Single-tree influences on soil properties in agroforestry: lessons from natural forest and savanna ecosystems

C. C. RHOADES
Institute of Ecology, University of Georgia, Athens, GA 30602, USA

Abstract. Climate, organisms, topographic relief, and parent material interacting through time are the dominant factors that control processes of soil formation and determine soil properties. In both forest and savanna ecosystems, trees affect soil properties through several pathways. Trees alter inputs to the soil system by increasing capture of wetfall and dryfall and by adding to soil N via N_2-fixation. They affect the morphology and chemical conditions of the soil as a result of the characteristics of above- and below-ground litter inputs. The chemical and physical nature of leaf, bark, branch, and roots alter decomposition and nutrient availability via controls on soil water and the soil fauna involved in litter breakdown. Extensive lateral root systems scavenge soil nutrients and redistribute them beneath tree canopies. In general, trees represent both conduits through which nutrients cycle and sites for the accumulation of nutrients within a landscape. From an ecological perspective, the soil patches found beneath tree canopies are important local and regional nutrient reserves that influence community structure and ecosystem function. Understanding species-specific differences in tree-soil interactions has important and immediate interest to farmers and agroforesters concerned with maintaining or increasing site productivity. Lessons from natural plant-soil systems provide a guide for predicting the direction and magnitude of tree influences on soil in agroforestry settings. The challenge for agroforesters is to determine under what conditions positive tree effects will accumulate simultaneously within active farming systems and which require rotation of cropping and forest fallows.

Introduction

Soil is the complex expression of physical, chemical and biological processes occurring across spatial and temporal scales. Soil properties at a specific location integrate and reflect both past and present conditions. Based on work of Dokuchaev in the late 1800's and Hildegard in the early 1900's, Jenny (1941) described a set of factors that control processes of soil formation and determine the state of the soil: climate, organizms, topographic relief, parent material, and time. Further development of the 'state factor approach' (Jenny, 1980) broadened the list of influences to include anthropogenic effects such as tillage or soil contamination. The main premise of this approach is that the properties measured within a particular soil profile result from the unique combination of the state factors. For example, as soil factors vary along precipitation or contamination gradients, or across a topographic sequence, soil conditions vary concomitantly. The relative importance of the different factors depends on the particular scale of interest (Robertson and Gross, 1994).

Climate and parent material are considered the most important determinants of soil conditions on a global or regional scale (Birkeland, 1984). At local or landscape levels, soils are more strongly influenced by changes in topography, microclimatic variation, soil fauna and vegetation.

At the forest stand or individual stem scale, trees alter chemical, physical and biological soil properties through their impact on energy and nutrients fluxes into, out of, and within ecosystems. In agroforestry, the premise is that soil improvement generated by trees can be exploited within production systems, either simultaneously, as in intercropping, or sequentially, as in rotational fallow systems. Several mechanisms for soil improvement by trees within agroforestry systems have been proposed and studied (Nair, 1984; Young, 1989; Sanchez, 1995; Breman and Kessler, 1995). The objectives of this review are to highlight research on tree effects in natural forest, savanna and agroforestry systems and to compare tree influence patterns and control mechanisms in natural systems, with examples from agroforestry systems.

Forest soil: stand level vegetation controls of soil properties

In temperate forest ecosystems, the first modern soil scientists and foresters began recording the effects of forest vegetation on soil morphology and fertility at the stand level. Dokuchaev (1900, cited in Remezov and Pogrebnyak, 1965) reported that '. . . different forest vegetation gives rise to different soil' and that local peasants '. . . are extremely conscious of the differences existing between soils formerly under linden, under oak, or under conifers'. Forest-soil associations such as 'pinery soil', 'hickory bottom', and 'white oak land' (Gast, 1937) were common labels given by European settlers describing North American forest soils. In Europe, Müller (1889, cited in Gast, 1937) differentiated distinct types of forest floor. Mull humus, usually found beneath broad-leaved trees, was associated with nutrient-rich, neutral-reaction soils, promoting thorough mixing of organic matter by worms; mor humus, commonly found beneath conifers, were relatively nutrient poor, acidic, and confined to the surface of the mineral soil.

Early research on the effects of tree species on soil began by characterizing forest floor and mineral soil properties beneath different forest types. In Minnesota, Alway and coworkers (1933) found species differences in the chemical composition of the forest floor layers and fresh litter, despite similar mineral soil conditions. For example, calcium and nitrogen content were 5 and 1.75 times higher in hardwood versus conifer forest floor. The pH of newly fallen litter was similar for all species, but pH was lower in the partially decomposed and humus layers of the pines. In forest plantations in the UK, Ovington (1954) found that a characteristic forest floor developed under a given species across a range of sites. He found thick mor humus under conifer and thin mull humus beneath hardwoods. He further differentiated mor humus into that found under pine (*P. nigra*) and spruce (*Picea abies*) from

that found beneath Douglas-fir (*Pseudotsuga taxifolia*). Ovington regarded the broad mor and mull categories as indicators of site fertility and the accumulation of C, N and other nutrients in the mor layer as a nutrient sink. Based on the objective of the British Forestry Commission to regenerate soils by afforestation, conifer stands were less favored for the task than hardwoods.

Resource managers concerned with the effects of forest conversion on soil productivity expanded their studies to include the mineral soil underlying various species. At Harvard forest, block plantations of various tree species were established to track soil changes in abandoned New England farmland (Gast, 1937). In general, research showed increases in organic matter in topsoil beneath hardwood species and decreases beneath pine. In Britain, Ovington (1956) compared hardwood and conifer forest plantations with unforested adjacent areas and reported increased soil carbon, nitrogen, and organic matter in 33 out of 36 plantations. He found considerable variation between species and was unable to draw a clear distinction between the influence of hardwoods and conifers on soil organic. He did however, find the highest soil N levels in native oak forest and the lowest in spruce plantations.

Recent research on forest vegetation effects on soil takes advantage of long-term data collected in replicated plots to quantify progressive soil change throughout the course of stand development (Challinor, 1968; Binkley and Valentine, 1991; Fisher, 1995). These studies support evidence of species differences and further emphasize that species effects cannot be aggregated into hardwood versus conifer effects. Challinor (1968) examined 30-year-old Yale forest plots in Connecticut and found that soil beneath Norway spruce (*Picea abies*) had higher levels of organic matter, N, K, and Ca than soil beneath red oak (*Quercus rubra*), white pine (*P. strobus*), and red pine (*P. resinosa*). The soil under pine species had higher infiltration rates than oak, spruce, or mixed hardwood stands. Binkley and Valentine (1991) returned to the Yale forest plantations 22 years after Challinor. They found that soil in green ash (*Fraxinus pennsylvanica*) plots contained more than twice the amount of Ca and Mg found in spruce plots. Spruce plots had higher levels of exchangeable acidity and aluminum and lower soil pH. They attributed the species effects on soil pH to differences in acid strengths and to depletion of soil base cations by spruce. These stand-level studies demonstrate the influence of uniform forest vegetation on soil conditions.

Mixed species forests: mosaics of soil properties

In dense, single-species forest stands, the effect of forest vegetation may be fairly uniform (Riha et al., 1986), but in mixed species stands an individual tree may affect soil conditions differently than surrounding vegetation. The outcome is a mosaic of soil conditions across the stand. Beneath a forest canopy, soil heterogeneity results from both the spatial and temporal effects of trees; for some soil properties, the effect on the soil template may extend

well beyond the life of the individual tree. Beneath Kauri (*Agathis australis*) canopies in New Zealand for example, intense local podzolization translocates organic material and clay to lower soil horizons, forming a lasting, visibly-bleached soil profile (Crocker, 1952). These tree-influence zones generate nutrient resource patches that can influence seedling establishment and under-story vegetation.

The idea of soil nutrient mosaics within forests was advanced by Zinke (Zinke, 1962; Zinke and Crocker, 1962). He measured radial variation in soil properties surrounding trees in northern California and described forest soils as the 'summation of individual influence patterns' (Zinke, 1962). He also found a general trend of increased soil pH, and decreased N and base cations with distance from *Pinus contorta* trunks (Table 1, Figure 1). After comparing an assortment of species, Zinke proposed that deposition patterns of bark and litter chemistry produce concentric rings of tree influence. Acidic stemflow and base element-poor bark dominate soil inputs adjacent to the bole, while base and N-rich leaf and branch litter form a fertile zone near the edge of the tree canopy. The radial extent of tree influence related to tree size, and the symmetric pattern was modified by slope and prevailing wind direction (Figure 1). For 1,500 to 3,000 year-old giant sequoias (*Sequoia gigantea*) with trunk diameters ranging from 6 to 9 m, Zinke and Crocker (1962) identified the zone of maximum tree influence at about 3 m from the bole.

In forest systems, throughfall and stemflow fluxes contribute to nutrient patterns beneath tree canopies by washing or leaching nutrients from leaf surfaces and concentrating them at the base of the trunk. Water soluble elements in stemflow are derived from dust and insect remains washed from the canopy and trunk. Chemical and textural properties of tree bark modify precipitation inputs and regulate stemflow quantity. Gersper and Holowaychuk (1971) examined 'biohydrologic factors' of soil formation by comparing
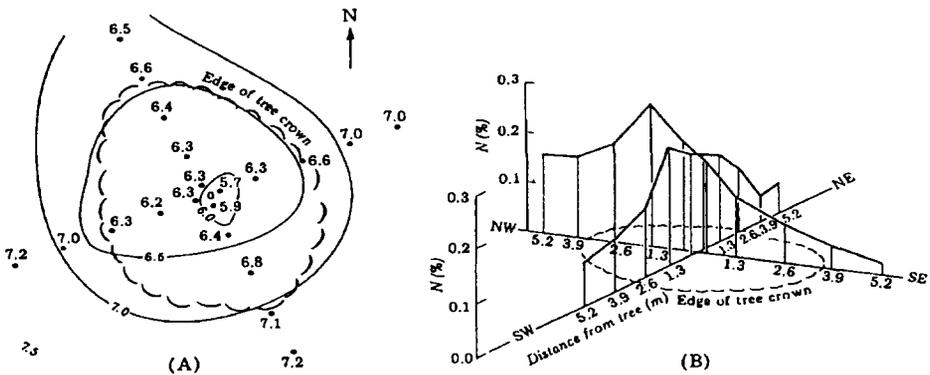

Figure 1. Pattern of soil pH (A) and percent total soil N (B) associated with *Pinus contorta* in northern California, USA. High N on NW axis is the effect of prevailing winds. *Source*: Zinke (1962).

subcanopy soil chemistry with incident stemflow beneath a variety of hard-woods (Table 4). Stemflow beneath American beech (*Fagus grandifolia*), white oak (*Quercus alba*), and sugar maple (*Acer saccharum*) was highly enriched in C, K, Ca, Na, Mg, and P. Where stemflow volume was high, soils had higher organic C and K, and had lower soil pH close to trunks. Smooth bark species such as American beech and red oak have greater stemflow volume and more distinct tree influence patterns than sugar maple, pignut hickory (*Carya glabra*) or white oak. Conversely, rough bark species generate more acidic stemflow than smooth bark species (Mina, 1967). In drier ecosystems where stemflow volume is lower, elements leaching from tree bark and canopy can generate tree effects. In an oak stand in France, Beniamino and coworkers (1991) found a soil acidity pattern beneath tree crowns similar to that reported by Zinke (1962). In these stands, where stemflow comprised only 0.62% of incident rainfall, acidification was attributed to slow diffusion of water soluble substances through the canopy and down the tree trunk.

Regional soil heterogeneity may result from processes occurring beneath the canopies of individual trees. In British Columbia, Crampton (1984) hypothesized that the high degree of local variability in soils may be the lasting impression of soil gleying beneath trees. Due to the architecture of hemlock (*Tsuga canadensis*) and cedar (*Thuja plicata*) canopies, rainwater is shed at the edge of the canopy; little precipitation penetrates the canopy and collects as stemflow. Soil at the canopy perimeter is frequently saturated, and mottling caused by reduction and transport of Fe is most pronounced in that zone (Table 1). Crampton noted that morphologic alteration was greatest under large trees, indicating that processes contributing to gleying were cumulative over the life of the tree.

Tree effects may vary across a landscape or be modified by understory vegetation. Boettcher and Kalisz (1990, 1991) looked at soil nutrient mosaics in the mountains of Kentucky (Table 1). Comparing tulip-poplar (*Liriodendron tulipifera*) and hemlock (*Tsuga canadensis*) they found that soil pH and mineralizable N were consistently higher under tulip-poplar regardless of topographic position or understory vegetation. Stands supporting *Rhododendron maximum* understories had lower pH and earthworm densities and showed little cation accumulation below the crowns of either overstory species. In the absence of rhododendron, earthworm densities and soil cations were higher under tulip-poplar.

Within a given species, genotypic or gender-specific variation may contribute to tree effects on soil properties. In Costa Rican lowland tropical rainforest, Rhoades et al. (1994) measured higher soil P associated with the dioecious tree *Simarouba amara*. Beneath female *S. amara* crowns, labile inorganic and organic soil P were higher than below male crowns or in surrounding forest. Gender differences may have resulted from increased P cycling in fruit or litter or differences in P transformations beneath female trees.

Table 1. Single-tree influences on soil properties in forest ecosystems

Site description/Source	Tree species	Soil property	Under canopy	Edge of canopy	Beyond canopy
California, USA	*Pseudotsuga menziesii*	Total N (%)	0.14–0.21	0.17–0.29	0.12–0.22
various sites	*Pinus ponderosa*	CEC (cmol$_c$ kg^{-1}	12–26	15–30	12–22
(Zinke, 1962)	*Libocedrus decurrens*	Ca+Mg+K+Na (cmol$_c$ kg^{-1})	5–25	8–35	14–24
		pH	4.9–6.1	5.1–6.8	5.5–6.9
California, USA	*Sequoia gigantea*	Total C (%)	8.47	5.46	4.06
Sierra Nevada mountains		Total N (%)	0.323	0.212	0.189
(Zinke and Crocker, 1962)		C/N	26.3	25	23
		pH	6.5	6.6	6.4
		Bulk density	0.6	0.86	0.86
British Colombia, Canada	*Tsuga heterophylla*	Mottling	2 mm dia	> 5 mm dia	–
coastal rainforest	*Thuja plicata*		reddish gray	yellowish red	–
(Crampton, 1984)		pH			
		A Horizon	4.9	5.4	–
		B Horizon	5.9	6.1	–

			LT	TC	LT	TC
			with rhododendron		without rhododendron	
Kentucky, USA	*Liriodendron tulipifera* (LT)	pH	4.7+	4.5	5.6**	5.0
Appalachian mountains	*Tsuga canadensis* (TC)	Mineralizable N (g kg^{-1})	0.110+	0.092	0.220+	0.150
temperate mixed mesophytic		Ca (cmol$_c$ kg^{-1})	2.2	2.3	5.5+	3.4
(Boettcher and Kalisz, 1990)		mg (cmol$_c$ kg^{-1})	0.5	0.4	0.9**	0.4
Significance levels:		K (cmol$_c$ kg^{-1})	0.2	0.2	0.3**	0.2
0.1(+), 0.05(*), and 0.01(**)		Forest floor mass (g m^{-2})	1515	1606	859**	1474

			Under tree canopies		Beyond	
			Females	Males	canopy	
La Selva, Costa Rica	*Simarouba amara*	Resin P	2.93 a	1.61 ab	1.13 b	
Lowland rainforest		Bicarbonate P				
(Rhoades et al., 1994)		Inorganic	3.14 a	2.47 ab	2.14 b	
Within a row, means		Organic	15.47 a	11.32 b	12.09 b	
followed by the same letter						
are not significantly						
different at $P = 0.05$						

Tree Savannas: islands of soil fertility

In semi-arid and arid regions, sparse water and frequent fire limit tree density and produce widely-spaced gallery forests or tree savannas. These ecosystems, where isolated trees are found within a grass matrix, offer a unique opportunity to quantify single-tree effects on soil resources and understory vegetation. The scattered trees represent islands within the surrounding landscapes, where differences in aboveground vegetative structure and longevity form corresponding below-ground patches in soil resources. Improved soil and microclimatic conditions beneath the canopies of isolated trees often provide visible benefit to subcanopy vegetation, giving rise to productive 'fertile islands' (Figure 2; Charley and West, 1975; Klemmedson and Barth, 1975). Modified microclimatic and nutrient conditions associated with the structural discontinuity of isolated savanna trees have been equated to the conditions found in forest gaps (Belsky and Canham, 1994). In contrast to forest gaps, however, the effect of the tree patch begins and grows in tandem with the tree rather than forming when a tree dies.

Improved soil nutrient and water conditions beneath isolated trees have been recorded in savanna ecosystems in Africa (Bernhard-Reversat, 1982; Weltzin and Coughenour, 1990; Belsky et al., 1993), Central and South America (Kellman, 1979; Garcia-Miragaya, 1994) and North America
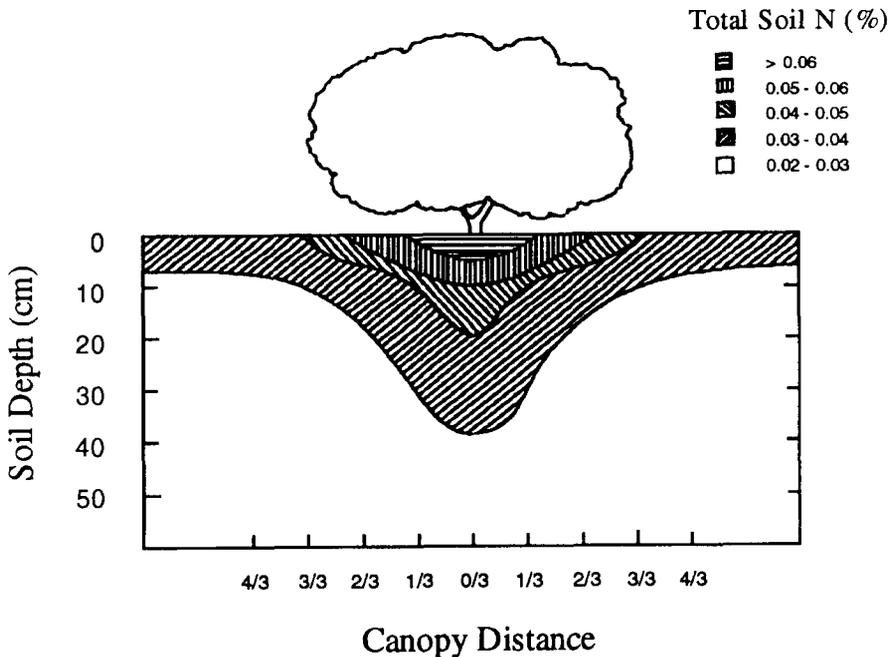

Figure 2. Nutrient isolines for total N% beneath isolated tree within a desert ecosystem in the south-western USA. Source: Klemmedson and Barth (1975).

(Tiedemann and Klemmedson, 1973a; Charley and West, 1975; Virginia, 1986; Everett et al., 1986; Klemmedson and Wienhold, 1992; Jackson et al., 1990; Table 2). The typical pattern near isolated trees is exemplified by the leguminous tree mesquite (*Prosopis juliflora*) which increases organic matter, total N, S, K and soluble salts at the soil surface (Tiedemann and Klemmedson, 1973a). Mesquite roots extend both deep into the soil profile and also over 10 m laterally where they nodulate and symbiotically fix nitrogen (Virginia, 1986). Improved nutrient content at the soil surface is attributed to redistribution of soil nutrients from both deep beneath and beyond the edge of mesquite canopies. Nutrient redistribution by extensive root systems (Figure 3) to surface soils results in increased abundance and production of understory perennial grasses beneath mesquite (Tiedemann and Klemmedson, 1973b), but may decrease grass production beyond the canopies (Paulsen, 1950). Comparing relative yields of understory grass planted in mesquite and non-mesquite soil, Tiedemann and Klemmedson (1973a) found that plants grown in non-mesquite soil were more limited by N, P, K, or S availability than those grown in mesquite soil. By experimentally maintaining optimal soil water levels they concluded that higher grass biomass production in mesquite soil was due to soil nutrient status rather than water relations.

Compared to zones of higher rainfall, where nutrients are leached deep into the soil profile, enrichment beneath trees in dryland regions is restricted to a thin band at the soil surface. The boundary of nutrient patches is less distinct here than in closed-canopy forest because the soil surface is exposed to eolian mixing and transport of litter and soil. Also, reduced wind velocity below tree crowns may settle airborne particles into soil mounds at the base of trees (Charley and West, 1975). This represents another form of redistribution of organic and inorganic nutrients from across the landscape to focal points beneath tree canopies.

Differences in soil influence beneath tree species relate both to nutrients recycled in litter and those captured by tree canopies. Leaf nutrient concentration, degree of nutrient reabsorption prior to leaf abscision, and litterfall mass determine the amount of nutrients recycled in litter (Vitousek and Sanford, 1986). The chemical quality of litter inputs then regulate organic matter decomposition and the formation of stable and labile soil organic matter pools (Parton et al., 1988). Species differences in N, P and lignin tissue concentrations explained greater soil nutrient buildup beneath a variety of savanna tree species in Venezuela (Garcia-Miragaya, 1994). Species with higher tissue C/N and C/P ratios and more lignin accumulated more soil organic matter. In the humid savannas of Belize, Kellman (1979) found that soil cation concentrations beneath clumps of certain tree species approached levels present in nearby rainforest (Table 2). *Clethra* sp. increased Ca, Mg and K by 50, 19, and 5% over savanna levels. Cations increased beneath *Quercus* and *Miconia* by only 2.4 to 8%. Of the trees studied, none had root systems that reached below 30 cm, and Kellman attributed the increment in soil nutrients to increased precipitation capture on tree foliage rather than nutrient pumping

Table 2. Single-tree influences on soil properties in savanna ecosystems

Site description/source	Tree species		Total C %	Total N %	Ca	Mg	K	Mineral N production (g N m^{-2})	Mineralized N (% of Total N)
					— (cmol$_c$ kg^{-1}) —				
Humid savanna	*Clethra hondurensis*	Tree canopies							
Belize, Central America	*Quercus* sp.	Clethra	5.0	0.21	5.10	3.50	0.35		
(Kellman, 1979)		Quercus	2.1	0.10	0.80	0.44	0.28		
Soil depth: 0–5 cm		Savanna	1.3	0.06	0.10	0.18	0.07		
		Rainforest	2.3	0.20	5.00	1.00	0.45		
Senegal	*Acacia senegal*	Tree canopies							
(Bernhard-Reversat, 1982)	*Balanites aegyptiaca*	Acacia	6.2	0.56	–	–	–	8.2	9.67
Soil depth: 10 cm		Balanites	5.8	0.52	–	–	–	4.9	7.03
		Open sites			–	–	–		
		Dune	2.2	0.18	–	–	–	2.2	7.10
		Foot slope	3.7	0.30	–	–	–	4.6	11.00

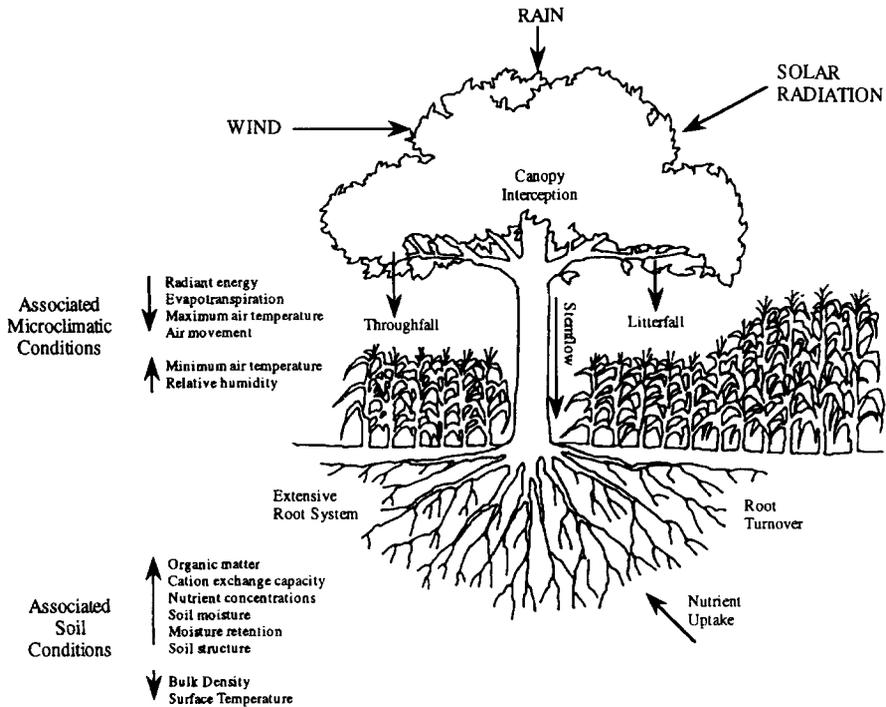|								Mineralizable N (g N g soil^{-1} week^{-1})	Microbial biomass C (g N g soil^{-1})
Western Kenya	*Acacia tortilis*	Low rainfall							
Tsavo National Park	*Adansonia digitata*	Canopy	1.49	0.13	3.62	1.68	0.89	4.1	262
(Belsky et al., 1989)		Open	0.78	0.06	2.94	1.38	0.68	1.7	172
and 1993		High rainfall							
Soil depth: 0–15 cm		Canopy	1.45	0.13	5.20	1.49	0.93	2.0	622
		Open	0.93	0.07	3.82	1.81	0.70	2.0	404
Southern Zimbabwe	*Combretum apiculatum*	Fine-texture soil							
(Campbell et al., 1994)	*Acacia nilotica*	Canopy	4.05	–	3.59	2.73	1.71		
Soil depth: 0–5 cm	*A. karroo*	Open	1.74	–	4.34	2.97	0.86		
	Terminalia sericea	Sandy soil							
	Burkea africana	Canopy	0.61	–	0.59	0.28	0.31		
		Open	0.40	–	0.37	0.18	0.20		
Llanos savanna, Venezuela		Evergreen	1.72	0.07	1.37	0.71	0.10		
(Garcia-Miragaya et al., 1994)		Deciduous	1.30	0.07	0.82	0.51	0.08		
		Forest	1.50	0.11	1.40	0.63	0.13		
		Grassland	0.78	0.07	0.22	0.28	0.06		

Figure 3. Summary of factors influencing soil processes beneath single trees growing in Mexican agroforestry systems. *Source*: Farrell (1990).

from deeper soil layers. Differences in canopy characteristics such as leaf area, angle and orientation determine a species' ability to scavenge nutrients from precipitation (Binkley, 1986). This, along with differences in nutrient concentrations in litterfall, may explain Kellman's species differences.

Shade beneath savanna tree canopies influences subcanopy microclimate and biomass production by reducing temperature maxima and evapotranspiration and by increasing relative humidity (Dancette and Poulain, 1969; Belsky et al., 1993; Amundson et al., 1995). In Kenyan savannas, soil temperatures declined by 5–12 °C under *Acacia tortilis* and *Adansonia digitata* canopies. Soil temperature maxima declined by 3.4 °C beneath *Faidherbia albida* in Senegal (Dancette and Poulain, 1969). The lower heat load beneath tree canopies reduces water stress and increases biomass of below-crown species (Amundson et al., 1995). Shade-cloth experiments in Australia showed that a 37% light reduction doubled grass production and increased N uptake by 53 kg N ha^{-1} (Wilson et al., 1986). Increased biomass production in the below-crown zone draws down the higher soil water resulting from reduced evapotranspiration below tree crowns, offsetting any increase relative to open sites (Belsky et al., 1993).

The improved microenvironmental conditions beneath savanna trees favor

soil biotic activity, nutrient transformations, and improved physical conditions. Coleman and coworkers (1991) measured higher soil microbial biomass, greater numbers of microbivorous nematodes, and larger amounts of mineralizable N beneath savanna tree canopies. Belsky and collaborators (1989, 1993, 1994) found higher rates of N mineralization beneath both *Adansonia digitata* and *Acacia tortilis* associated with lower bulk density and higher water infiltration. The tree influence on N availability was greater in more xeric environments. Lack of tree species differences on soil N shows the importance of microclimatic amelioration by tree canopies and that N-fixation by *Acacia* does not contribute significantly to the tree effect. Greater canopy-zone activity of earthworms and termites, in addition to augmented soil organic matter stocks, improved soil macroporosity and decreased bulk density beneath tree clumps in the Lamto savannas of the Ivory Coast (Mordelet et al., 1993).

In semi-arid systems, trees influence the availability of two limiting resources: water and nutrients. In the below-canopy environment, plant productivity is influenced by changes in soil fertility, water relations, and interspecific plant competition (Belsky, 1994). Beneath tree canopies, a 'two-layer model' delineates soil water uptake zones spatially; trees have exclusive access to deeper water stores while grasses utilize moisture held in surface soils. This example of niche partitioning has been used to explain the coexistence of savanna trees and below-crown grasses (Weltzin and Coughenour, 1990). In spite of partitioning of soil water resources, they concluded that increased soil fertility and higher herbaceous biomass production beneath tree canopies indicates a facultative interaction, surpassing that expected simply by soil water partitioning. Fertilizer experiments in Kenyan savannas demonstrated that plants grown in open sites were more nutrient limited than canopy-zone plants (Belsky, 1994). At the same sites, shade treatments generated smaller increases in understory vegetation production. Belsky was unable to firmly conclude whether nutrient enrichment or subcanopy microclimate was more important in increasing productivity of below-crown vegetation. Positive tree-effects on understory productivity are limited to those sites and species combinations where subcanopy tree and grass competition does not exceed site enrichment.

Tree effects on soils in agroforestry systems

The potential for soil improvement by trees is one of the central tenets of agroforestry (Palm, 1995). In both the semi-arid and humid tropics, soil-improving trees are often found scattered within crop and pastureland (Rocheleau et al., 1988; Nair, 1989; MacDicken and Vergara, 1990). In addition to production of fruit, forage, wood and other products, and shade for crops and animals, farmers often retain trees because of their positive impact on soil fertility and crop production. In a survey of African farming systems, Rocheleau and coauthors (1988) documented 36 dryland tree and shrub species growing

dispersed within farming systems and 20 in pastureland. Of these, more than half the cropland and a third of the pasture trees were reported as soil improvers. In Malawi, of 71 tree species found growing on cropland, farmers classified 27 as soil improvers (Maghembe and Seyani, 1991). In the tropical lowlands of south-eastern Nigeria, 5 of the 69 tree species found within home-garden plots were reported as soil improvers (Okafor and Fernandes, 1987). In Central and South America, nitrogen-fixing *Alnus, Inga* and *Erythrina* are managed within pasture and cropland for shade and improved soil fertility and forage quality (Galloway, 1986; Lojan Idrobo, 1992; Budowski, 1993). The following review will focus on semi-arid cropping systems where the bulk of cropland tree research has occurred.

Single-tree effects in dryland agroforestry

Semi-arid farmed parklands capitalize on the fertile soil islands found beneath trees in natural savanna ecosystems (Table 3). Trees are rarely planted delib-erately; rather, naturally regenerating trees are protected during tillage oper-ations (Poschen, 1986; Kerkhof, 1990; Tomilinson et al., 1995). The landusers' primary objective is food production, so tree species and density are managed to minimize negative impacts on crop production. Farmers selectively manage for trees that increase crop production either by improving soil fertility directly or by improving the subcanopy microenvironment.

Faidherbia albida is one the best known soil-improving trees of the semi-arid tropics (Felker, 1978; Vandenbelt, 1992). The tree's renown extends throughout its African range from the Sudano-Sahelian west African to the east Africa highland and south to Zimbabwe. The positive impact of *F. albida* on crop yields and soil fertility has long been recognized; scattered, mature *F. albida* are a common feature of areas with long cropping histories. Across Africa, yields of maize, millet, groundnuts and sorghum range from 30 to 200% higher beneath *F. albida* canopies compared to surrounding areas (Charreau and Vidal, 1965; Dancette and Poulain, 1969; Depommier et al., 1992; Saka et al., 1994). This remarkable increase in crop production, commonly referred to as the 'albida effect' results from both increases in soil fertility and improved soil water and microclimatic conditions below the tree.

Similar to other tree species, soil properties below the crowns of *F. albida* are higher in available nutrients (Rhoades, 1995) and in total soil pools of C and N (Radwanski and Wickens, 1967). The most unique feature of *F. albida* is that it exhibits 'reversed' leaf phenology by shedding its foliage during the cropping season. Its bare tree branches reduce evapotranspiration and increase relative humidity beneath the canopy without reducing crop produc-tion (Dancette and Poulain, 1969). Rhoades (1995) recorded increased soil water in the crop root zone beneath *F. albida* canopies in Malawi. The soil water difference beneath tree canopies rose from 4 to 53% higher than open sites during the course of the cropping season.

Table 3. Influence of parkland trees on soil and crops.

Site description/source	Tree species		Total C (%)	Total N (%)	Ca	Mg	K	pH	Crop response[a]
					— (cmol$_c$ kg^{-1}) —				
North-central Senegal	*Faidherbia albida*	Canopy	3.70	0.40	1.61	0.71	0.10	5.7	Groundnuts: +37%
(Dancette and Poulain, 1969) Soil depth: 0–20 cm		Open	2.70	0.30	1.13	0.62	0.07	5.5	Sorghum: +200%
Central Plateau,	*Faidherbia albida*	Canopy	0.90	0.13	5.80	2.08	0.65	6.7	Sorghum grain:
Burkina Faso (Depommier et al., 1992) Soil depth: 0–20 cm		Open	0.78	0.90	5.05	2.00	0.38	6.6	+115%
Lakeshore Plain, Malawi	*Faidherbia albida*	Canopy	2.50	0.22	5.71	1.50	0.98	6.3	Maize grain:
(Rhoades, 1995; Saka et al., 1994) Soil depth: 0–15 cm		Open	2.20	0.19	6.84	1.78	0.87	6.3	+100–400%
South Central Mexico	*Prunus capuli*	Canopy							Maize grain
(Farrell, 1990)	*Juniperus deppeana*	Prunus	1.34	0.09	6.50	1.29	0.58	6.6	Prunus: –50%
Soil depth: 0–15 cm		Juniperus	0.63	0.04	6.60	1.24	0.84	7.4	Juniperus: –50%
		Open	0.45	0.03	3.45	0.62	0.33	6.2	
South Eastern Mali	*Vitellaria paradoxa* (VP)	Canopy	0.66	0.06	1.68	0.67	0.27	6.0	Cotton: VP: –2%;
(Kater et al., 1992)	*Parkia biglobosa* (PB)	Open	0.51	0.05	1.45	0.42	0.16	6.0	PB: –65%
Soil depth: 0–20 cm									Sorghum: VP: –44%; PB: –66%
									Millet: VP & PB: –60%

[a] Yield difference under tree canopy and open sites.

The reversed leaf phenology of *F. albida* sets it apart from other tree species that also increase soil nutrients, but that reduce crop growth due to light or water competition (Farrell, 1990; Kater et al., 1992; Kessler, 1992). Crop production beneath common west African parkland trees *Parkia biglobosa* (Jacq. (Benth.)) and *Vitellaria paradoxa* (syn. *Butyrospermum paradoxum*) is known to drop by 40 to 70%, in spite of slight to moderate increases in total C, available P and exchangeable cations (Kater et al., 1992; Kessler, 1992; Table 3). A 50% reduction of light under the tree canopies explained most of the decline in crop production (Kessler, 1992) along with nutrient competition and higher incidence of crop pathogens (Kater et al., 1992). Species-related differences in shading relate to canopy architecture; trees with upright canopies reduces light levels less than those with low, spreading crowns. Farrell (1990) found comparable increases in total C, N, exchangeable cations, and CEC beneath the crowns of Mexican farmland trees, where maize yields declined by 50% of the open field levels. Soil water was also higher beneath the tree crowns, and the yield decline was attributed to light limitations. In the partial shade region at the canopy periphery, soil fertility and water content both improved slightly and crop yields remained equal to open site conditions (Farrell, 1990; Kater et al., 1992).

Beyond the 'albida effect'

The conditions that generate the 'albida effect' are a unique combination of increased soil fertility without the accompanying burden of light or water limitations. Why is it then, that farmers identify a wide variety of tree species with typical leaf phenology as soil improvers, since they may actually reduce crop yields? Agroforestry systems are classified as either simultaneous systems where trees and crops or pasture are integrated at the same time, or as sequential or rotational systems. The *F. albida* parkland system is an example of a system that simultaneously provides benefits to crop and animal production (Sanchez, 1995). Other species identified by farmers as soil improvers may ameliorate soil conditions gradually during the trees' life and only increase production after the tree is removed. These trees may represent the remnant of traditional tree fallows that have been abandoned due to increased population pressure. In traditional agroforestry systems, farmers' perceptions of soil improvement by trees may vary from those held by research scientists. Campbell and coworkers (1991) evaluated farmer surveys in Zimbabwe and discovered a strong link between trees identified as soil improvers and those valued for fruit or other products. In cases where farmers perceive trees as overwhelmingly beneficial components of their farm production, any effect of the tree on soil properties may be considered as incidental. In such cases, economic gains from cropland trees outweigh crop yield declines and explain their presence within farm fields. Kessler (1992) calculated that benefits resulting from the harvest of *Parkia biglobosa* products were twice as high as crop losses.

The challenge in agroforestry is to improve or introduce tree-crop combinations that will enhance farm productivity, diversity and sustainability. Critical concerns remain about the potential of scattered cropland trees to fulfill these objectives relative to other agroforestry alternatives. What certain species and biophysical conditions offer worthwhile opportunities to insure farmer adoption? Are there ways to maximize the beneficial attributes of soil-improving cropland trees while minimizing their potentially negative impacts? How long must farmers be willing to wait for soil amelioration to reach a point that it will improve crop production? Currently, too little information exists to make generalizations that address these questions. The following section will discuss considerations relevant to expansion of the cropland tree system and will offer research directives that will help to overcome the lack of knowledge in this system.

Species selection

Trees that benefit soil conditions within croplands can be placed into different categories based on their architecture and biophysical characteristics (Young, 1989; Breman and Kessler, 1995). For trees expected to improve soils concurrently with crop production, the degree of tree-crop competition will determine the success of the combination. In such cases, extensive, shallow root systems, and dense, spreading canopies are undesirable tree attributes. Trees with erect, sparse canopies and those that shed leaves during the rainy season

Table 4. Selected mechanisms regulating single-tree influence of soil properties.

Factor	Sources
Increased inputs	
Litter or fruit inputs	a, b, g, h, p, q, s
Nitrogen inputs from N-fixation	f, h, j
Stemflow and canopy throughfall inputs	a, b, d, g, h, l, m, o
Accumulation of windborne soil around trunks	e, h, n
Redistribution	
Root scavenging laterally or from deep soil levels	b, j, k, m, r, t
Fecal inputs from perching bird or grazing animals	b, k
Ameliorated canopy microclimate	b, c, k, l, o, s

a – Zinke, 1962.
b – Alban, 1969.
c – Dancette and Poulain, 1969.
d – Gersper and Holowaychuk, 1971.
e – Charley and West, 1975.
f – Felker, 1978.
g – Kellman, 1979.
h – Crampton, 1984.
i – Hogberg, 1986.
j – Virginia, 1986.

k – Belsky et al., 1989.
l – Beniamino et al., 1991.
m – Kessler and Breman, 1991.
n – Isichei and Muoghalu, 1992.
o – Belsky et al., 1993.
p – Mordelet et al., 1993.
q – Garcia-Miragaya et al., 1994.
r – Campbell et al., 1994.
s – Rhoades, 1995.
t – Tomilinson et al., 1995.

(similar to *F. albida*) will minimize light competition during the cropping season (Kessler, 1992). Synchronizing the release of nutrients from decomposing leaf litter with crop nutrient uptake requirements depends on both the phenology of leaf drop and the leaf litter quality. Trees whose canopies resprout after repeated pruning or coppicing may be managed for reduced light competition. Trees that fix nitrogen will not compete for soil N, and ideally will increase the soil N capital. Those with fruit or shade that attract animals during the dry season may become foci for increased nutrient deposition in the form of animal manure. The second category contains trees that improve soils but preclude crop production, as in a tree fallow system. Such trees should provide high-value products (food, wood) that offset lost crop production. Soil amelioration beneath these trees relates to increases in soil organic matter and associated changes in nutrient and soil water retention. In this case, trees with dense, low canopies that produce copious amount of leaf litter that is protected from wind removal are preferred. Trees with lower quality leaf litter (high C:N or high lignin content) will generate more stable forms of soil organic material that resist rapid oxidation (Campbell et al., 1994; Garcia-Miragaya et al., 1994).

Site selection

Plans to promote expansion of cropland tree plantings must consider the natural formation of savannas and traditional-cropped parklands. While soil amelioration occurs beneath the canopies of certain species, increasing the tree density may not extend these benefits (Kessler and Breman, 1991; Alstad and Vetaas, 1994). Such a benefit may occur in ecosystems where trees enhance soil fertility by increased inputs from external sources such as N-fixation, or interception of wet or dryfall nutrients. In semi-arid savannas or parklands, however, where trees often enrich soil through nutrient redistribution (Kessler and Breman, 1991; Belsky et al., 1989; Campbell et al., 1994) via lateral root scavenging or as deposition foci of animals, the upper limits on tree density are set by the finite amount of nutrients available in the system. Similarly, low water availability in natural and managed semi-arid systems limits tree and shrub density.

Survival and growth of farmland trees is highly variable (Kerkhof, 1990; Geiger et al., 1994). In natural savanna systems, tree species and distribution patterns are controlled by chemical and physical soil properties (Tinley, 1982; Ben-Shar, 1991; Coughenour and Ellis, 1993). Research in Niger has shown that establishment of *F. albida* on farmland relates to microsite variability in soil properties (Geiger et al., 1994). Rapid seedling growth was correlated with increased clay content and exchangeable bases, and decreased exchangeable acidity. The improved soil conditions were found at microtopographic high points, such as abandoned termite mounds.

The manner by which trees influence soil conditions depend on original. soil properties at both microsites and landscape scales. The findings in Niger

suggest that soil improvement credited to *F. albida* may result in part from the trees having established on relic termite mounds (Geiger and Manu, 1993). The increased clay content in the residual termiteria represent favorable microsites for the stabilization of organic matter cycled by the trees. At a broader scale, soil texture regulates the magnitude of tree influence. In Zimbabwe, Campbell et al. (1994) found that trees increased soil C levels to a greater extent in fine-textured rather than sandy soils. In sandier soils, even the moderate gain in soil organic matter beneath tree crowns greatly increased the size of the soil exchange complex and the amount of exchangeable cations. In finer-textured soils, trees had a minor impact, since the cation exchange complex is dominated by the mineral component, rather than by soil organic matter.

Tree establishment

Traditional scattered cropland tree systems are rarely planted (Felker, 1978; Kerkhof, 1990; Gijsbers et al., 1994; Bremen and Kessler, 1995). Seeds tend to germinate below seed-bearing adults or are dispersed by grazing animals. Recruitment of seedlings depends on grazing pressure, fire frequency and tillage practices. Encouraging natural regeneration by reducing or eliminating grazing represents a cost effective means of increasing tree stocking (Kerkhof, 1990; Vandenbeldt, 1992). Due to high soil variability, planting schemes should attempt to locate seedlings with regard to microsite conditions rather than on strict spacing guidelines. A combination of grazing-control practices and supplemental tree planting or direct seeding probably offers the most realistic strategy for expanding parkland agroforestry systems.

Management of cropland trees

Reducing light competition by canopy pruning can have a positive influence on crop yields. In Burkina Faso, Kessler (1992) found that while unpruned *Parkia* trees depressed sorghum yields by 80% of open site production, yields surrounding pruned trees dropped by only 40%. In northwestern India, shade from unpruned trees depressed bean yields (*Vigna mungo* and *Cyamopisis tetragonoloba*) by 20 to 60% (Shankarnarayan et al., 1987); under pruned trees yields were similar to open sites. Timmer et al. (1996) surveyed local pruning activities in parkland systems in Burkina Faso. They found that the major motivations for pruning trees related to improved tree survival and productivity. While farmers recognize the crop reduction beneath the cropland trees, less than one third of all trees are pruned and only 10% of the farmers surveyed did so to reduce shade. While pruning has a clear impact on above ground competition for light, changes in root morphology following pruning may increase competition for below-ground resources (van Noordwijk et al., 1991).

Within agroforestry systems, understanding the temporal impact of trees on soil nutrients is critical for determining the net benefit to crops. Crops

respond to available forms of nutrients that fluctuate over the course of a cropping season. The synchronization of seasonally-varying soil nutrient supply with plant demand is required for a tree to have a positive impact on crop production (Palm, 1995). In *F. albida* parklands in Malawi, Rhoades (1995) found that plant-available soil NO_3–N was 7 times higher during the first month of the cropping season. During the rest of the cropping season, soil NO_3–N was 2 to 3 times higher beneath tree crowns. Soil NO_3–N is highly mobile, so the large pulse of nitrification produced by the first rains may have leached beyond the crop root zone while the maize plants were still relying on seed resources. Mixing lower quality organic residue (high C:N ratio) with labile tree leaf material may help to regulate nutrient release by shunting nutrients into microbial biomass where nutrient release will be gradual rather than pulsed.

Time scale

A leading concern associated with wide-scale promotion of parkland agroforestry for increased soil fertility is the time required to produce the anticipated benefits. While it has been shown that soil improvement accrues with tree size or age (Bernhard-Reversat, 1982), there is no clear threshold beyond which the positive attributes of the tree will be conferred to the crops. In Senegal, Bernhard-Reversat (1982) found that total soil C and N pools increased linearly as a function of tree diameter for both *Acacia senegal* and *Balanites aegyptiaca*. Isichei and Muoghalu (1992) compared soil properties under trees above and below 7 m tall. They found significantly higher levels of soil organic matter, exchangeable cations, clay and silt under the larger trees and no difference in total N, available P or base saturation. *F. albida* growing in Tanzania reached a height of 8.8 m, after 6 years of growth (Okorio and Maghembe, 1994). By that age the trees had no positive or negative impact on maize or bean growth. In Malawi, *F. albida* trees 10–15 years of age averaged 13.7 m tall with a canopy radius of 3.3 m (Rhoades, 1995). Beneath these young trees, soil water and *in situ* nitrogen mineralization were no higher than levels measured in open sites. Twenty-meter tall mature trees with canopies extending 12 m dramatically increased both soil water and N cycling in the subcanopy zone. In the Ethiopian highlands, Poschen (1986) estimated that benefits from the 'albida effect' would require 20 years for fast-growing genotypes and up to 40 years at average growth rates. The long delay before realizing soil benefits in parkland agroforestry emphasizes the importance of protecting existing parklands while establishing new systems.

Conclusions

Understanding species-specific differences in tree-soil interactions has important and immediate interest to farmers and agroforesters concerned with

maintaining or increasing site productivity. From an ecological perspective, the soil patches found beneath tree canopies are important local and regional nutrient reserves that influence community structure and ecosystem function. Future research should integrate the action of tree-soil patches into a larger view of the ecosystem both spatially and temporally. Attempts to link species effects to whole ecosystem processes need to differentiate where tree effects can be aggregated and where species-specific differences must be considered. The challenge for agroforesters is to determine under what conditions positive tree effects will accumulate simultaneously within active farming systems and which require rotation of cropping and forest fallows.

Acknowledgements

References

Alstad G and Vetaas OR (1994) The influence of *Acacia tortilis* stands on soil properties in arid north-eastern Sudan. Acta Oecol 15(4): 449–460

Alway FJ, Kitteredge J and Methley WJ (1933) Composition of the forest floor layers under different forest types on the same soil type. Soil Sci 36: 387–398

Amundson RG, Ali AR and Belsky AJ (1995) Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. J Arid Environ 29: 139–153

Belsky AJ, Amundson RG, Duxbury JM, Riha SJ and Mwonga SM (1989) The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. J Appl Ecol 26: 1005–1024

Belsky AJ and Canham CD (1994) Forest gaps and isolated savanna trees. Bioscience 44: 77–84

Belsky AJ, Mwonga SM and Duxbury JM (1993) Effects of widely spaced trees and livestock grazing on understory environments in tropical savannas. Agrofor Syst 24: 1–20

Belsky AJ (1994) Influences of trees on savanna productivity: test of shade, nutrients, and tree-grass competition. Ecology 75: 922–932

Ben-Shar R (1991) Abundance of trees and grasses in a woodland savanna in relation to environment factors. J Veget Sci 2: 345–350

Beniamino F, Ponge JF and Arpin P (1991) Soil acidification under the crown of oak trees. I. Spatial distribution. For Ecol Manage 40: 221–232

Bernhard-Reversat F (1982) Biogeochemical cycle of nitrogen in a semi-arid savanna. Oikos 38: 321–332

Binkley D (1986) Forest Nutrient Management. John Wiley and Sons, New York, 290 pp

Binkley D and Valenine D (1991) Fifty-year biogeochemical effects of green ash, white pine, and Norway spruce in a replicated experiment. For Ecol Manage 40: 13–25

Birkeland PW (1984) Soils and Geomorphology. Oxford University Press, New York, 372 pp

Boettcher SE and Kalisz PJ (1990) Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology 71: 1365–1372

Boettcher SE and Kalisz PJ (1991) Single-tree influence on earthworms in forest soils in eastern Kentucky. Soil Sci Soc Am J 55: 862–865

Breman H and Kessler JJ (1995) Woody Plants in Agro-Ecosystems of Semi-Arid Regions. Springer-Verlag, Berlin, 340 pp

Budowski G (1993) The scope and potential of agroforestry in Central America. Agrofor Syst 23: 121–131

Campbell BM, Clarke JM and Gumbo DJ (1991) Traditional agroforestry practices in Zimbabwe. Agrofor Syst 14: 99–111

Campbell BM, Frost P, King JA, Mawanza M and Mhlanga L (1994) The influence of trees on soil fertility on two contrasting semi-arid soil types at Matopos, Zimbabwe. Agrofor Syst 28: 159–172

Challinor D (1968) Alteration of surface soil characteristics by four tree species. Ecology 49: 286–290

Charley JL and West NE (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. J Ecol 63: 945–963

Charreau C and Vidal P (1965) Influence de l'*Acacia albida* Del. sur le sol, nutrition minerale et rendements des mils Pennisetum au Senegal. L'Agronomie Tropicale 6–7: 600–626

Coleman DC, Edwards AL, Belsky AJ and Mwonga S (1991) The distribution and abundance of soil nematodes in East African savannas. Biol Fertil Soils 12: 67–72

Coughenour MB and Ellis JE (1993) Landscape and climate control of woody vegetation in a dry tropical ecosystem: Turkana District, Kenya. J Biogeogr 20: 383–398

Crampton CB (1984) Concentric zonation of gleyed soils under individual tree canopies in south-western British Columbia. Geoderma 32: 329–334

Crocker RL (1952) Soil genesis and the pedogenic factors. Q Rev Biol 27: 139–168

Dancette C and Poulain JF (1969) Influence of *Acacia albida* on pedoclimatic factors and crop yields. African Soils/Sols africains 14: 143–184

Depommier D, Janodet E and Oliver R (1992) *Faidherbia albida* parks and their influence on soils and crops at Watinoma, Burkina Faso. In: Vandenbelt RJ (ed) *Faidherbia Albida* in the West African Semi-Arid Tropics, pp 111–124. International Centre for Research in Agroforestry, Niamey, Niger

Everett R, Sharrow S and Thran D (1986) Soil nutrient distribution under and adjacent to single leaf pinyon crowns. Soil Sci Soc Am J 50: 788–792

Farrell J (1990) The influence of trees in selected agroecosystems in Mexico. In: Gliessman SR (ed) Agroecology: Researching the Ecological Basis for Sustainable Agriculture, pp 167–183. Springer-Verlag, New York

Felker P (1978) State of the Art: *Acacia albida* as a Complementary Permanent Intercrop with Annual Crops. Grant No. AID/afr-C-1361, University of California, Riverside, CA, 133 pp

Fisher RF (1995) Amelioration of degraded rain forest soils by plantations of native trees. Soil Sci Soc Am J 59: 544–549

Galloway G (1986) Guia sobre la repoblacion forestal en la sierra ecuatoriana. Proyecto USAID-DINAF, Quito, Ecuador, 291 pp

Garcia-Miragaya J, Flores S and Chacon N (1994) Soil chemical properties under individual evergreen and deciduous trees in a protected Venezuelan savanna. Acta Oecol 15(4): 477–484

Gast PR (1937) Contrasts between the soil profiles developed under pines and hardwoods. J For 35: 11–16

Geiger SC and Manu A (1993) Soil surface characteristics and variability in the growth of millet in the plateau and valley region of Western Niger. Agric Ecosyst Environ 45: 203–211

Geiger SC, Vandenbeldt RJ and Manu A (1994) Variability in the growth of *Faidherbia albida*: the soils connection. Soil Sci Soc Am J 58: 277–231

Gersper PL and Holowaychuck N (1971) Some effects of stem flow from forest canopy trees on chemical properties of soils. Ecology 52: 691–702

Gijsbers HJM, Kessler JJ and Knevel MK (1994) Dynamics and natural regeneration of woody species in farmed parklands in the Sahel region (Province of Passore, Burkina Faso). For Ecol Manage 64: 1–12

Högberg P (1986) Soil nutrient availability, root symbiosis and tree species composition in tropical Africa: a review. J Trop Ecol 2: 359–372

Isichei AO and Muoghalu JI (1992) The effects of tree canopy cover on soil fertility in a Nigerian savanna. J Trop Ecol 8: 329–338

Jackson LE, Strauss RB, Firestone MK and Bartolome JW (1990) Influence of tree canopies on grassland productivity and nitrogen dynamics in deciduous oak savanna. Agriculture, Ecosyst Environ 32: 89–105

Jenny H (1941) Factors of Soil Formation. McGraw-Hill, New York, 281 pp

Jenny H (1980) The Soil Resource-Origin and Behavior. Springer-Verlag, New York, 377 pp

Kater LJM, Kante S and Budelman A (1992) Karite (*Vitellaria paradoxa*) and nere (*Parkia biglobosa*) associated with crops in South Mali. Agrofor Syst 18: 89–105

Kellman M (1979) Soil enrichment by neotropical savanna trees. J Ecolo 67: 565–577

Kerkhof P (1990) Agroforestry in Africa: A Survey of Project Experience. Panos Publications, London, 216 pp

Kessler JJ and Breman H (1991) The potential of agroforestry to increase primary production in the Sahelian and Sudanian zones of West Africa. Agrofor Syst 13: 41–62

Kessler JJ (1992) The influence of karite (*Vitellaria paradoxa*) and nere (*Parkia biglobosa*) trees on sorghum production in Burkina Faso. Agrofor Syst 17: 97–118

Klemmedson JO and Barth RH (1975) Distribution and Balance of Biomass and Nutrients in Desert Shrub Ecosystems. US/IBP Desert Biome Research Memo 75-5, Utah State University, Logan, UT, 18 pp

Klemmedson JO and Wienhold BJ (1992) Aspect and species influences on nitrogen and phosphorus accumulation in Arizona chaparral soil-plant systems. Arid Soil Res Rehabilitation 6: 105–116

Lojan Idrobo L (1992) Arboles y arbustos nativos para le desarrollo forestal altoandino. Proyecto desarrollo forestal participativa en los andes, Quito, Ecuador, 217 pp

MacDicken KG and Vergara NT (1990) Agroforestry, Classification and Management. John Wiley and Sons, New York, 382 pp

Maghembe JA and Seyani JH (1991) Multipurpose trees used by smallholder farmers in Malawi: results form an ethnobotanical survey (AFRENA Report No. 42). International centre for Research in Agroforestry, Nairobi, Kenya, 30 pp

Mina VN (1967) Influence of stemflow on soil. Soviet Soil Sci 7: 1321–1329

Mordelet P, Abbadie L and Menaut JC (1993) Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Cote d' Ivoire). Plant and Soil 153: 103–111

Nair PKR (1984) Soil Productivity Aspects of Agroforestry. International Centre for Research in Agroforestry. Nairobi, Kenya, 85 pp

Okafor JC and Fernandes ECM (1987) The compound farms of south-eastern Nigeria: a predominant agroforestry homegarden system with crops and small livestock. Agrofore Syst 5: 153–168

Okorio J and Maghembe JA (1994) The growth and yield of *Acacia albida* intercropped with maize (*Zea mays*) and beans (*Phaseolus vulgaris*) at Morogoro, Tanzania. For Ecol Manage 64: 183–190

Ovington JD (1954) Studies of the development of woodland conditions under different trees. II. The forest floor. J Ecol 42: 71–80

Ovington JD (1956) Studies of the development of woodland conditions under different trees. IV. The ignition loss, water, carbon and nitrogen content of the mineral soil. J Ecol 44: 171–17

Palm CA (1995) Contribution of agroforestry trees to nutrient requirements of intercropped plants. Agrofor Syst 30: 105–124

Parton WJ, Stewart JWB and Cole CV (1988) Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5: 109–131

Poschen P (1986) An evaluation of the *Acacia albida*-based agroforestry practices in the Hararghe highlands of eastern Ethiopia. Agrofor Syst 4: 129–143

Paulsen HA (1950) A comparison of surface soil properties under mesquite and perennial grass. Ecology 34: 727–732

Radwanski SA and Wickens GE (1967) The ecology of *Acacia albida* on mantle soils in Zalingei, Jebel Marra, Sudan. J Appl Ecol 4: 569–579

Remezov NP and Pogrebnyak PS (1965) Forest Soil Science. Israel program for scientific translations, Jerusalem (1969). US Department of Commerce, Clearinghouse for Federal scientific and technical information, Springfield, MA, USA

Rhoades CC, Sanford Jr RL and Clark DB (1994) Gender dependant influences on soil phosphorus by the dioecious lowland tropical tree *Simarouba amara*. Biotropica 26: 362–368

Rhoades CC (1995) Seasonal patterns of nitrogen mineralization and soil moisture beneath *Faidherbia albida* (syn *Acacia albida*) in central Malawi. Agrofor Syst 29: 133–145

Riha SJ, James BR, Senesac GP and Pallent E (1986) Spatial variability of soil pH and organic matter in forest plantations. Soil Sci Soc Am J 50: 1347–1352

Robertson GP and Gross KL (1994) Assessing the heterogeneity of belowground resources: quantifying pattern and scale. In: Caldwell MM and Pearcy RW (eds) Exploitation of Environmental Heterogeneity by Plants, pp 237–253. Academic Press, New York

Rocheleau D, Weber F and Field-Juma A (1988) Agroforestry in Dryland Africa. International Council for Research in Agroforestry, Nairobi, Kenya, 311 pp

Saka AR, Bunderson WT, Itimu OA, Phombeya HSK and Mbekeani Y (1994) The effects of *Acacia albida* on soils and maize grain yields under smallholder farm conditions in Malawi. Agrofor Syst 64: 217–230

Sanchez PA (1995) Science in agroforestry. Agroforestry Systems 30: 5–55

Shankarnarayan KA, Harsh LN and Kathju S (1987) Agroforestry in the arid zones of India. Agrofor Syst 5: 69–88

Tiedemann AR and Klemmedson JO (1973a) Effect of mesquite on physical and chemical properties of the soil. J Range Manage 26: 27–29

Tiedemann AR and Klemmedson JO (1973b) Nutrient availability in desert grassland soils under mesquite *(Prosopis juliflora)* trees and adjacent open areas. Soil Sci Soc Am Procs 37: 107–111

Timmer LA, Kessler JJ and Slingerland M (1996) Pruning of nere trees *(Parkia biglobosa* (Jacq.) Benth.) on the farmlands of Burkina Faso, West Africa. Agrofor Syst 33: 87–98

Tinley KL (1982) The influence of soil moisture balance on ecosystem patterns in Southern Africa. In: Huntley BJ and Walker BH (eds) Ecology of Tropical Savannas, pp 175–192. Springer-Verlag, Berlin

Tomlinson H, Teklehaimanot Z, Traore A and Olapade E (1995) Soil amelioration and root symbioses of *Parkia biglobosa* (Jacq.) Benth. in West Africa. Agrofor Syst 30: 145–159

Vandenbelt RJ (ed) (1992) *Faidherbia Albida* in the West African Semi-Arid Tropics. ICRISAT, Patancheru, India, 206 pp

van Noordwijk M, Widianto, Heinen M and Hairiah M (1991) Old tree channels in acid soils in the humid tropics: important for crop penetration, water infiltration and nitrogen management. Plant and Soil 134: 37–44

Virginia RA (1986) Soil development under legume tree canopies. For Ecol Manage 16: 69–79

Vitousek PM and Sanford RL Jr (1986) Nutrient cycling in moist tropical forest. Annual Rev Ecol Syst 17: 137–167

Weltzin JF and Coughenour MB (1990) Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. J Veget Sci 1: 325–334

Wilson JR, Catchpoole VR and Weir KL (1986) Stimulation of growth and nitrogen uptake by shading a rundown green panic pasture in Brigalow clay soil. Trop Grassl 20: 134–144

Young A (1989) Agroforestry for Soil Conservation. CAB International, Wallingford, UK, 276 pp

Zinke PJ (1962) The pattern of influence of individual forest trees on soil properties. Ecology 43: 130–133

Zinke PJ and Crocker RL (1962) The influence of giant sequoia on soil properties. For Sci 8: 2–11