people in the world are malnourished (World Health Organization 1995; Pimentel and others 1997a).

Water

Water is a prime limiting factor for productivity in all terrestrial ecosystems because all vegetation requires enormous quantities of water for its growth and for the production of fruit (NSESPRPC 1981; Follett and Stewart 1985; Falkenmark 1989). For example, a hectare of corn or wheat will transpire more than 4 million L of water each growing season (Leyton 1983) and lose an additional 2 million L of water by evaporation from the soil (Waldren 1983; Donahue and others 1990).

Table 1. Water and Soil Loss Related to Various Conservation Technologies That Reduce Water Runoff and Soil Erosion

Treatments	Location	% Reduced Runoff	% Reduced Soil Erosion	References
4 t/ha mulch/No mulch	India	58	72	Kukal and others 1993
Contour cultivation/No contour cultivation	India	—	54	Kukal and others 1993
Wheat–oat–barley–hay–hay/Wheat–fallow	Canada	—	89	Monreal and others 1995
No grazing pasture/Very heavy grazing	Ethiopia	330	330	Mwendera and Saleem 1997
No till + cover crop/Conventional till	Brazil	400	130	Busscher and others 1996
Cover crop–corn/Conventional	USA	15	110	Martin and Cassel 1992
Cover crop–silage corn/Conventional silage corn	USA	—	244	Reeves 1994
No till cotton/Conventional cotton	USA	140	900	Langdale and others 1994
Alley cropping corn[a]/Conventional	Philippines	75	99	Comia and others 1994

[a] *Alley cropping corn with leguminous tree on 17% slope.*

When erosion occurs, the amount of water runoff significantly increases, and with less water entering the soil, less is available to support the growing vegetation (Table 1). Moderately eroded soils absorb 10–300 mm less water per hectare per year from rainfall than uneroded soils. This represents a decrease of 7%–44% in the amount of water available to the vegetation (Wendt and Burwell 1985; Wendt and others 1986; Murphee and McGregor 1991). A diminished absorption rate of 20%–30% of rainfall represents significant water shortages for all vegetation, including crops (Elwell 1985). Lal (1976) reported that erosion has reduced water infiltration in some tropical soils by up to 93%.

In general, when water availability for the agricultural ecosystem is reduced from 20% to 40% in the soil, plant productivity is reduced from 10% to 25%, depending also on total rainfall, soil type, slope, and other factors. Such major reductions in plant biomass also reduce the soil biota and the overall biodiversity within the ecosystem (Heywood 1995).

Nutrients

When soil is eroded, basic plant nutrients such as nitrogen, phosphorus, potassium, and calcium also are lost. Eroded soil typically contains about three times more nutrients than the soil left behind on the eroded land (Lal 1980; Young 1989). A ton of fertile topsoil typically contains 1–6 kg of nitrogen, 1–3 kg of phosphorus, and 2–30 kg of potassium, whereas soil on eroded land frequently has nitrogen levels of only 0.1–0.5 kg/t (Alexander 1977; Troeh and others 1991). Plant productivity is significantly reduced when soil nutrient levels are this low.

If the soil is relatively deep, such as 300 mm, and 10–20 tons of soil is lost per hectare, the nutrients lost in the erosded soil can be replaced with the application of commercial fertilizers and/or livestock manure (Pimentel and others 1995a). However, the loss of nutrients can be expensive for the farmer and nation. For instance, Troeh and colleagues (1991) estimate that the United States loses $20 billion annually in nutrients because of soil erosion.

Soil Organic Matter

Both wind and water erosion selectively remove the fine organic particles in the soil, leaving behind large particles and stones. Fertile soils frequently contain about 100 tons of organic matter per hectare (or 4% of the total soil weight) (Follett and others 1987; Young 1990). Because most of the organic matter is close to the soil surface in the form of decaying leaves and stems, erosion of the topsoil significantly decreases soil organic matter. Several studies have demonstrated that the soil removed by either wind or water erosion is 1.3–5.0 times richer in organic matter than the soil left behind (Barrows and Kilmer 1963; Allison 1973).

Soil organic matter facilitates the formation of soil aggregates and increases soil porosity. In this way, it improves soil structure, which in turn facilitates water infiltration and ultimately the overall productivity of the soil (Chaney and Swift 1984; Langdale and others 1992). In addition, organic matter aids cation exchange, enhances root growth, and stimulates the increase of important soil biota (Allison 1973). About 95% of the soil nitrogen and 25%–50% of the phosphorus are contained in the organic matter (Allison 1973).

Once the organic matter layer is depleted, the productivity of the ecosystem, as measured by crop-plant yields, declines both because of the degraded soil structure and the depletion of nutrients contained in the organic matter. For example, the reduction of soil organic matter from 1.4% to 0.9% lowered the yield potential for grain by 50% (Libert 1995).

When nutrient resources are depleted by erosion, plant growth is stunted and overall productivity declines (Pimentel and others 1995a). Soils that suffer severe erosion may produce 15%–30% lower crop yields than uneroded soils (Olson and Nizeyimana 1988; Schertz and others 1989; Follett and Stewart 1985; Langdale and others 1992). In addition to low yields, the total biomass of the biota and overall biodiversity of these ecosystems are substantially reduced (Heywood 1995).

Soil Depth

As plants grow, they need soils of adequate depth in which to extend their roots. Various soil biota also require a specific soil depth (Pimentel and others 1995a). Thus, when soil depth is substantially reduced by erosion from 30 cm to less than 1 cm, plant root space is minimal and, concurrently, valuable soil biota nearly disappear.

BIOMASS AND BIODIVERSITY

The biological diversity existing in any natural ecosystem is directly related to the amount of living and nonliving organic matter present in the ecosystem (Wright 1983, 1990). By diminishing soil organic matter and overall soil quality, erosion reduces biomass productivity in ecosystems. Ultimately, this has a profound effect on the diversity of plants, animals, microbes, and other forms of life present in the ecosystem.

Numerous positive correlations between biomass and species abundance have been established (Elton 1927; Odum 1978; Sugden and Rands 1990; M. Giampietro personal communication, 1997, Insituto Nazionale della Nutrizione, Rome, Italy). Vegetation is the main component of ecosystem biomass and provides the resources needed by animals and microbes. This relationship is summarized in Table 2.

Table 2. Biomass of Various Organisms per Hectare in a New York State Pasture[a]

Organism	Biomass (kg fresh weight)
Plants	20,000
Fungi	4000
Bacteria	3000
Annelids	1320
Arthropods	1000
Protozoa	380
Algae	200
Nematodes	120
Mammals	1.2
Birds	0.3

[a] *After Pimentel and colleagues (1992).*

Plants, animals, and microbes are a vital component of the soil, as mentioned, and constitute a large measure of the soil biomass. One square meter of soil may support about 200,000 arthropods and enchytraeids and billions of microbes (Wood 1989; Lee and Foster 1991). A hectare of productive soil may have a microbial and invertabrate biomass weighing nearly 10,000 kg/ha (Table 2). Anderson (1978) reported that a favorable temperate-forest soil with abundant organic matter supports up to 1000 species of animals per square meter, including arthropods, nematodes, and protozoa. Soil bacteria and fungi add another 4000–5000 species to the biodiversity in moist, organic forest soils (Heywood 1995).

Erosion rates that are 10–20 times higher than the sustainability rate (less than 0.5 to 1 t/ha/yr) decrease the diversity and abundance of soil organisms (Atlavinyte 1964, 1965), whereas agricultural practices that maintain adequate soil organic matter content favor the proliferation of soil biota (Reid 1985). For example, the simple practice of adding straw mulch on the soil surface increased soil organic matter and the number of living organisms as much as threefold (Teotia and others 1950). Similarly, the application of organic matter or manure enhanced earthworm and microorganism biomass as much as fivefold (Ricou 1979). In the former USSR, species diversity of macrofauna (mostly arthropods) increased 16% when organic manure was added to experimental wheat plots (Bohac and Pokarzhevsky 1987). Macrofauna (mostly arthropods) species diversity more than doubled when organic manure was added to grassland plots in Japan (Kitazawa and Kitazawa 1980).

Arthropod biomass increased significantly when soil organic matter was added to the agriculture. For example, the biomass of arthropods increased from twofold to sevenfold per hectare when organic matter in manure was added to wheat and mangold crops in the United Kingdom (Morris 1922; Raw 1967). Also, when organic manure was added to agricultural land in Hungary, soil microbial biomass increased tenfold (Olah-Zsupos and Helmeczi 1987). Because increased biomass generally is correlated with increased biodiversity, it is logical to assume that the increase in biomass of arthropods and microbes represents an increase in biodiversity (Pimentel and others 1992).

The relationship between biomass and biodiversity was further illustrated in field experiments with collards in which arthropod species diversity rose fourfold in the experimental plots that had the highest collard biomass compared with control collard plots (Pimentel and Warneke 1989). Ward and Lakhani (1977) reported that the number of arthropod species associated with an ecosystem containing juniper bushes increased fourfold when the number of bushes was increased 100-fold. Elsewhere, a strong correlation between plant biomass productivity and bird species diversity was reported when a 100-fold increase in plant biomass productivity yielded a tenfold increase in bird diversity (Wright 1983, 1990).

Indirect effects of erosion on ecosystems frequently may be nearly as damaging as the direct effects of reducing plant productivity. For example, the stability and biodiversity of grasslands were significantly reduced when plant species reduction occurred (Tilman and Downing 1994). As the number of plant species decreased from 25 species to five or fewer, the grassland became less resistant to drought and the total amount of biomass declined more than fourfold. As a result the grassland was more susceptible to drought conditions and recovery of productivity required more time than in the species-rich state.

The effects of erosion may be responsible for the loss of a keystone species, an absence that may have a cascading effect on a wide array of species within the ecosystem. Species that act as keystone species include plant types that maintain the productivity and integrity of the ecosystem; predators and parasites that control the feeding pressure of some organisms on vital plants; pollinators of various vital plants in the ecosystem; seed dispersers; and the plants and animals that provide a habitat required by other essential species, like biological nitrogen fixers (Heywood 1995; Daily 1996). Hence, the regular activities within an ecosystem may be interrupted or even eliminated. The impacts of this can be particularly severe especially in agroecosystems when, for instance, pollinators are drastically reduced and/or eliminated.

Soil biota perform many beneficial activities that improve soil quality and productivity. For example, soil biota recycle basic nutrients required by plants for their growth (Van Rhee 1965; Pimentel and others 1980, 1997b). In addition, the tunneling and burrowing activities of earthworms and other soil biota enhance productivity by increasing water infiltration into the soil. Earthworms, for instance, may produce up to 220 tunnel openings per square meter (3–5 mm in diameter). These channels enable water to run rapidly into the soil, thereby increasing infiltration rates (Anderson 1988).

Other soil biota contribute to soil formation and productivity by mixing soil components, enhancing aggregate stability, and preventing soil crusting. Earthworms bring between 10 and 500 t/ha/yr of soil from underground to the soil surface (Edwards 1981; Lavelle 1983; Lee 1985), while insects bring a smaller amount to the surface (Hole 1981; Zacharias and Grube 1984; Lockaby and Adams 1985). This churning and mixing of the upper soil redistributes nutrients, aerates the soil, exposes matter to the climate for soil formation, and increases infiltration rates, thus making conditions favorable for increased soil formation and plant productivity. In arid regions, species like the Negev desert snail (*Euchordrus* spp.) also help form soil by consuming lichens and the rocks on which the lichens are growing (Shachak and others 1995). This snail activity helps form about 1000 kg of soil per hectare per year, which is equal to the annual soil formation by windborne deposits.

Controlling erosion not only conserves the quality of soils but enhances vegetative growth and increases total biodiversity.

SEDIMENTS AND WIND-BLOWN SOIL PARTICLES

Beyond its direct effect on agricultural and forest ecosystems, the impact of erosion reaches far into the surrounding environment. Major off-site problems include earth-dam failures, eutrophication of waterways, siltation of harbors and channels, loss of reservoir storage, loss of wildlife habitat, disruption of stream ecology, and flooding of land and communities, plus increased costs for water treatment (Gray and Leiser 1989).

The most costly off-site damages occur when soil particles enter water systems (Lal and Stewart 1990). Of the billions of tons of soil lost from US and world cropland, nearly two-thirds finally are deposited in streams and rivers (USDA 1989; Pimentel 1997). These sediments harm aquatic ecosystems by contaminating the water with soil particles and the fertilizer and pesticide chemicals they contain (Clark 1987). Siltation of reservoirs and dams reduces water storage, increases the maintenance cost of dams, and shortens the lifetime of reservoirs (Pimentel and others 1995a).

Furthermore, heavy sedimentation frequently leads to river and lake flooding (Myers 1993). For example, some of the flooding that occurred in the midwestern United States during the summer of 1993 was caused by increased sediment deposition in the Mississippi and Missouri Rivers and their tributaries. These deposits raised the original depth of the waterways, making them more prone to overflowing and flooding the surrounding area (Allen 1994).

Wind-eroded soil is responsible for off-site damage because soil particles propelled by strong winds act as abrasives and air pollutants. Estimates are that soil particles sandblast US automobiles and buildings and cause about $8 billion in damages each year (Huszar and Piper 1985; Soil Conservation Service 1993; Pimentel and others 1995a). A prime example of the environmental impact of wind erosion occurs in New Mexico, where about two-thirds of the land is used for agriculture, including grazing, and erosion rates on pastures often exceed 6 t/ha/yr and sometimes reach as much as 100 t/ha/yr. Yearly off-site erosion costs in New Mexico, including health and property damage, are estimated as high as $465 million (Huszar and Piper 1985). Assuming similar costs for other states, the off-site damages from wind erosion alone could cost nearly $10 billion each year (Pimentel and others 1995a).

Soil erosion also contributes to the global warming problem by adding carbon dioxide to the atmosphere as enormous amounts of biomass carbon in the soil are oxidized (Phillips and others 1993). As mentioned, a hectare of soil may contain about 100 tons of organic matter or biomass. When the forces of erosion uncover the carbon from this organic matter, it is exposed and oxidizes. The subsequent release of carbon dioxide into the atmosphere contributes to the global warming problem (Phillips and others 1993). In fact, a feedback mechanism may exist wherein increased global warming intensifies rainfall, which, in turn, increases erosion and continues the cycle (Lal 1990).

CONSERVATION TECHNOLOGIES AND RESEARCH

Erosion adversely affects crop productivity by reducing water availability, the water-holding capacity of the soil, nutrient levels, soil organic matter, and soil depth (Pimentel and others 1995a). Estimates are that agricultural land degradation alone is expected to depress world food production between 15% and 30% during the next 25-year period (Buringh 1989), emphasizing the need to implement known soil conservation techniques, including biomass mulches, no till, ridge till, grass strips, shelterbelts, terracing, contour planting, crop rotations, and combinations of these. All of these techniques basically require keeping the land protected from wind and rainfall effects by some form of vegetative cover (Pimentel and others 1995a).

In the United States during the past decade, soil erosion rates on croplands have decreased nearly 25% using various soil conservation technologies (USDA 1989, 1994). Even with this decline, soil is still being lost on croplands at a rate 13-times greater than the sustainability rate (Pimentel and others 1995b). Although soil erosion has declined on croplands, soil erosion rates on pastures and rangelands have not declined during this same period (USDA 1989, 1994).

Soil erosion is known to affect water runoff, soil water-holding capacity, soil organic matter, nutrients, soil depth, and soil biota, and all of these factors influence soil productivity in natural and managed ecosystems. Little is known about the ecology of the interactions of these various soil factors and their interdependency (Lal and Stewart 1990; Pimentel 1993). In addition, more information is needed on the effects of soil erosion on the productivity of natural and managed ecosystems.

CONCLUSION

Soil erosion is a critical environmental problem throughout the world's terrestrial ecosystems. Erosion is a slow insidious process. One millimeter of soil, easily lost in one rainstorm or windstorm, is seemingly so minute that its loss goes unnoticed. Yet this loss of soil over a hectare of cropland amounts to 15 tons. Reforming that amount of soil under natural circumstances requires 20 years.

Erosion inflicts multiple, serious damages in managed ecosystems like crops, pastures, or forests—as well as in natural ecosystems. In particular, erosion reduces the water-holding capacity because of rapid water runoff, and reduces soil organic matter. As a result, nutrients and valuable soil biota are reduced. Separately or together, these factors diminish the productivity of all vegetation and animals in ecosystems. At the same time, species diversity of plants, animals, and microbes is significantly reduced.

Worldwide, soil erosion continues unabated while the human population and its requirements for food, fiber, and other resources expand geometrically. Indeed, achieving future food security for all people depends on conserving soil, water, energy, and biological resources. Conservation of these vital resources must receive high priority to ensure the effective protection of managed and natural ecosystems. If it is ignored, the quality of life for all humans will suffer.

REFERENCES

Aina PO, Lal R, Taylor GS. 1977. Soil and crop management in relation to soil erosion in the rainforest of western Nigeria. In:

soil erosion: prediction and control. Ankeny (IA): Soil Conservation Society of America. p. 75–82.

Alexander M. 1977. Introduction to soil microbiology. 2nd ed. New York: John Wiley and Sons.

Allen W. 1994. The flood of 1993 may rank as the worst weather disaster in U.S. history. St Louis: St Louis Post Dispatch; 01B.

Allison FE. 1973. Soil organic matter and its role in crop production. New York: Elsevier.

Alonso CV, Combs ST. 1989. Streambank erosion due to bed degradation. St Joseph (MI): American Society of Agricultural Engineers.

Anderson JM. 1978. Inter- and intra-habitat relationships between woodland cryptostigmata species diversity and the diversity of soil and litter microhabitats. Oecologia (Berl) 32:341–8.

Anderson JM. 1988. Spatiotemporal effects of invertbrates on soil processes. Biol Fertil Soils 6:216–27.

Atlavinyte O. 1964. Distribution of earthworms (Lumbricidae) and larval insects in the eroded soil under cultivated crops. Pedobiologia 4:245–50.

Atlavinyte O. 1965. The effect of erosion on the population of earthworms (Lumbricidae) in soils under different crops. Pedobiologia 5:178–88.

Barrow CJ. 1991. Land degradation. Cambridge: Cambridge University Press.

Barrows HL, Kilmer VJ. 1963. Plant nutrient losses from soils by water erosion. Adv Agron 15:303–15.

Bennett HH. 1939. Soil conservation. New York: McGraw-Hill.

Bohac J, Pokarzhevsky A. 1987. Effect of manure and NPK on soil macrofauna in chernozem soil. In: Szegi J, editor. Soil biology and conservation of biosphere: proceedings of the ninth international symposium. Budapest: Akademiai Kiado. p 15–9.

Bruijnzeel LA. 1990. Hydrology of moist tropical forests and effects of conversion: a state of knowledge review. Amsterdam: Free University and UNESCO.

Buringh P. 1989. Availability of agricultural land for crop and livestock production. In: Pimentel D, Hall CW, editors. Food and natural resources. San Diego (CA): Academic. p 70–85.

Busscher WJ, Reeves DW, Kochhann RA, Bauer PJ, Mullins GL, Clapham WM, Kemper WD, Galerani PR. 1996. Conservation farming in southern Brazil: using cover crops to decrease erosion and increase infiltration. J Soil Water Conserv 51:188–92.

Byington EK. 1986. Grazing land management and water quality. Harpers Ferry (WV): American Society of Agronomy and Crop Science Society of America.

Chaney K, Swift RS. 1984. The influence of organic matter on aggregate stability in some British soils. J Soil Sci 35:223–30.

Clark EH. 1987. Soil erosion: offsite environmental effects. In: Harlin JM, Bernardi GM, editors. Soil loss: processes, policies, and prospects. New York: Westview. p 59–89.

Comia RA, Paningbatan EP, Hakansson I. 1994. Erosion and crop yield response to soil conditions under allely cropping systems in the Philippines. Soil Tillage Res 31:249–61.

Crosson P. 1997. Will erosion threaten agricultural productivity? Environment 39(8):4–9 and 29–31.

Daily G. 1996. Nature's services: societal dependence on natural ecosystems. Washington (DC): Island.

Donahue RH, Follett RH, Tulloch RN. 1990. Our soils and their management. Danville (IL): Interstate.

Dregne HE. 1992. Erosion and soil productivity in Asia. J Soil Water Conserv 47:8–13.

Edwards CA. 1981. Earthworms, soil fertility and plant growth. In: Workshop on the role of earthworms in the stabilization of organic residues. Lansing (MI): Beach Leaf. p 61–85.

El-Swaify SA, Moldenhauer WC, Lo A. 1985. Soil erosion and conservation. Ankeny (IA): Soil Conservation Society of America.

Elton CS. 1927. Animal ecology. London: Sidgwick and Jackson.

Elwell HA. 1985. An assessment of soil erosion in Zimbabwe. Zimb Sci News 19:27–31.

Falkenmark M. 1989. Water scarcity and food production. In: Pimentel D, Hall CW, editors. Food and natural resources. San Diego (CA): Academic. p 164–91.

Follett RF, Gupta SC, Hunt PG. 1987. Conservation practices: relation to the management of plant nutrients for crop production. In: Soil fertility and organic matter as critical components of production systems. Special Publication 19. Madison (WI): Soil Science Society of America and American Society of Agronomy. p 19–51.

Follett RF, Stewart BA, editors. 1985. Soil erosion and crop productivity. Madison (WI): American Society of Agronomy and Crop Science Society of America.

Foster GR, Young RA, Ronkens MJM, Onstad CA. 1985. Processes of soil erosion by water. In: Follett FR, Stewart BA, editors. Soil erosion and crop productivity. Madison (WI): American Society of Agronomy and Crop Science Society of America. p 137–62.

Frye WW, Ebelhar SA, Murdock LW, Bevins RL. 1982. Soil erosion effects on properties and productivity of two Kentucky soils. Soil Sci Soc Am J 46:1051–5.

Gray DM, Leiser AT. 1989. Biotechnical slope protection and erosion control. Malabar (FL): Kreiger.

Gupta JP, Raina P. 1996. Wind erosion and its control in hot arid areas of Rajasthan. In: Buerkert B, Allison BE, von Oppen M, editors. Wind erosion in West Africa: the problem and its control. Berlin: Margraf. p 209–18.

Hawley JG, Dymond JR. 1988. How much do trees reduce landsliding? J Soil Water Conserv 43:495–8.

Heywood VH. 1995. Global biodiversity assessment. Cambridge: Cambridge University Press.

Hole FD. 1981. Effects of animals on soil. Geoderma 25:75–112.

Hood L, Morgan JK. 1972. Whose home on the range? Sierra Club Bull 57:4–11.

Huang X. 1996. Agroforestry in China to control desertification. Forthcoming.

Hudson NW. 1982. Soil conservation, research and training requirements in developing tropical countries. In: Soil erosion and conservation in the tropics. Special Publication 43. Madison (WI): American Society of Agronomy. p 121–43.

Hurni H. 1985. Ecosystem approach to soil conservation. In: El-Swaify WC editor. Soil erosion and conservation. Ankeny (IA): Soil Conservation Society of America. p 759–71.

Huszar PC, Piper SL. 1985. Off-site costs of wind erosion in New Mexico. In: Off-site costs of soil erosion: the proceedings of a symposium. Washington (DC): Conservation Foundation. p 143–66.

International Erosion Control Association (IECA). 1991. Erosion control: a global perspective—proceedings of conference XXII. Steamboat Springs (CO): IECA.

Kitazawa Y, Kitazawa T. 1980. Influence of application of a fungicide, an insecticide, and compost upon soil biotic community. In: Sindal DL, editor. Soil biology as related to land use practices. Washington (DC): Office of Pesticide and Toxic Substances, Environmental Protection Agency. p 94–9.

Klee GA. 1991. Conservation of natural resources. Englewood Cliffs (NJ): Prentice Hall.

Kukal SS, Khera KL, Hadda MS. 1993. Soil erosion management on arable lands of submontane Punjab India: a review. Arid Soil Res Rehabil 7:369–75.

Lal R. 1976. Soil erosion problems on an alisol in western Nigeria and their control. Lagos (Nigeria): IITA.

Lal R. 1980. Losses of plant nutrients in runoff and eroded soil. In: Rosswall T, editor. Nitrogen cycling in West African ecosystems. Uppsala: Reklan and Katalogtryck. p 31–8.

Lal R. 1984. Productivity assessment of tropical soils and the effects of erosion. In: Rijsberman FR, Wolman MG, editors. Quantification of the effect of erosion on soil productivity in an international context. Delft (The Netherlands): Delft Hydraulics Laboratory. p 70–94.

Lal R. 1990. Soil erosion and land degradation: the global risks. In: Lal R, Stewart BA, editors. Soil degradation. New York: Springer-Verlag. p 129–72.

Lal R. 1994. Water management in various crop production systems related to soil tillage. Soil Tillage Res 30:169–85.

Lal R, Stewart BA. 1990. Soil degradation. New York: Springer-Verlag.

Langdale GW, Alberts EE, Bruce RR, Edwards WM, McGregor KC. 1994. Concepts of residue management: infiltration, runoff, and erosion. In: Hatfield JL, Stewart BA, editors. Crops residue management. Boca Raton (FL): Lewis. p 109–24.

Langdale GW, West LT, Bruce RR, Miller WP, Thomas AW. 1992. Restoration of eroded soil with conservation tillage. Soil Techn 5:81–90.

Lavelle P. 1983. The soil fauna of tropical savannas. II. The earthworms. Ecosyst World 13:485–504.

Lee E, Foster RC. 1991. Soil fauna and soil structure. Aust J Soil Res 29:745–76.

Lee KE. 1985. Earthworms: their ecology and relationships with soils and land use. Orlando (FL): Academic.

Leyton L. 1983. Crop water use: principles and some considerations for agroforestry. In: Huxley PA, editor. Plant research and agroforestry. Nairobi: International Council for Research in Agroforestry. p 379–400.

Libert B. 1995. The environmental heritage of Soviet agriculture. Oxon (UK): CAB International.

Lockaby BG, Adams JC. 1985. Pedoturbation of a forest soil by fire ants. J Soil Sci Soc Am 49:220–3.

Maass JM, Garcia-Oliva F. 1990. La conservacion de suelos en zonas tropicales: el caso de Mexico. Cienc Desarrolio 15(90): 21–36.

Martin CK, Cassel DK. 1992. Soil loss and silage yield for three tillage management systems. J Prod Agric 5:581–6.

McLaughlin L. 1991. Soil conservation planning in the People's Republic of China: an alternative approach [dissertation]. Ithaca (NY): Cornell University.

McLaughlin L. 1993. A case study in Dingxi County, Gansu Province, China. In: Pimentel D, editor. World soil erosion and conservation. Cambridge: Cambridge University Press. p 87–107.

Mokma DL, Sietz MA. 1992. Effects of soil erosion on corn yields on Marlette soils in South-Central Michigan. J Soil Water Conserv 47:325–7.

Monreal CM, Zentner RP, Robertson JA. 1995. The influence of management on soil loss and yield of wheat in Chernozemic and Luvisolic soils. Can J Soil Sci 75:567–74.

Morris HM. 1922. The insect and other invertebrate fauna of arable land at Rothamsted. Ann Appl Biol 9:1441–305.

Murphee CE, McGregor KC. 1991. Runoff and sediment yield from a flatland watershed in soybeans. Trans ASAE 34:407–11.

Mwendera EJ, Saleem MAM. 1997. Hydrologic response to cattle grazing in the Ethiopian highlands. Agric Ecosyst Environ 64:33–41.

Myers N. 1989. Deforestation rates in tropical forests and their climatic implications. London: Friends of the Earth Report.

Myers N. 1993. Gaia: an atlas of planet management. Garden City (NY): Anchor/Doubleday.

NSESPRPC (National Soil Erosion–Soil Production Research Planning Committee). 1981. Soil erosion effects on soil productivity: a research perspective. J Soil Water Conserv 32:82–90.

Odum EP. 1978. Fundamentals of ecology. New York: WB Saunders.

Olah-Zsupos A, Helmeczi B. 1987. The effect of soil conditioners on soil microorganisms. In: Szegi J, editor. Soil biology and conservation of the biosphere, proceedings of the ninth international symposium. Budapest: Akademiai Kiado. p 829–37.

Oldeman LR. 1997. Soil degradation: a threat to food security? Paper presented at the international conference on time ecology: time for soil culture—temporal perspectives on sustainable use of soil, Tutzing, Germany, 6–9 April 1997.

Olson KR, Nizeyimana E. 1988. Effects of soil erosion on corn yields of seven Illinois soils. J Prod Agric 1:13–9.

Parrington JR, Zoller WH, Aras NK. 1983. Asian dust: seasonal transport to the Hawaiian Islands. Science (Washington DC) 246:195–97.

Phillips DL, White D, Johnson B. 1993. Implications of climate change scenarios for soil erosion potential in the USA. Land Degrad Rehabil 7:61–72.

Pimentel D, editor. 1993. World soil erosion and conservation. Cambridge: Cambridge University Press.

Pimentel D. 1997. Soil erosion. Environment 39(10):4–5.

Pimentel D, Garnick E, Berkowitz A, Jacobson S, Napolitano S, Black P, Valdes-Cogliano S, Vinzant B, Hudes E, Littman S. 1980. Environmental quality and natural biota. Bioscience 30:750–5.

Pimentel D, Harvey C, Resosudarmo P, Sinclair K, Kurz D, McNair M, Crist S, Sphpritz L, Fitton L, Saffouri R, Blair R. 1995a. Environmental and economic costs of soil erosion and conservation benefits. Science (Washington DC) 267:1117–23.

Pimentel D, Harvey C, Resosudarmo P, Sinclair K, Kurz D, McNair M, Crist S, Sphpritz L, Fitton L, Saffouri R, Blair R. 1995b. Response to letter by Pierre Crosson about "Environmental and economic costs of soil erosion and conservation benefits" (no. 430). Science (Washington DC) 269:461–5.

Pimentel D, Huang X, Cardova A, Pimentel M. 1997a. Impact of population growth on food supplies and environment. Popul Environ 19:9–14.

Pimentel D, Stachow U, Takacs DA, Brubaker HW, Dumas AR, Meaney JJ, O'Neil J, Onsi DE, Corzilius DB. 1992. Conserving biological diversity in agricultural/forestry systems. Bioscience 42:354–62.

Pimentel D, Warneke A. 1989. Ecological effects of manure, sewage sludge, and other organic wastes on arthropod populations. Agric Zool Rev 3:1–30.

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B. 1997b. Economic and environmental benefits of biodiversity. Bioscience 47:747–57.

Raw F. 1967. Arthropods (except *Acari* and *Collembola*). In: Burges A, Raw F, editors. Soil biology. London: Academic. p 323–62.

Reeves DW. 1994. Cover crops and rotations. In: Hatfield JL, Stewart BW, editors. Crops residue management. Boca Raton (FL): Lewis. p 125–72.

Reid WS. 1985. Regional effects of soil erosion on crop productivity: northeast. In: Follett RF, Stewart BA, editors. Soil erosion and crop productivity. Madison (WI): American Society of Agronomy. p 235–50.

Ricou GAE. 1979. Consumers in meadows and pastures. In: Coupland RT, editor. Grassland ecosystems of the world: analysis of grasslands and their uses. Cambridge: Cambridge University Press. p 147–53.

Risser J. 1981. A renewed threat of soil erosion: it's worse than the Dust Bowl. Smithsonian 11:120–2, 124, and 126–30.

Roose E. 1988. Soil and water conservation lessons from steep-slope farming in French speaking countries of Africa. In: Conservation farming on steep lands. Ankeny (IA): Soil and Water Conservation Society. p 130–1.

Schertz DL, Moldenhauer WC, Livingston SJ, Weesies GA, Hintz EA. 1989. Effect of past soil erosion on crop productivity in Indiana. J Soil Water Conserv 44:604–8.

Shachak M, Jones CG, Brand S. 1995. The role of animals in an arid ecosystem: snails and isopods as controllers of soil formation, erosion and desalinization. In: Blume HP, Berkowicz SM, editors. Arid ecosystems. Cremlingen-Destedt (Germany): Catena. p 37–50.

Simons M. 1992 Oct 29. Winds toss Africa's soil, feeding lands far away. New York Times; Sect A:1 and 16.

Singh TV, Kaur J. 1989. Studies in Himalayan ecology and development strategies. New Dehli: Himalayan.

Soil Conservation Service (SCS). 1993. Wind erosion report (Nov. 1992–May 1993). Washington (DC): SCS, US Department of Agriculture.

Southgate D, Whitaker M. 1992. Promoting resource degradation in Latin America: tropical deforestation, soil erosion, and coastal ecosystem disturbance in Ecuador. Econ Dev Cultural Change 40:787–807.

Speth JG. 1994. Towards an effective and operational international convention on desertification. New York: United Nations, International Convention on Desertification, International Negotiating Committee.

Sugden AM, Rands GF. 1990. The ecology of temperate and cereal fields. Trends Ecol Evol 5:205–6.

Teotia JP, Duky FL, McCalla TM. 1950. Effect of stubble mulch on number and activity of earthworms. Nebr Agric Exp Stn Res Bull.

Tilman D, Downing JA. 1994. Biodiversity and stability in grasslands. Nature 367:363–5.

Trimble SW. 1994. Erosional effects of cattle on streambanks in Tennessee, USA. Earth Surf Process Landforms 19:451–64.

Trimble SW, Mendel AC. 1995. The cow as a geomorphic agent: a critical review. Geomorphology 13:233–53.

Troeh FR, Thompson LM. 1993. Soils and soil fertility. 5th ed. New York: Oxford University Press.

Troeh FR, Hobbs JA, Donahue RL. 1991. Soil and water conservation. Englewood Cliffs (NJ): Prentice Hall.

US Department of Agriculture (USDA). 1989. The second RCA appraisal: soil, water, and related resources on nonfederal land in the United States—analysis of conditions and trends. Washington (DC): USDA.

US Department of Agriculture (USDA). 1993. Agricultural statistics. Washington (DC): USDA.

US Department of Agriculture (USDA). 1994. Summary report 1992 national reseources inventory. Washington (DC): Soil Conservation Service, USDA.

US Forest Service (USFS). 1936. The major range problems and their solution. Washington (DC): USFS.

Van Rhee JA. 1965. Earthworm activity and plant growth in artificial cultures. Plants Soil 22:43–8.

Waldren RP. 1983. Corn. In: Teare ID, Peet MM, editors. Crop–water relations. New York: John Wiley and Sons. p 187–212.

Ward LK, Lakhani KH. 1977. The conservation of juniper: the fauna of food-plant island sites in southern England. J Appl Ecol 14:121–35.

Wen D. 1993. Soil erosion and conservation in China. In: Pimentel D, editor. Soil erosion and conservation. New York: Cambridge University Press. p 63–86.

Wen D. 1997. Agriculture in China: water and energy resources. Shenyang (China): Institute of Applied Ecology, Chinese Academy of Sciences. Forthcoming.

Wendt RC, Alberts EE, Helmers AT. 1986. Variability of runoff and soil loss from fallow experimental plots. Soil Sci Soc Am J 50:730–6.

Wendt RC, Burwell RE. 1985. Runoff and soil losses from conventional, reduced, and no-till corn. J Soil Water Conserv 40:450–4.

Wood M. 1989. Soil biology. New York: Blackie, Chapman and Hall.

World Health Organization (WHO). 1995. Bridging the gaps. Geneva: WHO.

World Resources Institute (WRI). 1994. World resources. New York: Oxford University Press.

Wright DH. 1983. Species-energy theory: an extension of the species-area theory. Oikos 41:4996–506.

Wright DH. 1990. Human impacts on energy flow through natural ecosystems, and replications for species endangerment. Ambio 19:189–94.

Young A. 1989. Agroforestry for soil conservation. Wallingford (UK): CAB.

Young A. 1990. Agroforestry, environment and sustainability. Outlook Agric 19:155–60.

Zacharias TP, Grube AH. 1984. An economic evaluation of weed control methods used in combination with crop rotations: a stochastic dominance approach. North Cent J Agric Econ 6:113–20.

Zhang X, Walling DE, Quine TA, Wen A. 1997. Use of reservoir deposits and caesium-137 measurements to investigate the erosional response of a small drainage basin in the rolling loess plateau region of China. Land Degrad Devel 8:1–16.

Oecologia (2001) 129:21–30
DOI 10.1007/s004420100760

**Michael L. Roderick · Graham D. Farquhar
Sandra L. Berry · Ian R. Noble**

On the direct effect of clouds and atmospheric particles on the productivity and structure of vegetation

Received: 11 May 2001 / Accepted: 1 June 2001 / Published online: 28 July 2001

Abstract The volume of shade within vegetation canopies is reduced by more than an order of magnitude on cloudy and/or very hazy days compared to clear sunny days because of an increase in the diffuse fraction of the solar radiance. Here we show that vegetation is directly sensitive to changes in the diffuse fraction and we conclude that the productivity and structure of vegetation is strongly influenced by clouds and other atmospheric particles. We also propose that the unexpected decline in atmospheric [CO_2] which was observed following the Mt. Pinatubo eruption was in part caused by increased vegetation uptake following an anomalous enhancement of the diffuse fraction by volcanic aerosols that would have reduced the volume of shade within vegetation canopies. These results have important implications for both understanding and modelling the productivity and structure of terrestrial vegetation as well as the global carbon cycle and the climate system.

Keywords Global carbon cycle · Diffuse radiation · Global change · Light use efficiency · Mt. Pinatubo

Introduction

Models which attempt to predict broad-scale variations in the productivity and/or structure of vegetation as a function of climate and other environmental factors have not generally considered the effects of clouds and other atmospheric particles. Instead, such models describe the weather and climate using factors like solar radiation, rainfall, evaporation and temperature, which have generally been assumed to exert a dominant influence over the productivity and structure of vegetation. However, measurements, particularly from forest ecosystems, have consistently shown that the efficiency of canopy gas exchange increases with, and is very sensitive to, the diffuse component of the incoming solar radiance (Hollinger et al. 1994, 1998). These observations suggest that models which ignore the diffuse component of solar radiance, such as the so-called big-leaf models, will not correctly predict changes in CO_2 uptake as a consequence of changes in diffuse radiance (De Pury and Farquhar 1997). That is important because the diffuse fraction of the solar radiance incident at the earth's surface has increased substantially in many regions as a consequence of increases in both cloudiness and the concentration of aerosols in the atmosphere (Suraqui et al. 1974; Abakumova et al. 1996).

The basic concept that canopy photosynthesis models must separately account for diffuse and beam radiance has long been realised by canopy modellers (Sinclair et al. 1976; Goudriaan 1977). However, the broader ecological and earth science communities have not yet appreciated the fundamental importance of the diffuse component of global solar irradiance. This may in part be caused by the apparently complex mathematics that is often used to describe the propagation of beam and diffuse radiance within vegetation canopies and through the atmosphere. While that mathematical complexity is often necessary for many purposes, the fundamental biological significance of diffuse radiance is related to shadows and this can be easily understood from casual observations. For example, when light is mostly diffuse, such as on cloudy days, there are minimal shadows. In contrast, when the solar disk is clearly visible, the shadows are well-defined and occupy a much larger volume because most of the radiance is coming from a single direction. A second basic fact that has not yet been fully exploited in climate-vegetation models is that the fraction of the global solar irradiance that is diffuse is negatively correlated with the fractional transmission of solar radiance through the atmosphere (Liu and Jordan 1960; Spitters et al. 1986; Roderick 1999). Thus, there is a robust relationship between the diffuse and global solar irradiance at the top of vegetation canopies.

M.L. Roderick (✉) · G.D. Farquhar · S.L. Berry · I.R. Noble
CRC for Greenhouse Accounting,
Research School of Biological Sciences,
Institute of Advanced Studies, Australian National University,
Canberra ACT 0200, Australia
e-mail: michael.roderick@anu.edu.au
Tel.: +61-2-61254020, Fax: +61-2-61255095

The aim of this paper is to show that variations in the diffuse fraction of solar radiation are an important, but largely ignored factor in understanding global scale variations in vegetation productivity and structure. To do that we initially use semi-quantitative arguments to show why the diffuse fraction is very important in determining the rates of canopy gas exchange. We then combine estimates of the sensitivity of canopy photosynthesis to the diffuse fraction, with the direct relation between the diffuse and global solar irradiance noted above, to derive a simplified version of the widely used light use efficiency model. The application of this new formulation is demonstrated by estimating the productivity over Australia using satellite and solar irradiance data. Following that, we apply the theory by showing that the unexpected decrease in atmospheric CO_2 that was observed following the Mt. Pinatubo volcanic eruption was most likely caused by an increased uptake of CO_2 by the vegetation. The increased uptake would have been a consequence of a reduction in the volume of shade within vegetation canopies that resulted from the anomalous nature of the increase in the diffuse fraction following the eruption.

The importance of diffuse radiance

Canopy shade and the diffuse fraction

The shadow cast by an object has a three-dimensional structure that is determined by the optical properties of the object and the geometry of the incoming radiance. Individual leaves typically absorb about 80% of the incident visible solar radiance (Monteith and Unsworth 1990) so that the (visible) component which is scattered by the leaves is relatively small. Because of that, the three-dimensional structure of shadows within a canopy, which can be described in terms of the volumes of umbra (full shade), sunflecks (full sun) and penumbra (part sun-part shade) (Horn 1971), is largely determined by the geometry of the incoming solar radiance. When the solar disk is totally obscured, such as commonly occurs on cloudy days, vegetation canopies at the surface are located within the shadows cast by clouds and the irradiance is predominantly diffuse. Consequently, the length of the umbra under each leaf is very short and there is only a very small volume of shade within vegetation canopies (Fig. 1B). In contrast, when the solar disk is clearly visible, the length of the umbra under each leaf is much longer because most of the solar radiance is coming from a single direction (Fig. 1C). Estimating the volume of penumbra on sunny days is a very difficult practical problem because it mostly depends on the spatial arrangement of the leaves (Smith et al. 1989; Ross and Mottus 2000) which is highly variable. Despite that, it is easy to see from Fig. 1 that the volume of shade within a vegetation canopy will be at least an order of magnitude larger on a sunny day compared to a cloudy day.

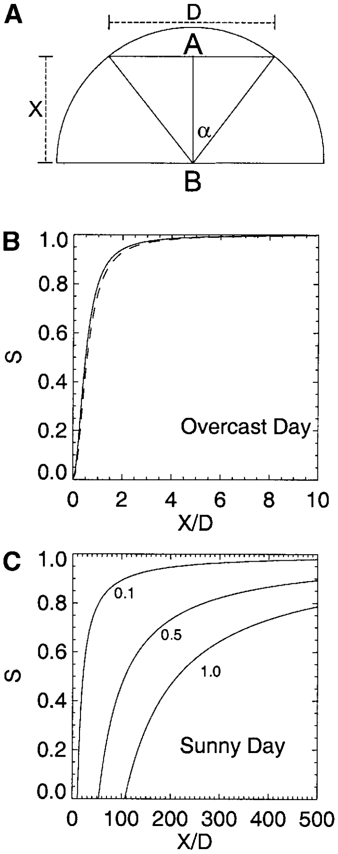

Fig. 1A–C A simplified method for estimating the reduction in solar irradiance caused by shadows. **A** Radiance coming from the upper hemisphere is intercepted by an opaque horizontal circular object of diameter D, centred at A and there is a reduction in the irradiance at B (R_B) located a distance X below A. The relative loss of irradiance at B, defined as R_B/R_A is denoted S. **B** S is plotted as a function of X/D for overcast days using two different radiance distributions; isotropic distribution (*full line*) in which the radiance is assumed to be the same in all directions and the standard overcast sky (*dashed line*) in which the radiance at the zenith is assumed to be 2.2 times the radiance at the horizon. Calculations to define these curves are described in the Appendix. Note that S is very similar for both distributions and when X/D is ≈ 2, R_B is about 95% of R_A and there is virtually no shade. **C** Relatively simple analytical expressions like those used above cannot be derived for sunny days. However, on sunny days most of the radiance is coming directly from the sun and the calculation can be greatly simplified without too much error by assuming that all of the radiance is coming from the solar disk. Accordingly, the semi-diameter of the sun is $\approx 16'$ so the length of the umbra is $\approx 107D\cos\beta$ where β is the angle between the sun and the surface normal, and $S\approx\max\{0,1-107D\cos\beta/X\}$. This formula is used to plot S as a function of X/D for a sunny day at three different values of $\cos\beta$ (0.1, 0.5, 1.0). Note that even if the umbra was only half as long as the above calculations suggest (Horn 1971), the volume of shade within a vegetation canopy is still at least an order of magnitude larger for a sunny sky compared to a cloudy sky

It follows from the above discussion that the volume of shade within a vegetation canopy must largely depend on the relative magnitude of the beam (R_b) and diffuse (R_d) solar irradiance at the top of a vegetation canopy where:

$$R_s=R_b+R_d \tag{1}$$

and R_s is the global solar irradiance. Thus when the solar disk is not obstructed by clouds or other atmospheric

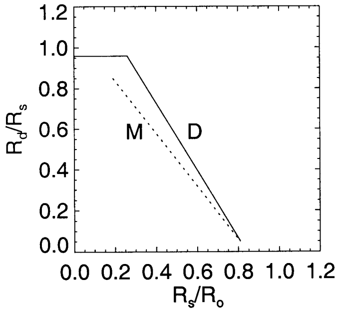

Fig. 2 Relationship between the diffuse fraction (R_d/R_s) and the atmospheric transmission (R_s/R_o) where R_d, R_s and R_o are the diffuse, global and top of the atmosphere solar irradiance using daily (D, *full line*) and monthly (M, y=1.11-1.31x) totals (Roderick 1999). The relation shown for daily data is for 40° latitude but there are only minor differences for other latitudes and the daily and monthly curves shown here typically account for at least 90% of the observed variation (Roderick 1999). The daily and monthly curves have a different form and slope because of differences in the inter- and intra-day distribution of cloud over a month. See Roderick (1999) for a theoretical treatment. Note that the relationship for annual data is virtually identical to the relation given for monthly data (Roderick 1999)

particles, the beam fraction, R_b/R_s, approaches unity and the diffuse fraction, R_d/R_s, must approach zero. In contrast, when the solar disk is totally obscured by clouds and/or very thick haze, R_d/R_s approaches unity and R_b/R_s approaches zero. These limits set the bounds on variation in the diffuse fraction. In that context, it has long been known that the diffuse fraction is negatively correlated with the atmospheric transmission, R_s/R_o where R_o is the global solar irradiance at the top of the atmosphere (Liu and Jordan 1960). More recently, it has been shown that the parameters of that relationship are more or less globally invariant (but see later for exceptions following volcanic eruptions) (Fig. 2). It follows that relative to the solar irradiance at the top of the atmosphere, high levels of solar irradiance at the top of vegetation canopies must be nearly all beam radiance, while low levels must be nearly all diffuse radiance.

Canopy photosynthesis and the diffuse fraction

Canopy scale photosynthesis depends amongst other things on the spatial distribution of irradiance in relation to the biochemical capacity (e.g. Rubisco and other enzymes) for photosynthesis. Models that account for these factors as well as the saturating response of leaf scale photosynthesis to the instantaneous irradiance at the leaf show that canopy scale photosynthesis is very sensitive to the diffuse fraction (De Pury and Farquhar 1997). One way to examine the direct effect of the diffuse irradiance on canopy photosynthesis is to use the so-called light-use efficiency model (Monteith 1972) where the daily net assimilation rate of the canopy (A, mol CO$_2$ m^{-2} day^{-1}) is given by:

$$A = efCR_s \qquad (2)$$

where e (mol CO$_2$ mol^{-1} PAR) is commonly known as the efficiency of the canopy, f is the fraction of photosynthetically active radiation (PAR) absorbed by the canopy, C is a more or less constant factor (*c*. 2.3 mol PAR MJ^{-1}) used to convert from global solar irradiance to quanta in the PAR part of the spectrum and R_s is the daily global solar irradiance at the top of the canopy. The effect of the diffuse fraction on e is more easily assessed by rewriting Eq. 2 as:

$$A = efC\frac{R_s}{R_o}R_o \qquad (3)$$

Thus, as R_s/R_o declines, there is typically less irradiance on individual leaves at the top of the canopy relative to that at the top of the atmosphere. However, the decline in R_s/R_o is accompanied by an increase in the diffuse fraction (Fig. 2) so that there will also be concurrent reduction in the volume of shade within the canopy. Further, because the photosynthetic rate of individual leaves usually saturates at high irradiance, it follows that individual leaves in low irradiance will have a higher e, and the reduction in the volume of shade within the canopy means that the canopy as a whole will also be more efficient in low irradiance. On that basis, we expect that e should generally increase as R_s/R_o decreases.

The above prediction is consistent with measurements above crop (Murata 1981; Sinclair et al. 1992; Rochette et al. 1996) and forest canopies (Price and Black 1990; Hollinger et al. 1994, 1998; Fan et al. 1995; Baldocchi et al. 1997) which show that e does increase as the irradiance at the top of the canopy declines. In many of these studies, the observed increase in e was attributed to increases in the diffuse fraction (Hollinger et al. 1994). That proposition has been confirmed by modelling studies of both crop and forest canopies that have found that e increases more or less linearly with the diffuse fraction (Norman and Arkebauer 1991; Choudhury 2000, 2001a, b).

As a further qualitative test of the above theoretical framework, we note that some forests have a leaf area index (L, defined as the total projected leaf area per unit ground area) as high as 7–10, or sometimes even higher (Anderson 1981). These values are extraordinary because both measurements (Ross et al. 1998; Ross and Mottus 2000) as well as estimates from relatively simple models indicate that on sunny days, most of the leaves in such canopies are in deep shade, presumably with marginal or negative carbon balances (Fig. 3). However, forests with a large L are often located in cloudy climates and the large values of L could be sustained by a reduction in the volume of shade within the canopy resulting from a higher diffuse fraction, as suggested by H. Horn (Horn 1971). If that were true, then we would expect forests with large L to have higher rates of CO$_2$ uptake on cloudy days than on sunny days. This accords with measurements over a dense forest canopy (L≈7) in New Zealand (Hollinger et al. 1994).

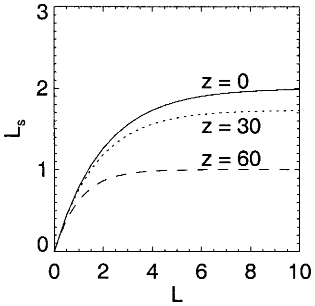

Fig. 3 Sunlit leaf area index (L_s) as a function of leaf area index (L) at three different solar zenith angles (z). The calculation is based on a simplified formula that has been recommended for general use in forest studies (Landsberg and Gower 1997); $L_s=(1-e^{-Lk \sec z})(k \sec z)$ where k is the canopy extinction coefficient. Values of k typically vary from 0.2 (i.e. near vertical leaves) to 1.1 (i.e. near horizontal leaves) but 0.5 has been recommended as a general value suitable for most forest canopies (Landsberg and Gower 1997) and was used to prepare the curves. The important conclusion is that L_s saturates at relatively small values of L and decreases as z increases. That general conclusion also holds for other values of k

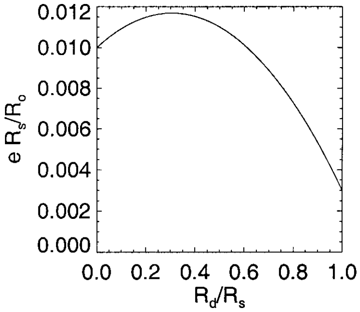

Fig. 4 Variation in $e'(R_s'/R_o')$ as a function of the annual diffuse fraction as predicted from Eq. 8. Note that Eq. 8 is in part dependent on Eq. 7, and the parameters of Eq. 7 do vary between different vegetation canopies (Choudhury 2001a). Consequently, the predicted maximum will also vary for different vegetation canopies. (See the main text for further discussion of this important point)

Estimating productivity using the diffuse fraction

Formulation of a simplified light use efficiency model

The above analyses suggest that it is possible to develop an (approximate) generic function relating e with the diffuse fraction and to use that relation in an integrated form of Eqs. 2 and 3 to estimate the annual gross and net productivity of plant communities. To do that, we can express the annual net production (N, mol CO_2 m^{-2} $year^{-1}$) of a plant community as the difference between gross photosynthesis (P_G, mol CO_2 m^{-2} $year^{-1}$) and autotrophic respiration (P_R, mol CO_2 m^{-2} $year^{-1}$):

$$N=P_G-P_R \tag{4}$$

P_R is usually found to be 30–70% of P_G and observations suggest that 45% is close to a typical average value (Landsberg and Gower 1997) which is consistent with theoretical expectations (Dewar 2000). The gross photosynthesis is given by:

$$P_G = e' f' C' \frac{R_s'}{R_o'} R_o' \tag{5}$$

where the superscripts denote that we are using annual totals or averages as appropriate. Both R_s'/R_o' and e' can be expressed as functions of the diffuse fraction. For annual (and monthly) totals, we have (see Fig. 2):

$$\frac{R_d'}{R_s'} \approx 1.11 - 1.31 \frac{R_s'}{R_o'} \tag{6}$$

Choudhury (2001a) modelled the CO_2 uptake for a wide variety of different crop and (native) forest canopies (n=57) spanning a large range of different climatic zones. His summary suggests that e' was on average about 0.015 and 0.036 under sunny and overcast conditions, respectively. Assuming that the diffuse fraction is 13% and 100% on sunny and overcast days respectively (Roderick 1999), those data can be used to derive the following relation:

$$e' \approx 0.024 \frac{R_d'}{R_s'} + 0.012 \tag{7}$$

By using Eqs. 6 and 7, it is straightforward to write a single expression for the product, $e'(R_s'/R_o')$, as a sole function of either R_s'/R_o' or R_d'/R_s' depending on which is more convenient for the purpose at hand. In terms of the diffuse fraction, that function is:

$$e' \left(R_s'/R_o'\right) \approx 0.010 + 0.011 \frac{R_d'}{R_s'} - 0.018 \left(\frac{R_d'}{R_s'}\right)^2 \tag{8}$$

and by substitution into Eq. 5, we have:

$$P_G \approx f' C' R_o' \left(0.010 + 0.011 \frac{R_d'}{R_s'} - 0.018 \left(\frac{R_d'}{R_s'}\right)^2\right) \tag{9}$$

for the gross annual productivity of a plant community. The quadratic function in Eqs. 8 and 9 predicts that at fixed values of f', C' and R_o', the gross productivity would have a maximum value at a diffuse fraction of about 31% (Fig. 4). In the context of this paper, the precise value of the maximum is not important because there is variation in Eq. 7, and hence Eqs. 8 and 9, between different plant communities (Choudhury 2001a). For example, the measurements from New Zealand forests which were cited earlier (Hollinger et al. 1994) show that the maximum would occur at a much higher diffuse fraction, because the uptake of CO_2 was higher on cloudy days. Nevertheless, it is important to note here that the quadratic function predicts that a broad optimum will occur and this is consistent with observations (Gu et al. 1999).

Estimating continental scale annual productivity: a case study using Australia

Equation 9 is convenient for practical applications because (ignoring orbital perturbations) R_o' is only a func-

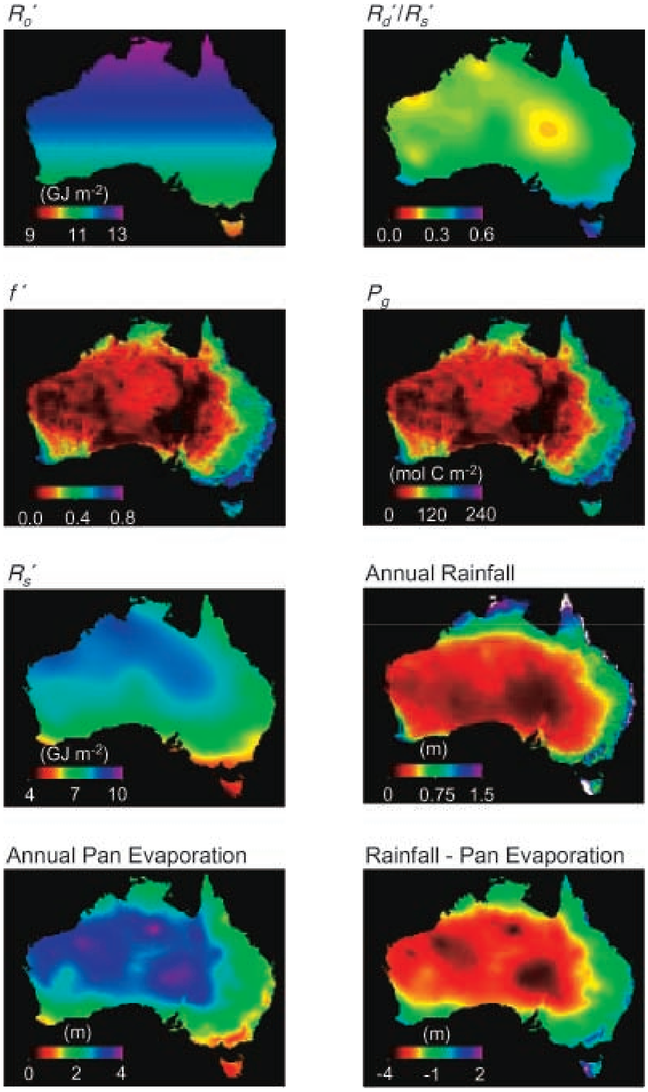

Fig. 5 Top four panels include the estimate of gross annual productivity for the period 1982–1990 (P_G) and the data used to make that estimate (per Eq. 9). *The lower four panels* are ancillary climate data that are included to highlight the inter-relationships between the radiation and water balance and the vegetation cover. (Note that the annual rainfall is greater than 1.5 m in the 'white' areas on the rainfall image and that the pan evaporation is for a Class A pan.) The 'Rainfall – Pan Evaporation' image was computed as the difference between the respective images. The *upper left* and *lower right* corners of each image are at 110°E, 10°S and 155°E, 45°S respectively

tion of latitude and C′ is reasonably constant (*c.* 2.3 mol PAR MJ^{-1}), leaving only the annual diffuse fraction, R_d'/R_s' and f', the fraction of the incident annual PAR absorbed by the vegetation, to be estimated. The diffuse fraction can be estimated from measurements of global solar irradiance (per Fig. 2) and f' can be estimated using satellite observations.

To demonstrate this approach, we estimated the average f' for 1982–1990 using 9 years of monthly satellite images following the method of Roderick et al. (1999) as modified by Berry and Roderick (2001). The average annual global solar irradiance, and the other average annual climatic data (Fig. 5), were computed using monthly averages from the ESOCLIM database available from the Centre of Resource and Environmental Studies at the Australian National University. The average annual diffuse fraction was calculated by estimating the diffuse irradiance for each month, using the method of Roderick (1999) and then summing the diffuse and global solar irradiance for each month to calculate the ratio of the annual values.

Using these data, and Eq. 9, we estimated the annual average gross production for Australia for the period 1982–1990 as 66 mol C m^{-2} year^{-1} corresponding to about 5.9 GtC year^{-1} for the whole country (Fig. 5). Assuming that autotrophic respiration was 45% of the gross production, the corresponding average net production would be about 36 mol C m^{-2} year^{-1} or about 3.2 GtC year^{-1} over the whole country. From sensitivity analysis (results not shown) we found that our estimate of gross (and net) production would be most sensitive to errors in estimating f' over the partially vegetated surfaces that cover most of Australia. Our estimates of e' based on Eq. 7 were generally consistent with estimates for Australian forests made using other means (Landsberg and Hingston 1996) but we expect that Eq. 7 could be improved for specific vegetation types and environmental conditions (Choudhury 2001a), especially during droughts. Note that in cloudy environments such as tropical rainforests, the variation in e' would generally be larger than the variation in f'. Our estimate of *c.* 3.2 GtC year^{-1} for the average annual net primary production of Australia is higher than, but still of the same order as, estimates made using a variety of other approaches, e.g. *c.* 2.8 GtC year^{-1} (Gifford et al. 1992), *c.* 2.7 GtC year^{-1} (Pittock and Nix 1986), *c.* 2.0 GtC year^{-1} (Field et al. 1998; DeFries et al. 1999), *c.* 1.6 GtC year^{-1} (Kirschbaum 1999). However, here we emphasise the underlying relationships and methods that are used in subsequent analysis, rather than the absolute accuracy of the results, given that we have not addressed the effects of, for example, water stress on e'.

Mt. Pinatubo – the effect of perturbations in the diffuse-global relationship

The data in Fig. 5 highlight the interrelationships between the water balance (rainfall, pan evaporation) and the radiation balance (global solar irradiance, diffuse fraction). In particular, as cloud cover increases, rainfall and the diffuse fraction typically increase, and the atmospheric transmission of solar radiance declines as does the pan evaporation. These interrelationships are at the heart of the light use efficiency model because it is ultimately based on the (reasonable) assumption that the interception of light by leaves will be accompanied by the uptake of water and nutrients necessary for photosynthesis and transpiration (Roderick et al. 2000). Nevertheless, that does not mean that diffuse radiance, and hence the diffuse fraction, is only important because it is correlated with changes in the radiation and water balance. On the contrary, the earlier theoretical analysis predicted, and the existing data showed, that canopy photosynthesis is sensitive to changes in the diffuse fraction. One way to explicitly test the direct effect of diffuse irradiance on canopy photosynthesis would be to conduct experiments in which the diffuse fraction was varied using artificial means, independently from the global solar irradiance. Plot-scale agricultural experiments of this sort have been conducted, and the results showed that plant productivity increases dramatically when the diffuse fraction is artificially increased while the global solar irradiance is held constant (Healey et al. 1998). While that is important confirmation of the significance of diffuse radiance, it is important to note that in nature, these various combinations do not usually occur (at the top of vegetation canopies) because increases in the diffuse fraction occur concurrently with decreases in atmospheric transmission (Fig. 2). However, there is (at least) one spectacular exception.

Following volcanic eruptions the solar irradiance at the surface usually remains more or less constant but there is a large increase in the diffuse fraction because the volcanic aerosols predominantly forward scatter the incoming solar radiance (Garrison 1995). Thus, for a period of time following a volcanic eruption there is a greater amount of diffuse irradiance at any given global solar irradiance than predicted by the relationship in Fig. 2. Of particular interest here is the Mt. Pinatubo (120°E, 15°N) eruption which occurred in June 1991 at the height on the northern hemisphere growing season, because there was a distinct change in atmospheric [CO_2] (Sarmiento 1993) that lasted for about 2 years after that eruption (Keeling and Whorf 1999). The decline is unique in the atmospheric [CO_2] (Keeling) measurements and surprised many scientists because it also coincided with an El Niño event and previous and subsequent such events have been associated with *increases* in atmospheric [CO_2]. Initial analysis of this anomaly concluded that the effect was probably a terrestrial one (Sarmiento 1993). Subsequent work has suggested a combined terrestrial-oceanic sink (Keeling et al. 1996) or an oceanic sink because of fertilisation by iron ejected in the eruption (Watson 1997) and/or changes in wind patterns over the Pacific ocean (Murray et al. 1994). Here we propose an additional/alternative mechanism, based on the perturbation in the diffuse-global relationship (Fig. 2) that would lead to a terrestrial sink.

Following the Mt. Pinatubo eruption the solar irradiance at the surface typically declined by a few percent (Molineaux and Ineichen 1996). This reduction was most pronounced in the latter half of 1991 and in 1992 and had begun to disappear by the end of 1993 (Michalsky et al. 1994; Molineaux and Ineichen 1996; Adeyefa et al. 2000). There was also a large anomalous increase in the diffuse fraction (Michalsky et al. 1994; Molineaux and Ineichen 1996; Adeyefa et al. 2000) during the same period that accords with the time scale of the observed atmospheric CO_2 anomaly. Thus, there would have been a reduction in the volume of shade within vegetation canopies as a result of the anomalous increase in the diffuse fraction. Because this occurred without a large reduction in the amount of global solar irradiance, the combination of events should have resulted in an increased uptake of CO_2 by vegetation worldwide.

While we have little doubt about the direction of change following Pinatubo, the key issue here is to establish whether the expected increase in CO_2 uptake by vegetation would have been of sufficient magnitude to explain a significant part of the observed atmospheric anomaly. To do that, we attempt a simple analysis by estimating the perturbation in net production (dN) resulting from the increased diffuse fraction as:

$$\frac{\mathrm{d}N}{N}=\frac{\mathrm{d}P_\mathrm{G}-\mathrm{d}P_\mathrm{R}}{P_\mathrm{G}-P_\mathrm{R}} \tag{10}$$

By expressing the autotrophic respiration as a fraction (α) of gross production:

$$P_\mathrm{R}=\alpha\,P_\mathrm{G} \tag{11a}$$

and for the perturbation in those quantities:

$$\mathrm{d}P_\mathrm{R}=\beta\,\mathrm{d}P_\mathrm{G} \tag{11b}$$

we can rewrite Eq. 10 as:

$$\frac{\mathrm{d}N}{N}=\frac{(1-\beta)\mathrm{d}P_\mathrm{G}}{(1-\alpha)P_\mathrm{G}} \tag{12}$$

We make the assumption that C' and f' remained constant after the eruption. Based on those assumptions, Eq. 12 can be rewritten as:

$$\frac{\mathrm{d}N}{N}=\left(\frac{(1-\beta)}{(1-\alpha)}\right)\left(\frac{\mathrm{d}e'}{e'}+\frac{\mathrm{d}R_\mathrm{s}'}{R_\mathrm{s}'}\right) \tag{13}$$

By differentiating Eq. 7, we have:

$$\mathrm{d}e'\approx 0.024\,\mathrm{d}(R_\mathrm{d}'/R_\mathrm{s}') \tag{14}$$

Note that Eq. 7 was derived for conditions where the diffuse fraction would have followed the usual pattern as depicted in Fig. 2. The extensive calculations of Choudhury (2001a) need to be repeated for the conditions discussed here, and the slope (0.024) may need to be altered. In the absence of such calculations we assume that Eq. 14 is still a useful approximation.

Measurements of global and diffuse solar irradiance in New Zealand in March 1992, just after the Pinatubo eruption, showed a much higher diffuse fraction than expected (Kelliher et al. 1996), and are generally consistent with the widespread distribution of volcanic aerosols after the Pinatubo eruption (Minnis et al. 1993). Using data for Geneva (Switzerland, 46°N) and Albany (N.Y., USA, 43°N) (Molineaux and Ineichen 1996) we estimate that d($R_\mathrm{d}'/R_\mathrm{s}'$) was 0.08 and 0.10 respectively when averaged over the year following the Mt. Pinatubo eruption. Adopting 0.09, we get:

$$\frac{\mathrm{d}e'}{e'}\approx\frac{(0.024)(0.09)}{0.024\left(R_\mathrm{d}'/R_\mathrm{s}'\right)+0.012} \tag{15}$$

If R_d'/R_s' is assumed to be in the range 0.2–0.6 (Roderick 1999), then de'/e' would be between 0.13 and 0.08, say $de'/e' \approx 0.10$. Following volcanic eruptions, there is typically a small reduction in global solar irradiance (R_s') and here we assume 3% (Garrison 1995; Olmo et al. 1999). Assuming that global N is about 60 GtC year^{-1} (Field et al. 1998), we can rewrite Eq. 13 using the above estimates as:

$$dN \approx \frac{(1-\beta)}{(1-\alpha)}(0.10-0.03)(60) \approx \frac{(1-\beta)}{(1-\alpha)}(4.2) \qquad (16)$$

in units of GtC year^{-1}. Thus, assuming that there was no change in the fraction of autotrophic respiration, we estimate that dN would be about 4.2 GtC year^{-1}. Even if we make the (unlikely) assumption that the average autotrophic respiration increased from 45 to 65% of gross productivity, the estimate of dN is still of the same order (*c*. 2.7 GtC year^{-1}).

To estimate the effect of this change in net production on the atmospheric [CO_2], we also need to consider the decomposition of the increment as well as changes in heterotrophic (the so-called soil) respiration. To consider decomposition of the increment, we assume that the net carbon fixed by woody plants is incorporated in long-lived structures (e.g. woody stems) while the additional carbon fixed by herbaceous plants is decomposed and returns to the atmosphere. Assuming that approximately 60% of the global net production is attributed to woody plants (Potter and Klooster 1998), we can reduce our estimate of 4.2 GtC year^{-1} to 2.5 GtC year^{-1}. (Note that while it is the case that some of the primary production of woody plants is allocated to leaves, which in temperate conditions are often lost within a few months, we have been conservative by treating the response in terms of net primary productivity. For example, in practice, the autotrophic respiration, P_R, that diminishes P_G to N will not occur instantaneously as assumed here. Also, as noted above, the increase in the diffuse fraction persisted for at least two years and will have been promoting P_G over that period. This may explain the persistence of the CO_2 anomaly.) Soil respiration has traditionally been assumed to increase with temperature. Observations show that the average global surface air temperature decreased by about 0.1–0.2°C in the year following the Mt. Pinatubo eruption (Keeling et al. 1995), but this change would not be sufficient to significantly alter the order of magnitude of the above estimate.

While the above calculations are approximate, the estimate of the ‘Pinatubo pertubation’ on atmospheric CO_2 in the year following the eruption is a reduction of about 2.5 GtC which equates to about 1.2 ppmv CO_2 in the atmosphere and is of the same order as the observed effect (Sarmiento 1993). It is important to note that while the parameters we have used seem to have given a high estimate of Australian annual net primary production, the estimate of the Mt. Pinatubo effect is not generally sensitive to the assumed values of the parameters because the calculations are based on the proportional change in the parameter values. One caveat identified earlier is that further calculations of the dependence of e' on the diffuse fraction need to be made for conditions of extreme haze. Further, we acknowledge that there were probably many other subtle effects of the eruption on the climate and biosphere, including those noted by Watson (1997) and Murray et al. (1994). Nevertheless, we conclude that a decrease in the volume of shade caused by an anomalous increase in the diffuse fraction as a consequence of the scattering properties of volcanic aerosols is a major reason for the atmospheric CO_2 anomaly that was observed after the Mt. Pinatubo eruption.

Discussion

In most existing global scale climate-vegetation models, many of the gross effects of clouds are indirectly included via changes in variables like the global solar irradiance, or via the reduction in the vapour pressure deficit which is usually observed under cloudy conditions (Hammer and Wright 1994; Gu et al. 1999). While these indirect effects are important, clouds and other atmospheric particles also have an important direct effect on vegetation productivity and structure because changes in the diffuse fraction, resulting from variations in both cloudiness and aerosol concentrations, lead to large changes in the volume of shade within vegetation canopies. This direct effect can be readily incorporated into models because there is a robust relationship linking the diffuse fraction with the fractional transmission of solar radiance through the atmosphere (Fig. 2).

These latter results are very important in the context of global climate change, because there is now substantial evidence that the solar irradiance incident at the surface has declined substantially over the last 50 years (Stanhill and Cohen 2001). To put those observations in perspective, the radiative forcing at the surface as a consequence of the increase in CO_2 and other greenhouse gases since the start of the industrial era is believed to be about 1–3 W m^{-2}, while increases in aerosols are suspected to have decreased the radiative forcing by about the same amount (Hansen et al. 1998, 2000). These estimated changes are small by comparison with the *observed* changes in global solar irradiance. For example, Stanhill and Cohen (2001) estimate that since 1950, the global solar irradiance has decreased on average by about 25 W m^{-2}. According to the diffuse-global relationship (Fig. 2), that should have resulted in substantial increases in the diffuse fraction. Although estimates of diffuse irradiance are relatively scarce, observations made over the former Soviet Union are consistent with the predicted increase in the diffuse fraction (Fig. 6).

Because the diffuse radiance is very important in determining canopy photosynthesis, and because the globally observed trends in the diffuse fraction over the last 50 years are large, it is important that climate-vegetation models, including global scale carbon balance models,

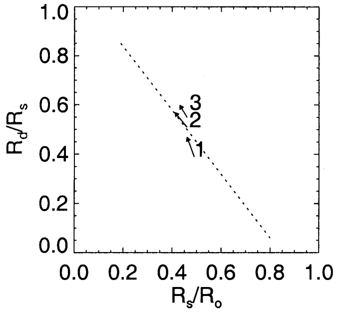

Fig. 6 Observed increases in the annual diffuse fraction at three sites (1, 2, 3) located in the former Soviet Union (Abakumova et al. 1996). *Dotted line* (y=1.11-1.31x) is the estimated relation for annual data (see Fig. 2). The base of each arrow signifies the observed relation in 1960 while the tip of the *arrowhead* is the observed relation in 1985 for sites 1 and 2, and 1990 is used for site 3. Sites are; 1 (Odessa, 46°24′ N, 30°48′ E), 2 (Toropets, 56°30′ N, 31°48′ E), 3 (Moscow, 55°42′ N, 37°30′ E). Data for the nine other sites reported in Abakumova et al. (1996) also follow the same trend reported here

be modified to include this important direct effect on vegetation productivity and structure.

We conclude that atmospheric scattering has important effects on the global carbon cycle and we support the recent call by Broecker (2000) for intense study of a possibly pivotal role of atmospheric dust in the global climate system.

Acknowledgements We thank Stephen Roxburgh, Frank Kelliher and two anonymous referees for helpful comments on the manuscript.

Appendix

Mathematical expressions for shadows

The irradiance of a surface receiving radiance from the upper hemisphere can be computed by integrating the intercepted radiance over the visible hemisphere. In the most general case, the radiance is a function of both azimuth and zenith angles. However, under overcast skies it is usually assumed that the radiance (I) is only a function of the zenith angle (z) and that dependence is usually expressed as (Monteith and Unsworth 1990):

$$I(z) = \frac{I(0)(1+b\cos z)}{(1+b)} \qquad \text{(A1)}$$

where (1+b) is the ratio of the radiance at the zenith, $I(0)$ to that at the horizon, $I(\pi/2)$. With reference to Fig. 1A, the irradiance at A, denoted R_{A}, is (Monteith and Unsworth 1990):

$$R_{\mathrm{A}} = \pi \int_{0}^{\pi/2} I(z)\sin z \cos z \, \mathrm{d}z \qquad \text{(A2)}$$

$$R_{\mathrm{B}} = \pi \int_{\alpha}^{\pi/2} I(z)\sin z \cos z \, \mathrm{d}z \qquad \text{(A3)}$$

where:

$$\tan\alpha = \frac{D}{2X} \qquad \text{(A4)}$$

Equation A3 is evaluated as:

$$R_{\mathrm{B}} = \frac{2\pi I(0)}{(1+b)}\left(\frac{\cos 2\alpha - \cos\pi}{4} + \frac{b}{3}\left(\cos^3\alpha - \cos^3 \pi/2\right)\right) \qquad \text{(A5)}$$

which reduces to:

$$R_{\mathrm{B}} = \frac{2\pi I(0)}{(1+b)}\left(\frac{\cos 2\alpha + 1}{4} + \frac{b}{3}\left(\cos^3\alpha\right)\right) \qquad \text{(A6)}$$

The integral of Eq. A2 can be derived from Eq. A6 by replacing α with zero throughout and is:

$$R_{\mathrm{A}} = \frac{2\pi I(0)}{(1+b)}\left(\frac{2}{4} + \frac{b}{3}\right) \qquad \text{(A7)}$$

The reduction in irradiance at B, relative to that at A, denoted S, is given by:

$$S = \frac{R_{\mathrm{B}}}{R_{\mathrm{A}}} \qquad \text{(A8)}$$

For an isotropic distribution of radiance, b equals zero, and from Eqs. A6, A7 it follows that:

$$S_i = \frac{\cos 2\alpha + 1}{2} \qquad \text{(A9)}$$

For the standard overcast sky, b equals 1.2 (Monteith and Unsworth 1990) and it can be shown that:

$$S_{\mathrm{sos}} = \frac{1}{0.9}\left(\frac{\cos 2\alpha + 1}{4} + 0.4\cos^3\alpha\right) \qquad \text{(A10)}$$

Equations. A4, A9 and A10 have been used to prepare Fig. 1B in the main text.

References

Abakumova GM, Feigelson EM, Russak V, Stadnik VV (1996) Evaluation of long-term changes in radiation, cloudiness, and surface temperature on the territory of the former Soviet Union. JClim 9:1319–1327

Adeyefa ZD, Holmgren B, Adedokun JA (2000) Spectral solar irradiance in northern Scandinavia before and after Pinatubo. Atmosfera 13:133–146

Anderson MC (1981) The geometry of leaf distribution in some south-eastern Australian forests. Agric Meteorol 25:195–205

Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric For Meteorol 83:147–170

Berry SL, Roderick ML (2001) Estimating mixtures of leaf functional types using continental-scale satellite and climatic data. Global Ecol Biogeogr 10(in press)

Broecker WS (2000) Abrupt climate change: causal constraints provided by the paleoclimate record. Earth-Sci Rev 51:137–154

Choudhury BJ (2000) A sensitivity analysis of the radiation use efficiency for gross photosynthesis and net carbon accumulation by wheat. Agric For Meteorol 101:217–234

Choudhury BJ (2001a) Estimating gross photosynthesis using satellite and ancillary data: Approach and preliminary results. Remote Sensing Environ 75:1–21

Choudhury BJ (2001b) Modeling radiation- and carbon-use efficiencies of maize, sorghum and rice. Agric For Meteorol 106: 317–330

De Pury DGG, Farquhar GD (1997) Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ 20:537–557

DeFries RS, Field CB, Fung I, Collatz GC, Bounoua L (1999) Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. Global Biogeochem Cycles 13:803–815

Dewar R (2000) A model of the coupling between respiration, active processes and passive transport. Ann Bot 86:279–286

Fan S-M, Goulden ML, Munger JW, Daube BC, Bakwin PS, Wofsy SC, Amthor JS, Fitzjarrald DR, Moore KE, Moore TR (1995) Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole ecosystem exchange measurements by eddy correlation. Oecologia 102:443–452

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: Integrating terrestrial and oceanic components. Science 281:237–239

Garrison J (1995) An evaluation of the effect of volcanic eruption on the solar radiation at six Canadian stations. Solar Energy 55:513–525

Gifford RM, Cheney NP, Noble JC, Russell JS, Wellington AB, Zammit C (1992) Australian land use, primary production of vegetation and carbon pools in relation to atmospheric carbon dioxide concentration. In: Gifford RM, Barson MM (eds) Australia's renewable resources sustainability and global change. Bureau of Rural Resources and CSIRO Division of Plant Industry, Canberra, pp 151–187

Goudriaan J (1977) Crop micrometeorology: a simulation study. PUDOC, Wageningen

Gu L, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. J Geophys Res 104:31421–31434

Hammer GL, Wright GC (1994) A theoretical analysis of nitrogen and radiation effects on radiation use efficiency in peanut. Aust J Agric Res 45:575–589

Hansen JE, Sato M, Lacis A, Ruedy R, Tegen I, Mathews E (1998) Climate forcings in the industrial era. Proc Natl Acad Sci USA 95:12753–12758

Hansen JE, Sato M, Ruedy R, Lacis A, Oinas V (2000) Global warming in the twenty-first century: an alternative scenario. Proc Ntl Acad Sci USA 97:9875–9880

Healey KD, Rickert KG, Hammer GL, Bange MP (1998) Radiation use efficiency increases when the diffuse component of incident radiation is enhanced under shade. Aust J Agric Res 49:665–672

Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology 75:134–150

Hollinger DY, Kelliher FM, Schulze E-D, Bauer G, Arneth A, Byers JN, Hunt JE, McSeveny TM, Kobak KI, Milukova I, Sogatchev A, Tatarinov F, Varlargin A, Ziegler W, Vygodskaya NN (1998) Forest-atmosphere carbon dioxide exchange in eastern Siberia. Agric For Meteorol 90:291–306

Horn HS (1971) The adaptive geometry of trees. Princeton University Press, Princeton

Keeling CD, Whorf TP (1999) Atmospheric CO_2 records from sites in the SIO air sampling network. In: Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge

Keeling CD, Whorf TP, Wahlen M, van der Pilcht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. Nature 375:666–670

Keeling RF, Piper SC, Heinmann M (1996) Global and hemispheric CO_2 sinks deduced from changes in atmospheric CO_2. Nature 381:218–221

Kelliher FM, Owens IF, Sturman AP, Byers JN, Hunt JE, McSeveny TM (1996) Radiation and ablation on the névé of Franz Josef Glacier. J Hydrol (Dunedin) 35:131–150

Kirschbaum MUF (1999) The effect of climate change on forest growth in Australia. In: Howden SM, Gorman JT (eds) Impacts of global change on Australian temperate forests. BRS Working Paper Series No. 99/08, Canberra, pp 62–68

Landsberg JJ, Gower ST (1997) Applications of physiological ecology to forest management. Academic Press, San Diego

Landsberg JJ, Hingston FJ (1996) Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus globulus* plantations in Western Australia. Tree Physiol 16: 801–808

Liu BYH, Jordan RC (1960) The interrelationship and characteristic distribution of direct, diffuse and total solar radiation. Solar Energy 4:1–19

Michalsky JJ, Perez R, Seals R, Ineichen P (1994) Degradation of solar concentrator performance in the aftermath of Mt Pinatubo. Solar Energy 52:205–213

Minnis P, Harrison EF, Stowe LL, Gibson GG, Denn FM, Doelling DR, Smith WL Jr (1993) Radiative climate forcing by the Mount Pinatubo eruption. Science 259:1411–1415

Molineaux B, Ineichen P (1996) Impact of Pinatubo aerosols on the seasonal trends of global, direct and diffuse irradiance in two northern mid-latitude sites. Solar Energy 58:91–101

Monteith JL (1972) Solar radiation and productivity in tropical ecosystems. J Appl Ecol 9:747–766

Monteith JL, Unsworth M (1990) Principles of environmental physics. Edward Arnold, London

Murata Y (1981) Dependence of potential productivity and efficiency for solar energy utilization on leaf photosynthetic capacity in crop species. Jpn J Crop Sci 50:223–232

Murray JW, Barber RT, Roman MR, Bacon MP, Feely RA (1994) Physical and biological controls on carbon cycling in the equatorial pacific. Science 266:58–65

Norman JM, Arkebauer TJ (1991) Predicting canopy light-use efficiency from leaf characteristics. In: Hanks J, Ritchie JT (eds) Modelling Plant and Soil Systems, Agronomy Monograph No. 31. ASA-CSSA-SSSA, Madison, pp 125–143

Olmo FJ, Tovar J, Alados-Arboledas L, Okulov O, Ohvril HO (1999) A comparison of ground level solar radiative effects of recent volcanic eruptions. Atmos Environ 33:4589–4596

Pittock AB, Nix HA (1986) The effect of changing climate on Australian biomass production – a preliminary study. Clim Change 8:243–255

Potter CS, Klooster SA (1998) Dynamic global vegetation modelling for prediction of plant types and biogenic trace gas fluxes. Global Ecol Biogeogr 8:473–488

Price DT, Black TA (1990) Effects of short-term variation in weather on diurnal canopy CO_2 flux and evapo-transpiration of a juvenile Douglas-fir stand. Agric For Meteorol 50:139–158

Rochette P, Desjardins RL, Pattey E, Lessard R (1996) Instantaneous measurement of radiation and water use efficiencies of a maize crop. Agron J 88:627–635

Roderick ML (1999) Estimating the diffuse component from daily and monthly measurements of global radiation. Agric For Meteorol 95:169–185

Roderick ML, Noble IR, Cridland SW (1999) Estimating woody and herbaceous vegetation cover from time series satellite observations. Global Ecol Biogeogr 8:501–508

Roderick ML, Berry SL, Noble IR (2000) A framework for understanding the relationship between environment and vegetation based on the surface area to volume ratio of leaves. Funct Ecol 14:423–437

Ross J, Mottus M (2000) Statistical treatment of sunfleck length inside the willow coppice. Agric For Meteorol 104:215–231

Ross J, Sulev M, Saarelaid P (1998) Statistical treatment of the PAR variability and its application to willow coppice. Agric For Meteorol 91:1–21

Sarmiento JL (1993) Atmospheric CO_2 stalled. Nature 365:697–698

Sinclair TR, Murphy CE, Knoerr KR (1976) Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. J Appl Ecol 13:813–829

Sinclair TR, Shiraiwa T, Hammer GL (1992) Variation in crop radiation use efficiency in response to increased proportion of diffuse radiation. Crop Sci 32:1281–1284

Smith WK, Knapp AK, Reiners WA (1989) Penumbral effects on sunlight penetration in plant communities. Ecology 70:1603–1609

Spitters CJT, Toussaint HAJM, Goudriaan J (1986) Separating the diffuse and direct component of global radiation and its implication for modelling canopy photosynthesis. I. Components of incoming radiation. Agric For Meteorol 38:217–229

Stanhill G, Cohen S (2001) Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. Agric For Meteorol 107:255–278

Suraqui S, Tabor H, Klein WH, Goldberg B (1974) Solar radiation changes at Mt. St. Katherine after forty years. Solar Energy 16:155–158

Watson AJ (1997) Volcanic iron, CO_2, ocean productivity and climate. Nature 385:587–588

Ecosystems

10.1007/s10021-005-0167-6

Drainage Size, Stream Intermittency, and Ecosystem Function in a Sonoran Desert Landscape

Ryan A. Sponseller[1] and **Stuart G. Fisher**[1]

(1) School of Life Sciences, Arizona State University, Tempe, Arizona 85287, USA

Ryan A. Sponseller
Email: rsponse@asu.edu
Phone: +480-965-6478

Received: 7 December 2004 **Accepted:** 11 February 2005

Abstract Understanding the interactions between terrestrial and aquatic ecosystems remains an important research focus in ecology. In arid landscapes, catchments are drained by a channel continuum that represents a potentially important driver of ecological pattern and process in the surrounding terrestrial environment. To better understand the role of drainage networks in arid landscapes, we determined how stream size influences the structure and productivity of riparian vegetation, and the accumulation of organic matter (OM) in soils beneath plants in an upper Sonoran Desert basin. Canopy volume of velvet mesquite *(Prosopis velutina)*, as well as overall plant cover, increased along lateral upland–riparian gradients, and among riparian zones adjacent to increasingly larger streams. Foliar $\delta^{13}C$ signatures for *P. velutina* suggested that landscape patterns in vegetation structure reflect increases in water availability along this arid stream continuum. Leaf litter and annual grass biomass production both increased with canopy volume, and total aboveground litter production ranged from 137 g m^{-2} y^{-1} in upland habitat to 446 g m^{-2} y^{-1} in the riparian zone of the perennial stream. OM accumulation in soils beneath *P. velutina* increased with canopy volume across a broad range of drainage sizes; however, in the riparian zone of larger streams, flooding further modified patterns of OM storage. Drainage networks represent important determinants of vegetation structure and function in upper Sonoran Desert basins, and the extent to which streams act as sources of plant-available water and/or agents of fluvial disturbance has implications for material storage in arid soils.

Keywords Sonoran Desert - intermittent streams - primary production - soil organic matter - scale - *Prosopis velutina*

INTRODUCTION

Understanding the relationships between fluvial ecosystems and the catchments they drain has been a major research focus in stream ecology for over 30 years (*Hynes 1975*; *Fisher and others 2004*). Recently, efforts have focused on learning how the spatial structure of channel networks influences ecological patterns in streams (*Power and Dietrich 2002*; *Benda and others 2004*), and the surrounding terrestrial landscape (*Fisher and others 2001*). Arid landscapes are heavily dissected by drainage networks (*Graf 1988*), and the influence of aquatic ecosystems on terrestrial biota is evident from the conspicuous growth of riparian vegetation along streams and rivers that drain catchments that are otherwise poorly vegetated. Flow regimes within arid stream networks vary dramatically in space and time (*Stanley and others 1997*), however, and the importance of these hydrologic dynamics to ecological patterns considered at basin scales is largely unknown.

A variety of biotic and abiotic factors may influence plant communities in arid landscapes (*McAuliffe 1994*; *Whitford 2002*), but water availability is considered the prominent driver of vegetation pattern and process (for example, *Noy-Meir 1973*; *Schlesinger and Jones 1984*; *Reynolds and others 1999*). Water is routed across arid basins via a continuum of channels that drain subcatchments of increasingly greater area, and constitute a gradient in stream intermittency (*Fisher and others 2001*). The smallest channels (that is, rills) in the stream network receive runoff from surrounding hillslopes when rainfall is in excess of infiltration in soils, and thus support surface flow only in direct response to precipitation. Infiltration losses in the beds of rills can be substantial (for example, *Parsons and others 1999*); this water moves downstream along subsurface flow paths and represents an important mechanism for the recharge of alluvial aquifers (for example, *Khazaei and others 2003*). Surface and subsurface discharge from alluvial aquifers in turn supports intermittent and perennial flow in high-order stream and wetland ecosystems. Because channels divert water vertically and laterally, the productivity of near-stream vegetation can be augmented relative to that in upland habitats (for example, *Ludwig 1987*; *Martinez-Yrizar and others 1999*). It is not known how this disparity in production varies along the entire continuum flow regimes, which includes not only ephemeral washes, but also large intermittent and perennial streams.

Landscape gradients in plant productivity that result from differential access to water may in turn influence the storage of material in arid soils. Historically, research in desert ecosystems has emphasized the role of plants in sequestering carbon (C), nitrogen (N), and other nutrients into ‘islands of fertility’ (for example, *Crawford and Gosz 1982*; *Schlesinger and others 1996*). This concentration of material beneath vegetation is thought to derive from local plant productivity, the capture of dissolved and particulate components of overland sheet flow, and the trapping of particles transported by wind (*Schlesinger and Pilmanis 1998*). Therefore, to the extent that material storage beneath plants is driven by local production, the concentration of organic matter (OM) and nutrients in soils should increase along landscape gradients in plant productivity. Deposition and scour during floods, however, may further influence the storage of material in soils beneath vegetation in productive riparian habitats (*Malanson 1993*). These fluvial processes are likely to be particularly important in arid catchments, where rivers are characterized by flash floods that represent important agents of disturbance along channel margins (for example, *Stromberg and others 1991*).

In this paper, we seek to better understand the role of stream networks in arid landscapes by exploring how stream size and intermittency affect the structure and function of riparian zones in an upper Sonoran Desert basin. Our first objective was to determine how differences in drainage area influence vegetation size, cover, and production in streamside habitats, as well as the strength of lateral upland–riparian gradients in plant structure. A second objective was to learn whether gradients in plant size and productivity influence the concentration of resources in underlying soils, and determine how relationships between vegetation structure and soil properties in riparian zones change with stream size and hydrologic regime. To meet these objectives, we quantified plant and soil features in upland and riparian habitats of subcatchments drained by streams that encompass the range of flow characteristics commonly found in arid basins of the upper Sonoran Desert. We then used a scaling analysis (sensu *Ludwig and others 2000*) to determine whether soil organic matter (SOM) concentration increases with plant size, and to evaluate how these plant–soil relationships change as the window of observation is expanded to include increasingly larger catchments, with more frequently flooded riparian terraces.

METHODS

Study Site

Sycamore Creek is located 52 km northeast of Phoenix, AZ, USA, and drains a 505-km^2 basin that ranges in elevation from 427 to 2,164 m. Mean annual precipitation varies with elevation, ranging from approximately 30 cm at 500 m to approximately 60 cm above 1,200 m (*Thomsen and Schumann 1968*). Annual precipitation is distributed bimodally, with approximately 70% of rainfall associated with Pacific frontal storms (November–April), and 30% associated with convective monsoon storms in the summer (June–September; *Welter 2004*). Stream flow across the Sycamore Creek basin is spatially and temporally intermittent (*Stanley and others 1997*). Surface water in the mainstem is typically continuous throughout the winter and spring (for example, December–April), but can be reduced by more than 50% during summer months. The largest tributaries to the mainstem may also support surface flow for extended periods of time (for example, weeks to months) during the winter and spring. For the vast majority of smaller channels in the stream network, however, surface flow is ephemeral and coincides with precipitation events.

We quantified vegetation structure, litter production, and SOM storage from five nested subcatchments ranging in area from 0.006–393.0 km^2 (sites 1–5, Figure 1). We selected sites drained by channels that encompass the spectrum of flow regimes found in the basin. Channels at sites 1–3 drain relatively small subcatchments (0.006–0.6 km^2), and produce surface flow for short periods of time, only in response to precipitation. Previous research at these sites has shown that flow characteristics and drying patterns for channel sediments are tied to the characteristics of the precipitation regime (that is, the duration, magnitude, and intensity of events; *Welter 2004*). Site 1 had no obvious riparian terrace, and was only used for a subset of the analyses described below.

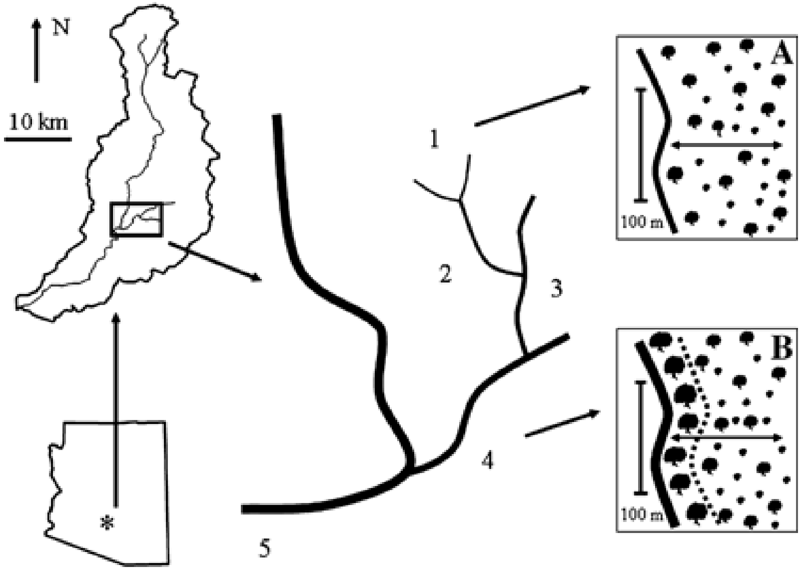

Figure 1 Depiction of study sites in the Sycamore Creek basin, located NE of Phoenix, AZ, USA. Sites were organized along a stream continuum, and site numbers (1–5) and line thickness correspond to increased catchment area and stream size: site 1 = 0.006 km^2, site 2 = 0.05 km^2, site 3 = 0.6 km^2, site 4 = 40.0 km^2, site 5 = 390.0 km^2. Each site consisted of a 100 m stream reach; plant and soil features were quantified from stream channel to ridge-top. Site 1 was an upland catchment with no apparent riparian terrace (*inset A*); sites 2–5 all had obvious streamside terraces (*inset B*, shown as *dotted line*).

Channels at sites 4 and 5 drain larger subcatchments and can retain streamflow long past individual precipitation events. Site 4 lies adjacent to one of the major tributaries of Sycamore Creek (drainage area = 40 km^2). The stream here can sustain surface water for months at a time during the winter and spring—sufficient to support a variety of benthic fish and invertebrates (*Stanley 1993*). Following the cessation of surface flow, subsurface flow continues through early summer, although this eventually becomes restricted to deeper (> 3 m) strata (*Thomsen and Schumann 1968*; *Clinton 1996*). Site 5 is located on Sycamore Creek proper (390 km^2). Here the stream retains some surface water throughout the year, in all but the driest years, and supports a diverse assemblage of benthic and hyporheic organisms, as well as obligate wetland and riparian vegetation. In addition to these five sites, we also completed a broader survey of plant structure in nine additional riparian zones from six major subcatchments in the Sycamore Creek basin (drainage size range = 0.02–50 km^2).

Velvet Mesquite as a Model System

We used velvet mesquite (*Prosopis velutina*) as a model system to ask how stream intermittency influences the structure and function of riparian zones. *P. velutina* is a deciduous legume that is ubiquitous across upper Sonoran desert landscapes, being a common member of the Arizona upland desert–scrub association, and the dominant tree species along intermittent and permanent stream channels (*Campbell and Green 1968*; *Stromberg and others 1993*). *P. velutina* is a facultative phreatophyte (*Campbell and Green 1968*), meaning that it is able to access deep groundwater sources where possible, but can also utilize water from upper soil layers when deeper sources are not available (for example, *Snyder and Williams 2000*). In addition to this, *Prosopis* sp. in the Sonoran desert are known to (1) facilitate the growth of understory annual grasses (*Yavitt and Smith 1983*; *Schade and others 2003*), and (2) accumulate C, N, and other nutrients in underlying soils, relative to interplant spaces (for example, for *P. glandulosa*, *Virginia and Jarrell 1983*; for *P. velutina*, *Schade and Hobbie 2005*). For these reasons, *P. velutina* is ideal for investigating relationships between basin scale patterns in water availability and aboveground productivity, and asking how these interactions influence the accumulation of materials in soil beneath desert plants.

Survey of *P. velutina* Canopy Volume and Plant Cover

In each of the five subcatchments, we identified a study site bounded by a 100-m stream reach, extending laterally from channel-edge to ridge-top (Figure 1, inset). Within these boundaries, we estimated *P. velutina* canopy volume for all individuals using:

$$V\ (\mathrm{m}^3) = \frac{2}{3} \times \tau \times H \times \left(\frac{A}{2} \times \frac{B}{2}\right)$$

Where *H* represents tree height, and *A* and *B* the major and minor axes measured at 50% *H* (as developed for rangeland shrubs by *Thorne and others 2002*). Heights and widths of small individuals were measured with a meter stick; dimensions for larger individuals were estimated using a clinometer and meter tape.

We used data from sites 2–5 to compare *P. velutina* size between upland and riparian zones, and to ask whether this disparity varies with longitudinal position. For this, *P. velutina* were classified as either upland or riparian based on their position relative to the terrace–upland slope-break. Mean canopy volume was compared among sites and habitats (upland vs. riparian) using a two-way ANOVA, followed by *t* tests and a one-way ANOVA to compare averages between upland and riparian habitats within sites, and among riparian zones of increasingly larger streams, respectively. The total number of individuals sampled at these sites ranged from 38 (site 2) to 116 (site 3); canopy volume data were not normally distributed, and log-transformed values were used for analyses.

To further evaluate the influence of stream size on vegetation structure, we quantified total plant cover in upland and riparian habitats at sites 2–5 using the line intercept method (*Mueller-Dombois and Ellenberg 1974*). Total cover, relative cover by *P. velutina*, and the total number of plant patches (hereafter referred to as patch number) were quantified from three 100 m transects that ran parallel to the stream channel at each site and for both habitats (that is, upland and riparian terrace). We compared mean plant cover variables among sites and habitats using a two-way MANOVA. This was followed by two-way ANOVAs for each dependent variable separately, and post-hoc analyses as described for canopy volume.

To determine how riparian *P. velutina* size varies across a more complete range of drainage areas, canopy volume was surveyed from nine additional streams draining subcatchments of variable size, shape, slope, and parent material. For this, 100 m stream reaches were selected near the base of each subcatchment. Using the methods described above, canopy volume was measured for all individuals within the riparian zones of these study sites (within site *n* range = 15–34). Bivariate regression on site means was used to relate riparian canopy volume to drainage area.

Water Availability and Aboveground Productivity

To determine whether changes in stream size translate to increased water availability for *P. velutina* growing on adjacent terraces, we surveyed foliar δ^{13}C in riparian zones for three consecutive years. Stable C isotope signatures provide a temporally integrative descriptor of water use efficiency (WUE), and have been used widely to describe patterns in water stress, where low water availability leads to reduced stomatal conductance, less discrimination of ^{13}C, and heavier C isotopic signatures in C3 plants (for example, *Ehleringer and Cooper 1988*; *Stewart and others 1995*; *Wainwright and others 2002*). We include here the results of a pilot study conducted in August of 2002, where three to five trees were sampled from the riparian zone of sites 2, 4, and 5. In May 2003 and 2004, we expanded this survey to include ten trees at each site (that is, sites 2–5). For all 3 years, samples were also taken from upland individuals at site 1. Leaves were collected from five individual stems at the north side of each plant; individuals were selected that encompassed the spectrum of *P. velutina* size at each site. Leaves were dried, ground by ball mill, and ^{13}C/^{12}C ratios measured on a PDZ-Europa Hydra GSL 20/20 Isotope Ratio Mass Spectrometer (Europa Scientific, Cheshire, UK). Carbon isotope ratios in parts per thousand (‰) are expressed relative to Pee Dee Belemnite (PDB) as:

$$\delta^{13}\mathrm{C} = [(R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1) \times 1{,}000]$$

where δ^{13}C is the C isotope ratio of the sample; R_{sample} and R_{standard} are the ^{13}C/^{12}C ratios of the sample and standard (peach leaf, NIST # 1547), respectively. Within years, one-way ANOVA was used to compare δ^{13}C among sites. Linear regression was used with data from all years to ask how foliar δ^{13}C signatures in riparian terraces varied as a function of drainage size.

We estimated *P. velutina* leaf litter production in the fall and spring of 2002–2003 and 2003–2004. For both years, litter fall was quantified from approximately 25 trees across the Sycamore Creek basin. The objective was to select trees that encompassed the range of habitats (that is, upland and riparian) and canopy volumes found in the broader survey, and then use statistical relationships between plant size and litter fall to estimate patterns of leaf production for each site and habitat. In 2002–2003, we used individual *P. velutina* from sites 1, 2, and 3, and from the riparian zone of an adjacent catchment approximately 50 km^2 in area. For 2003–2004, we used five individuals each from sites 1–5. At each tree, circular (0.02 or 0.03 m^2) litter traps were placed along two transects extending from the bole to the canopy edge. Litter was collected from traps monthly (leaves only) from October to April, encompassing the entire duration of leaf fall for *P. velutina* in this system. Leaves were dried at 60°C, and ashed to determine organic content.

The aboveground biomass of winter annuals was also quantified beneath *P. velutina* at the peak of growing season in 2003 and 2004. Because herbaceous plants are essentially absent prior to the winter rain season, we used grass biomass at the end of the growing season as a proxy for the production of winter annuals (for example, *Schade and others 2003*). For both years, we quantified grass biomass beneath 20 trees, 5 each from sites 1, 2, 4, and 5. Individuals selected from sites 2, 4, and 5 were located in the riparian terrace; all individuals from site 1 were located in upland habitat. Triplicate grass samples were harvested from beneath each tree using a 0.25 m^2 quadrat. Material was dried, and ashed to determine organic content. Linear regression was used to relate winter annual grass biomass production to *P. velutina* canopy volume; as described previously, regression equations were then used to estimate grass production for each site and habitat.

Resource Accumulation in Soils

Soil organic matter concentration at 0–2 cm depth was used as a proxy for material accumulation beneath *P. velutina*. Soils were sampled from beneath a subset of upland and riparian plants at sites 1–5. Site 1 included only upland individuals ($n = 33$); at sites 2–5, 18–20 riparian and 8–10 upland individuals were sampled. Triplicate samples were taken from within 1 m of the bole using a 10 cm diameter PVC core, inserted to 2 cm depth. Surface litter (O horizon) was removed before soils were collected. Interplant soils were also sampled at the same depth from five locations distributed across each upland and riparian site. Soils were air-dried in the laboratory and passed through a 2 mm sieve. The less than 2 mm fraction was subsampled, and OM content determined gravimetrically after combustion at 550°C for 4 h. Triplicate samples were averaged to generate an SOM concentration (% OM) for each tree. Within sites and habitats, we used *t* tests to compare mean % OM between plant and interplant patches. To determine whether patterns of SOM concentration were diagnostic for biogeochemically important elements, we measured total N on a subset of soils ($n = 40$) used in the survey. For this, subsamples from sieved soils were ground by ball mill, and analyzed for total N on a Perkin-Elmer 2400 CHNS/O Analyzer (Perkin-Elmer, Wellesly, MA, USA). Linear regression was used to evaluate relationships between SOM and total soil N.

Regression scaling plots (sensu Ludwig and others 2000) with canopy volume on the *x*-axis and SOM concentration on the *y*-axis were used to ask (1) how the concentration of SOM beneath *P. velutina* changes with plant size, and (2) whether and how these plant–soil relationships change as the spatial extent of the analysis expands to include riparian plants from increasingly larger, more permanent streams. To answer this second question, we compared slopes of regression lines relating the (ln-transformed) accumulation of SOM and canopy volume from plant–soil pairs organized at five different spatial scales. To generate these plots, we started with data from site 1 only, and sequentially increased the spatial extent of the analysis by adding plant–soil pairs from the next largest subcatchment. The broadest spatial extent, therefore, was the entire Sycamore Creek basin (393 km^2 at the study site), and consisted of all plant–soil pairs generated in the study. ANCOVA was used to compare slopes of the relationship between canopy volume and SOM as we increased the spatial extent. A Bonferroni adjustment was used to control for Type I error in slope comparisons.

To determine the extent to which fluvial processes influence soil features in riparian zones, particle size distribution was quantified from beneath a subset of trees in upland and streamside habitats at sites 2–5 ($n = 5$ for upland, $n = 7$ for terrace). Here, a bucket auger was used to collect soils to 10 cm. Percent gravel was determined gravimetrically from the larger than 2 mm size fraction. Clay content was quantified from 50 g subsamples using the density hydrometer method and sand was determined gravimetrically after rinsing the same subsamples through a 53 µm sieve and drying at 60°C. Both % clay and sand then scaled to the original bulk soil sample. A two-way MANOVA was used to compare mean % gravel, sand, and clay among sites and habitat. As described for the analysis of plant cover, this was followed by univariate statistics for each variable separately. All statistical analyses were conducted with

SYSTAT 10 (SYSTAT 2000). In all cases, transformations were used when bivariate relationships were nonlinear, or otherwise failed to meet regression assumptions.

RESULTS

Spatial Patterns in Vegetation Structure

Average canopy volume ranged from 14.7 m^3 in the uplands at site 5 to 201.1 m^3 in the riparian zone at site 5, and generally increased along both upland–riparian and upstream–downstream gradients (Table 1). Results from the two-way ANOVA with canopy volume showed no site effect ($F_{3,315} = 1.8$, $P = 0.146$), but did reveal significant habitat, and site by habitat effects ($F_{1,315} = 64.3$, $P < 0.001$, $F_{3,315} = 10.6$, $P < 0.001$, respectively). Multiple comparison tests show that average *P. velutina* canopy volume was greater in riparian zones when compared to adjacent uplands for sites 3, 4, and 5, but not site 2. Furthermore, average canopy volume varied among riparian zones ($F_{3,178} = 7.7$, $P < 0.001$); means at sites 2 and 3 were lower than those at sites 4 and 5 (Table 1). Results from the broader survey of riparian *P. velutina* canopy volume showed that average plant size increased with drainage area ($n = 13$, $r^2 = 0.82$, $P < 0.001$, Figure 2).

Table 1 Summary Statistics for Canopy Volume and Line-transect Data from Upland and Riparian Habitats at Sites 2–5

Site	Habitat	2	3	4	5
Canopy volume (m^3)	U	28.7 (5.3)	28.2 (2.6)	32.0 (5.4)	14.7 (1.6)
Canopy volume (m^3)	R	47.4 (5.2)^b	***72.2 (9.5)^b	***150.7 (18.0)^a	***201.1 (30.0)^a
Plant cover (%)	U	45.5 (1.7)	38.4 (2.0)	37.7 (4.8)	41.1 (1.5)
Plant cover (%)	R	*52.6 (1.5)^b	**52.8 (1.8)^b	*63.3 (4.3)^b	***77.8 (2.8)^a
P. velutina (%)	U	20.7 (9.3)	21.7 (5.0)	22.5 (11.7)	22.1 (5.6)
P. velutina (%)	R	*57.8 (7.0)^a	*63.0 (7.8)^a	*78.3 (7.7)^a	67.5 (16.3)^a
Patch #	U	38.3 (0.9)	39.0 (3.8)	24.3 (1.5)	35.0 (0.6)
Patch #	R	***20.0 (0.6)^b	**13.0 (1.2)^{ab}	*13.3 (2.0)^{ab}	***9.0 (2.5)^a

$*P < 0.05$, $** P < 0.01$, $*** P < 0.001$.

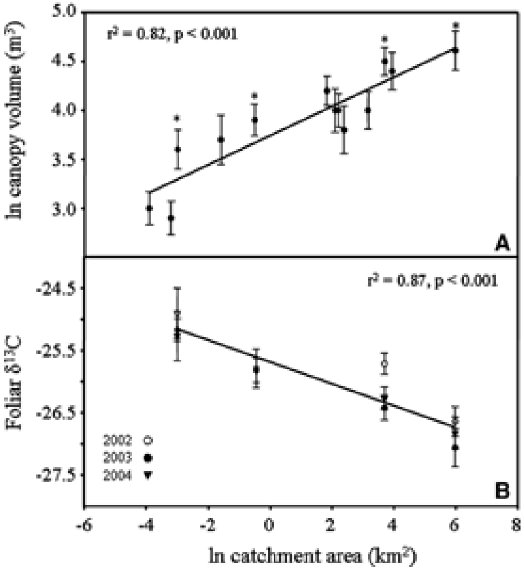

Figure 2 Relationships between riparian *P. velutina* canopy volume (m^3) (**A**) and foliar $\delta^{13}C$ (‰) (**B**) and catchment area (km^2). For (**A**), data are mean (± SE) for 13 streams of varying drainage area, *points with asterisks* represents sites also used in the intensive survey of plant and soil properties. For (**B**), data are mean (± SE) for surveys conducted in three consecutive years at four sites. *Lines* represent the best-fit least squared means regression equations.

Vegetation cover and the number of plant patches varied among upland and riparian habitats. Percent cover generally increased (37.7–77.8 %), and patch number decreased (39–9) along both upland–riparian and upstream–downstream gradients (Table 1). The percentage of plant cover comprised by *P. velutina* also varied among sites and ranged from 20.7 (site 2, upland) to 78.3 (site 4, riparian). Taken together, we found significant differences in plant cover variables among sites (Wilks $\Lambda = 0.10$, $F_{9,34} = 5.9$, $P < 0.0001$), habitats (Wilks $\Lambda = 0.05$, $F_{3,14} = 84.9$, $P < 0.0001$), as well as a significant site by habitat interaction term (Wilks $\Lambda = 0.10$, $F_{9,31} = 6.2$, $P < 0.0001$). Similarly, univariate tests showed that, analyzed individually, total plant cover and patch number both varied among sites and habitats, with significant site by habitat interaction terms ($F_{3,16} = 10.6$, $P = 0.001$; $F_{3,16} = 6.9$, $P = 0.001$, respectively). For all sites, we found that percent cover was greater, and patch number lower, in riparian versus upland habitats (Table 1). There were also significant differences in plant cover and patch number among riparian zones ($F_{3,8} = 17.9$, $P < 0.001$; $F_{3,8} = 6.8$, $P < 0.01$, respectively). Percent cover by *P. velutina* typically increased along upland–riparian gradients, but not among riparian zones adjacent to different-sized channels (Table 1).

Water Availability and Aboveground Productivity

Average foliar $\delta^{13}C$ in riparian terraces ranged from −24.9‰ at site 2 (2002) to −27.1‰ at site 5 (2003); values for upland trees (site 1) ranged from −24.3‰ (2002) to −24.7 ‰ (2003) (Table 2). Within years, $\delta^{13}C$ values differed among sites (2002: $F_{3,11} = 19.4$, $P < 0.0001$; 2003: $F_{4,39} = 32.4$, $P < 0.0001$; 2004: $F_{4,43} = 9.2$, $P < 0.0001$). Furthermore, using data for all years, foliar $\delta^{13}C$ decreased in riparian zones with ln catchment area ($r^2 = 0.87$, $P < 0.001$, Figure 2). Leaf litter production ranged from 21.4 to 187.3 g AFDM m^{-2} in 2003 and from 67.4 to 238.3 g AFDM m^{-2} in 2004, increasing both years with ln canopy volume ($r^2 = 0.79$, $P < 0.001$, and $r^2 = 0.74$, $P < 0.001$, 2003 and 2004, respectively, Figure 3A). The biomass of winter annuals varied from 76.0 to 428.3 g AFDM m^{-2} in 2003, and from 34.7 to 175.4 g AFDM m^{-2} in 2004, again, increasing with ln canopy volume both years ($r^2 = 0.76$, $P < 0.001$, and $r^2 = 0.89$, and $P < 0.001$, respectively, Figure 3B). We applied statistical relationships between canopy volume and litter and grass production to all upland trees from site 1 and riparian trees at sites 2–5, and estimated that total litter inputs (leaves + grass) beneath *P. velutina* ranged from 166.0 g m^{-2} y^{-1} (site 1) to 446.4 g m^{-2} y^{-1} (site 5) in 2003 and from 136.6 g m^{-2} y^{-1} (site 1) to 341.8 g m^{-2} y^{-1} (site 5) in 2004 (Table 3).

Table 2 Foliar δ^{13}(‰) Values for *P. velutina* in Upland (site 1) and Riparian (sites 2–5) Habitat

Year	**Site**				
	1*	**2**‡	**3**‡	**4**‡	**5**‡
2002	−24.4 (0.12)^{c}	−24.9 (0.4)^{bc}	NA	−25.7 (0.17)^{ab}	−26.6 (0.24)^{a}
2003	−24.3 (0.12)^{d}	−25.2 (0.18)^{c}	−25.8 (0.19)^{bc}	−26.4 (0.19)^{ab}	−27.1 (0.30)^{a}
2004	−24.7 (0.15)^{c}	25.3 (0.39)^{bc}	−25.7 (0.31)^{bc}	−26.3 (0.18)^{ab}	−26.8 (0.25)^{a}

Values are mean (± SE). Within years, values that share superscripts are not significantly different from each other.

*Data from upland P. velutina.

‡Data from riparian P. velutina.

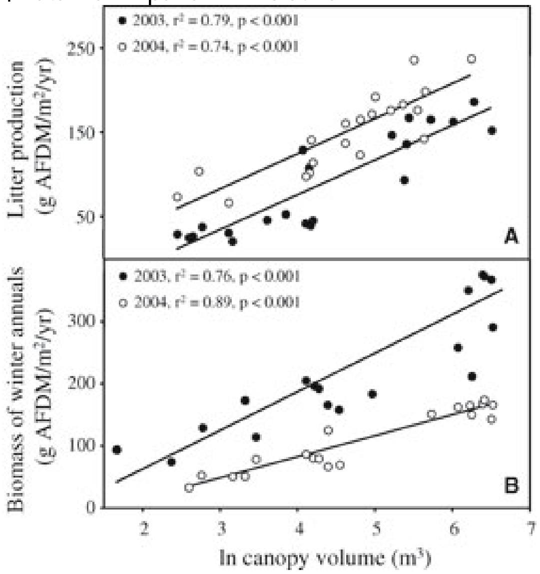

Figure 3 Relationship between ln canopy volume of *P. velutina* (m^3) and **A** leaf-litter production (g AFDM m^{-2} y^{-1}), and **B** biomass production of winter annuals (g AFDM m^{-2} y^{-1}). Each panel includes data from two consecutive growing seasons. *Lines* represent the best-fit least squared means regression equations.

Table 3 Estimates of Leaf and Annual Grass Inputs (g AFDM/m^2/yr) beneath *P. velutina* in Uplands (site 1), and Riparian Zones Adjacent to Increasingly Larger Streams (sites 2–5)

Season		**Site**				
		1*	**2**‡	**3**‡	**4**‡	**5**‡
2002–2003	Leaf	37.1 (3.4)	84.0 (5.0)	103.5 (5.5)	129.5 (6.7)	149.1 (5.6)
	Grass	128.9 (5.1)	199.2 (7.5)	228.9 (8.3)	267.9 (10.1)	297.3 (8.4)

Season		**Site**				
		1*	**2‡**	**3‡**	**4‡**	**5‡**
	Total	166.0 (8.5)	283.3 (11.9)	332.6 (13.8)	397.5 (16.7)	446.4 (14.0)
2003–2004	Leaf	85.3 (3.4)	132.6 (4.8)	152.7 (5.6)	178.9 (6.7)	198.7 (5.7)
	Grass	51.4 (2.8)	89.6 (3.9)	105.8 (4.5)	127.0 (5.4)	143.1 (4.6)
	Total	136.6 (6.2)	222.3 (8.9)	258.5 (10.1)	305.6 (12.2)	341.8 (12.0)

Values are mean (± SE), and obtained by applying equations that describe relationships between leaf and grass production and canopy volume to all trees surveyed at each site.
*Data for uplands.
‡Data for riparian habitat.

Average surface SOM concentration beneath *P. velutina* ranged from 5.4% at site 1, to 13.1% at site 4 (riparian); values in interplant spaces varied from 1.8% at site 5 (upland) to 5.3% at site 5 (riparian). SOM concentration was significantly greater beneath *P. velutina* when compared to interplant spaces for all sites and habitats except in the riparian zone of site 5 (Table 4). Furthermore, ln % SOM beneath *P. velutina* increased with ln canopy volume across a broad range of subcatchment sizes (Figure 4A–E). We found that scaling relationships between *P. velutina* canopy volume and SOM content remained statistically constant across five orders of magnitude in drainage area (Figure 4A–D; F scores range: 0.31–1.9, P values range: 0.17–0.58, when comparing slopes). When evaluated at the scale of the entire basin, however, the slope of the relationship between canopy volume and SOM storage decreased significantly ($F_{1,255} = 10.4$, $P = 0.001$, Figure 4E). Finally, we found that our measure of combustible OM successfully predicted patterns in total soil N, where: % N = 0.04 (% OM)–0.01 ($r^2 = 0.89$, $P < 0.001$).

Table 4 Estimates of % SOM for Plant and Interplant Spaces, and the Difference between These Patch types, for All sites and Habitats (U = upland, R = riparian)

Site	**Habitat**	**Plant**	**Inter-plant**	**Difference**
1	U	5.39 (0.3)*	2.15 (0.1)	3.2
	R	NA	NA	–
2	U	5.48 (0.5)*	2.47 (0.2)	3.0
	R	9.10 (0.6)*	2.35 (0.06)	6.8
3	U	6.10 (0.4)*	2.98 (0.1)	3.1
	R	12.51 (1.2)*	2.37 (0.2)	10.1
4	U	7.83 (0.3)*	4.65 (0.2)	3.2
	R	13.10 (1.1)*	3.8 (0.9)	9.3
5	U	5.47 (0.4)*	1.8 (0.2)	3.7
	R	7.12 (0.8)	5.30 (1.0)	NS

Asterisks indicate where mean % SOM beneath P. velutina was significantly greater than that from interplant spaces. In this case, P < 0.001 for all significant t tests.

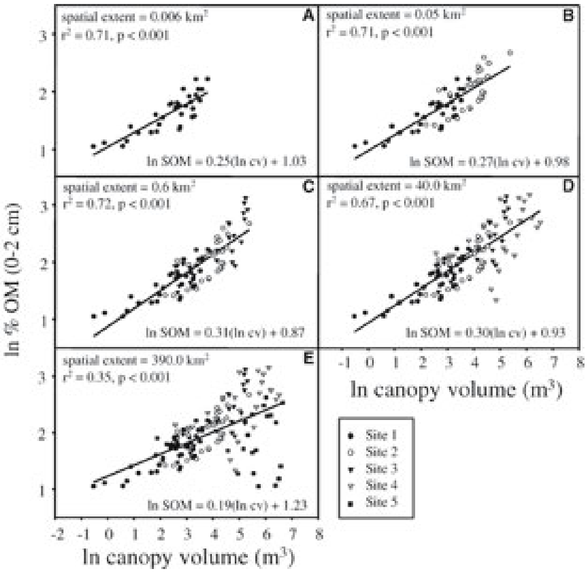

Figure 4 Scaling plots that show relationships between ln soil organic matter (% SOM) and ln *P. velutina* canopy volume (m^3) at five spatial scales. **A** shows data from site 1 only; consecutive panels add all points from the next largest catchment, and **E** includes all data points in the survey. *Regression lines* represent the equations for scaling relationships at each spatial extent; results from the ANCOVA indicate that slope of the line in **E** is significantly different than those in all other panels ($F_{1,255} = 9.8$, $P = 0.002$).

Soil particle-size distribution varied significantly among sites and habitats (Table 5). Percent gravel ranged from 6.4 (site 5, riparian) to 41.4 (site 3, upland), % sand from 33.5 (site 4, upland) to 71.0 (site 5, riparian), and % clay from 4.8 (site 5, upland) to 9.7 (site 4, upland). Using the three variables simultaneously, we found significant differences in particle-size composition among sites (Wilks $\Lambda = 0.075$, $F_{9,92} = 19.55$, $P < 0.001$), habitats (Wilks $\Lambda = 0.52$, $F_{3,38} = 11.6$, $P < 0.001$), as well as a site by habitat interaction (Wilks $\Lambda = 0.51$, $F_{9,92} = 3.2$, $P = 0.002$). Univariate analyses indicated that, analyzed separately, average % gravel, sand, and clay each varied among sites ($F_{3,40} = 20.3$, $P < 0.001$; $F_{3,40} = 36.0$, $P = 0.001$; $F_{3,40} = 7.05$, $P = 0.001$, respectively). Mean % gravel and sand also varied significantly among habitats ($F_{1,40} = 32.7$, $P < 0.001$; $F_{1,40} = 14.3$, $P = 0.001$, respectively). Only % gravel showed a significant site by habitat interaction ($F_{3,40} = 7.02$, $P = 0.001$). Relative to respective uplands, average % gravel was significantly lower in the riparian terrace of sites 4 and 5, and % sand was significantly greater in the riparian terrace of sites 3 and 5. There were also significant differences in mean % gravel and sand among riparian zones ($F_{3,24} = 17.9$, $P < 0.001$, $F_{3,24} = 27.4$, $P < 0.001$, respectively); here, % gravel was significantly lower in the terrace of site 5 when compared to all other sites. Similarly, average % sand was significantly greater in the riparian zone of site 5 when compared to all other terrace habitats.

Table 5 Percent Composition of Gravel, Sand, and Clay beneath *P. velutina* in Upland and Riparian habitats at sites 2–5

Site	Habitat	2	3	4	5
% Gravel	U	38.5 (2.4)	41.4 (2.3)	37.8 (2.5)	31.8 (2.8)
% Gravel	R	37.8 (1.8)^{c}	32.9 (3.8)^{cb}	*27.9 (2.2)^{b}	***6.4 (1.9)^{a}
% Sand	U	41.0 (2.2)	37.9 (2.4)	33.5 (2.2)	57.8 (2.7)

Site	Habitat	2	3	4	5
% Sand	R	42.5 (1.7)^b	*47.5 (2.3)^b	39.3 (3.3)^b	*71.0 (3.4)^a
% Clay	U	9.4 (0.6)	9.7 (1.0)	6.9 (0.6)	4.8 (0.5)
% Clay	R	8.2 (0.5)	8.3 (0.9)	9.2 (0.8)	6.5 (0.8)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

DISCUSSION

Landscape Patterns in Plant Cover and Aboveground Production

The drainage networks that dissect arid landscapes influence basin-scale pattern of vegetation structure and function. In the Sycamore Creek basin, we found that the size and cover of dominant riparian vegetation increased 4- and 1.5-fold, respectively, along a channel continuum. These downstream changes in vegetation size and cover in turn increased the disparity in plant structure between adjacent upland and riparian habitats. Because we do not have replication at the catchment level, caution should be used when attributing observed differences in plant characteristics to drainage area alone. Indeed, site-specific features acting independently of drainage size, such as geomorphic structure (for example, *Hupp 1992*), nutrient availability (for example, *Harner and Stanford 2003*), and disturbance (for example, *Stromberg and others 1991*) all likely interact to influence the dynamics of riparian vegetation at small spatial-scales. Results from the spatially extensive survey of riparian canopy volume, however, support the idea that at basin scales the channel network is an important organizer of plant structure in arid landscapes (*Caylor and others 2004*).

Results from the survey of foliar δ^{13}C suggest that longitudinal and lateral patterns in plant size and cover are the consequence of increased water availability adjacent to larger intermittent and perennial streams. In all years, foliar δ^{13}C of *P. velutina* decreased among riparian zones adjacent to streams of increasing size and hydrological permanence. The observed change in C isotope values, from approximately −24‰ in uplands to approximately −27‰ in the riparian zone site 5, likely reflects increases in stomatal conductance and discrimination of ^{13}C by plants adjacent to streams with greater duration of surface and subsurface flow, as well as an increased capacity to store water in near-channel alluvial sediments. Other studies in arid environments have shown that features of intermittent drainage networks can influence plant–water relations. For example, *Wainwright and others (2002)* found that δ^{13}C signatures for *Larrea tridentata* were significantly higher for upland individuals when compared to those growing in depositional areas of upland rills (beads), which proved to be locations of high water infiltration and storage. Observed patterns of δ^{13}C for *P. velutina* among riparian habitats in this study are also consistent with the results from *Snyder and Williams (2000)* and *Stromberg and others (1993)* who found that predawn leaf water potentials for the same species were significantly lower in desert uplands and along ephemeral and intermittent streams than near perennial streams in southern Arizona.

Differences in plant size and water availability influenced patterns of leaf litter and understory annual grass production, which increased from 2.3- to 4-fold from desert uplands to perennial riparian zones. Values for leaf production across the landscape were within the range of those reported for *P. glandulosa* in the Sonoran Desert of

California (30–188 g m^{-2} y^{-1}, Sharifi and others 1982). Grass biomass values were similar to those reported by Schade and others (2003) in a nearby drainage (150–325 g m^{-2} y^{-1}), and represented approximately 70 and 40% of the total litter production in 2003 and 2004, respectively. The observed range in total aboveground litter production (leaves + annual grasses) in this study corresponds well to that given by Martinez-Yrizar and others (1999) for upland (60 g m^{-2} y^{-1}) and arroyo (357 g m^{-2} y^{-1}) sites along a southern Sonoran desert drainage. Production numbers reported here also resemble those given by Ludwig (1987) and Austin and Sala (2002) for total aboveground net productivity in upland and lowland habitats in the Chihuahuan Desert (range: 30–592 g m^{-2} y^{-1}), and along an aridity gradient in Patagonia (range: 15.9–338.4 g m^{-2} y^{-1}), respectively.

Previous research in arid landscapes has shown that plant productivity can be augmented along ephemeral stream channels, when compared to surrounding uplands (for example, Ludwig 1987; Martinez-Yrizar and others 1999). Ludwig (1987) suggests that precipitation regimes dictate these spatial patterns: when rainfall is sufficient to generate runoff in the rill network, transmission losses from low-order channels infiltrate terrace soils, and riparian plant productivity is stimulated. In dry years, stream flow in rills is limited, and rates of productivity along channels are unlikely to differ from those in adjacent uplands. This runoff/runon model would likely apply across the range of drainage sizes at Sycamore Creek where stream flow is tied directly to precipitation (for example, sites 1–3). Surface and subsurface flow in high-order streams of larger drainages, however, is supported by discharge from upstream alluvial aquifers, persists long past individual precipitation events, and acts to further stimulate the productivity of riparian vegetation. Our results also suggest that plants able to access these more permanent groundwater stores are less sensitive to intra-annual variation in precipitation. Between 2002 and 2003, estimates of *P. velutina* litter production in the uplands increased by 2.3-fold, corresponding to an approximate doubling in annual precipitation in the Sycamore Creek basin (15.7 vs. 32.5 cm). For the same time interval, leaf production in the riparian zone of sites 4 and 5 increased by only 1.4- and 1.3-fold, respectively, suggesting that the availability of water at depth may effectively buffer climatically driven variation in productivity along more permanent stream channels.

We focused our efforts on a single, ubiquitous species so that we could ask questions about patterns of ecological function along landscape gradients using standardized response variables and metrics. Caution should be used, however, when extrapolating production estimates from a single species to a community that is (1) taxonomically and physiologically diverse, and (2) includes members that may respond to different aspects of the precipitation regime (for example, Ehleringer and others 1991; but also see Reynolds and others 1999). Our estimates of relative cover suggest this is particularly the case in the uplands, where *P. velutina* only represents about 20–25% of the total assemblage. The remaining members of this community include other deciduous shrubs that may behave similarly to *P. velutina* (for example, Palo Verde, *Cercidium microphyllum*), as well as evergreen shrubs (for example, Jojoba, *Sommondsia chinensis*) and several species of cacti (*Optuntia* sp.) that may have different production dynamics. In riparian zones, however, relative cover by *P. velutina* ranges from about 60 to 80% of the total plant assemblage, thus the dynamics of this species may effectively represent those of streamside habitats as a whole.

Spatial Context for Islands of Fertility

Variation in plant size and productivity, along lateral upland–riparian gradients, and among riparian zones of increasingly larger streams, influenced the storage of SOM and N in soils beneath *P. velutina*. We found that the concentration of material in soils beneath plants increased with plant size (*Ludwig and others 2000*); these plant–soil scaling relationships were statistically similar across five orders of magnitude in catchment area. This represents a spatially extensive scaling domain (sensu *Wiens 1989*) within which material accumulation beneath *P. velutina* in both upland and riparian habitats increases as a constant function of patch size. Although *Ludwig and others (2000)* base predicted relationships between patch size and soil storage on the capture of material in runoff, in this study the concentration of soil resources beneath *P. velutina* is likely driven by local productivity (litter, roots, annual grasses, and so on), a finding consistent with research on isolated deciduous trees and shrubs in other arid and semiarid ecosystems (*Belsky and others 1993*; *Facelli and Brock 2000*). One consequence of increased material storage beneath larger plants is that the extent of fertility island development (that is, relative to interplant spaces) increases along both upland-riparian and upstream-downstream gradients. These results support the idea that fertility islands can spatial context (*Schade and Hobbie 2005*, in press); in this case, patterns of resource accumulation within this scaling domain reflect a landscape gradient in aboveground productivity.

Although material concentrated in soils beneath *P. velutina* may derive from local plant and grass production, mechanisms driving relationships between plant size and SOM concentration are likely to change with catchment size. In small upland catchments (for example, site 1), where plant size and productivity are unlikely to vary with proximity to channels, plant–soil scaling relationships likely arise from differences in the date of establishment, with older, larger individuals accumulating more resources in underlying soils (*Facelli and Brock 2000*). In larger subcatchments, stream channels provide a water source that stimulates the growth of riparian vegetation, and within-site relationships between SOM concentration and canopy volume likely reflect these lateral gradients in litter and grass production. With further increases in drainage area, longitudinal changes in SOM concentration with plant size correspond to downstream gradients in productivity of riparian plants that result from greater hydrologic permanence.

At the scale of the entire Sycamore Creek basin, we observed a shift in the statistical relationship between plant size and SOM concentration in underlying soils. Specifically, this scale-break occurs because SOM concentration beneath *P. velutina* in the riparian terrace of the perennial stream was lower than expected, given plant size and productivity. In addition, this was the only location where we found no significant differences in % SOM between plant and interplant spaces. These results suggest that, at the scale of the entire Sycamore Creek basin, additional processes emerge to alter the fate of detritus and the spatial pattern of material storage in soils. One potential explanation is that SOM turnover via biotic processes increases beneath trees in the riparian zone of site 5, when compared to other sites and patches. However, rates of litter decomposition and CO_2 flux from surface-soils (0–2 cm) at this site do not support this hypothesis (R.A. Sponseller, unpublished data). We argue that the scale-break is more likely the consequence of flooding in the riparian zone of site 5 that (1) removes and/or buries surface litter and SOM that would otherwise accumulate beneath vegetation (*Steiger and others 2001*), and (2) acts to homogenize the distribution of soil resources across terrace habitats. This hypothesis is supported by sediment particle size data, which show a dramatic reduction in percent gravel, and corresponding increase in percent sand, in the riparian zone of site 5, suggesting an abrupt increase in fluvial deposition at this site relative to riparian zones of smaller streams.

Riparian zones may act as sources or sinks for fluvial sediments, although deposition and sediment accrual typically outweigh erosion and sediment loss (*Trimble and Knox 1984*; *Lowrance and others 1988*; reviewed by *Malanson 1993*). Moreover, *Graf (1985)* suggests that, in arid catchments, phreatophytes growing along stream margins tend to augment sediment deposition onto riparian terraces. Our results indicate that depositional processes are indeed important in the riparian zone of Sycamore Creek, and that these are likely to have implications for the fate of riparian detritus, and the trajectory of soil development beneath plants. Results from the survey of SOM and texture, however, suggest that fluvial processes adjacent to small and medium size streams used in this study do not have important consequences for soil structure. Flooding appeared to act as an important determinant of soil properties only in the riparian zone of the largest stream considered here. We hypothesize that the role of over-bank flooding as a driver of soil features in riparian zones emerges at some threshold in drainage size. This argument is consistent with principles of catchment hydrology that suggest increases in drainage area, from small to midsized catchments, correspond to a greater frequency and severity of floods and flood-associated disturbance (*Graf 1988*; *Leopold 1994*; *Bendix 1997*; *Dodds and others 2004*).

Conclusion: Stream Networks and Scale Dependencies

Our results support the hypothesis that, at basin scales, water availability (and stress) is the major driver of vegetation pattern in arid landscapes; these plant-water interactions are mediated in space by stream networks (*Caylor and others 2004*). In the Sycamore Creek catchment, we found that plant size, cover, and aboveground productivity increases along both upland–riparian and upstream–downstream gradients. Because differences in stream size have profound implications for the ecology of adjacent terrestrial habitats, the relative number and lengths of different-sized channels may influence functional properties (for example, net primary productivity) of the broader catchment. In other words, the geomorphic structure of drainage basins (for example, distribution of sizes, shape, slope, parent material), and the resulting drainage density and configuration of channel networks become significant landscape features to consider when evaluating the importance of arid streams to ecological patterns and processes at broad spatial scales (*Benda and others 2004*).

Results also show that patterns of plant size and productivity among upland and riparian habitats influence the development of fertility islands in arid landscapes. Moreover, the role of streams in arid landscapes, with respect to the accumulation of material beneath plants, shifts with drainage size. From small to midsized catchments, streams act to stimulate productivity and promote material accumulation beneath plants. At some threshold in drainage area the frequency and magnitude of flooding acts to further influence the fate of riparian detritus—altering plant–soil scaling relationships and the spatial pattern of resource storage in soils. Thus, the accumulation of OM and nutrients beneath vegetation is driven by water as both a resource for plant growth and detritus production, and an agent of disturbance that buries, removes, and redistributes materials during floods. These contrasting modes of action are distributed in space by stream networks, and operate across a different range of catchment sizes.

Acknowledgements This work was supported by grants from the National Science Foundation (NSF DEB 0075650, to SGF), and the Environmental Protection Agency Science to Achieve Results (STAR) Program (# 91613101, to RAS). Sam Norlin, Jim Heffernan, and John Schade provided assistance in the field and/or lab. Comments by David Lewis, Jim Heffernan, and two anonymous reviewers improved the quality of this manuscript.

References

Austin AT, Sala OE. 2002. Carbon and nitrogen dynamics across a natural precipitation gradient in Patagonia, Argentina. J Veg Sci 13:351–60

Belsky AJ, Mwonga SM, Amundson RG, Duxbury JM, Ali AR. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low rainfall savannas. J Appl Ecol 30:143–55

Benda L, Poff NL, Miller D, Dunne T, Reeves G, Pess G, Pollock M. 2004. The network dynamics hypothesis: how channel networks structure riverine habitats. BioScience 54:413–27

Bendix J. 1997. Flood disturbance and the distribution of riparian species diversity. Geographical Rev 87:468–83

Campbell CJ, Green W. 1968. Perpetual succession of stream-channel vegetation in a semi-arid region. J Ariz Acad Sci 5:86–98

Caylor KK, Scanlon TM, Rodriguez-Iturbe I. 2004. Feasible optimality of vegetation patterns in river basins. Geophys Res Lett 31(31):LI34502

Clinton SM, Grimm NB, Fisher SG. 1996. Response of hyporheic invertebrate assemblage to drying disturbance in a desert stream. J N Am Benthol Soc 15:700–12

Crawford CS, Gosz JR. 1982. Desert ecosystems: their resources in space and time. Environ Conserv 9:181–95

Dodds WK, Gido K, Whiles MR, Fritz KM, Mathews WJ. 2004. Life on the edge: the ecology of Great Plains prairie streams. Bioscience 54:205–15

Ehleringer JR, Cooper TA. 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76:562–66

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991. Differential utilization of summer rains by desert plants. Oecologia 88:430–34

Facelli J, Brock DJ. 2000. Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of south Australia. Ecography 23:479–91

Fisher SG, Welter J, Schade J, Henry J. 2001. Landscape challenges to ecosystem thinking: creative flood and drought in the American Southwest. In: Gili JM, Pretus JL, Packard TT, Eds. A marine science odyssey into the 21st century. Scienta Marina 65(2):181–92

Fisher SG, Sponseller RA, Heffernan JB. 2004. Horizons in stream biogeochemistry: flowpaths to progress. Ecology 85:2369–79

Graf WL. 1985. The Colorado River: instability and basin management. Washington D.C.: American Association of Geographers

Graf WL. 1988. Fluvial processes in dryland rivers. Berlin Heidelberg New York: Springer

Harner MJ, Stanford JA. 2003. Differences in cottonwood growth between a losing and gaining reach of an alluvial floodplain. Ecology 84:1453–58

Hupp CR. 1992. Riparian vegetation patterns following channelization: a geomorphic perspective. Ecology 73:1209–26

Hynes HBN. 1975. The stream and its valley. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 19:1–15

Khazaei E, Spink AEF, Warner JW. 2003. A catchment water balance model for estimating groundwater recharge in arid and semiarid regions of south-east Iran. Hydrogeol J 11:333–42

Leopold L. 1994. A view of the river. Cambridge (MA): Harvard University Press. p 298

Lowrance R, McIntyre S, Lance C. 1988. Erosion and deposition in a forest/field system estimated using cesium-137 activity. J Soil Water Conserv 43:195–99

Ludwig JA. 1987. Primary productivity in arid lands: myths and realities. J Arid Environ 13:1–7

Ludwig JA, Wiens JA, Tongway DJ. 2000. A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. Ecosystems 3:84–97

Malanson GP. 1993. Riparian landscapes. Cambridge (UK): University Press. p 293

Martinez-Yrizar A, Nunez S, Miranda H, Burquez A. 1999. Temporal and spatial variation of litter production in Sonoran Desert communities. Plant Ecol 145:37–48

McAuliffe JR. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert bajadas. Ecol Monogr 64:111–48

Mueller-Bombios D, Ellenberg H. 1974. Aims and methods of vegetation ecology. New York (NY): Wiley. p 547

Noy-Meir I. 1973 Desert ecosystems: enviornment and producers. Annu Rev Ecol Syst 4:25–52

Parsons AJ, Wainwright J, Stone PM, Abrahams AD. 1999. Transmission losses in rills on dryland hillslopes. Hydrol Processes 13:2897–905

Power ME, Dietrich WE. 2002. Food webs in river networks. Ecol Rese 17:451–71

Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:69–106

Schade JD, Sponseller RA, Collins SL, Stiles A. 2003. The influence of Mesquite canopies on understory vegetation: effects of landscape position. J Veg Sci 14:743–50

Schade JD, Hobbie SE. 2005. Spatial and temporal variation in islands of fertility in the Sonoran Desert. Biogeochemistry 73:541–553

Schlesinger WH, Jones CS. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Bot Gaz 145:116–24

Schlesinger WH, Raikes JA, Hartley AE, Cross AF. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364–74

Schlesinger WH, Pilmanis A. 1998. Plant–soil interactions in deserts. Biogoechemistry

42:169–87

Sharifi MR, Nilsen ET, Rundel PW. 1982. Biomass and net primary production of *Prosopis glandulosa* (Fabaceae) in the Sonoran Desert of California. Am J Bot 69:760–67

Snyder KA, Williams DG. 2000. Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. Agric Forest Meteorol 105:227–40

Stanley EH. 1993. Drying disturbance and stability in a desert stream ecosystem. Dissertation, Arizona State University

Stanley EH, Fisher SG, Grimm NB. 1997. Ecosystem expansion and contraction in streams. Bioscience 47:427–35

Steiger J, Gurnell AM, Petts GE. 2001. Sediment deposition along the channel margins of a reach of the Middle River Severn, UK. Regul Rivers Res Manage 17:443–60

Stewart GR, Turnbull MH, Schmidt S, Erskine PD. 1995. ^{13}C Natural abundance in plant communities along a rainfall gradient: a biological integrator of water availability. Aust J Plant Physiol 22:51–55

Stromberg JC, Patten DT, Richter BD. 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers 2:221–35

Stromberg JC, Wilkins SD, Tress JA. 1993. Vegetation-hydrology models: implications for management of *Prosopis velutina* (velvet mesquite) riparian ecosystems. Ecol Appl 3:307–14

Thomsen BW, Schumann HH. 1968. The Sycamore Creek watershed, Maricopa County, Arizona. Washington, D.C.: Water Supply Paper 1861, United States Geological Survey

Thorne MS, Skinner QD, Smith MA, Rogers JD, Laylock WA, Cerekci SA. 2002. Evaluation of a technique for measuring canopy volume of shrubs. J Range Manage 55:235–41

Trimble SW, Knox JC. 1984. Comment on “Erosion, redeposition, and delivery of sediment to Midwestern streams” by D.C. Wilkin and S.J. Hebel. Water Resour Res 20:1317–18

Virginia RA, Jarell WM. 1983. Soil properties in a mesquite-dominated Sonoran desert ecosystem. Soil Sci Soc Am J 47:138–44

Wainwright J, Parsons AJ, Schlesinger WH, Abrahams AD. 2002. Hydrology-vegetation interactions in areas of discontinuous flow on a semi-arid bajada, Southern New Mexico. J Arid Environ 51:319–38

Welter JR. 2004. Nitrogen transport and processing in the intermittent drainage network: linking terrestrial and aquatic ecosystems. Dissertation, Arizona State University

Whitford WG. 2002. Ecology of desert systems. London (UK): Academic. p 343

Wiens JA. 1989. Spatial scaling in ecology. Funct Ecol 3:385–97

Yavitt JB, Smith L. 1983. Spatial patterns of mesquite and associated herbaceous species in an Arizona desert grassland. Am Midl Nat 109:98–3