Interspecific interactions in temperate agroforestry

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Abstract

The ecological principles that define the competitive and complementary interactions among trees, crops, and fauna in agroforestry systems have received considerable research attention during the recent past. These principles have not yet, however, been adequately integrated and synthesized into an operational approach. This paper reviews the ecological and ecophysiological bases for interspecific interactions based on data from site-specific research and demonstration trials from temperate agroforestry systems, primarily from temperate North America. The review shows that information on ecological interactions in several temperate agroforestry systems is inadequate. It is recommended that the future research should focus on exploring new species and systems that have received little attention in the past. Priority research areas should include cultural practices and system designs to minimize interspecific competition and maximize environmental benefits such as improved water quality. Potential for genetic modification of components to increase productivity and reduce competition also needs to be explored. Process-oriented models may be used increasingly to predict resource-allocation patterns and possible benefits for a suite of site and species combinations.

Introduction

The search for highly productive, yet sustainable and environmentally responsible agricultural systems has led to a renewed interest in agroforestry practices in temperate regions of the world (Matson et al. 1997; Moffat 1997; Noble and Dirzo 1997). Increasing environmental, ecological, and economic concerns have been providing momentum for this shift in paradigm away from 'chemical agriculture.' As in the tropical regions, the major objectives for establishing agroforestry systems in temperate regions are also somewhat similar (production of tree or wood products, agronomic crops or forage, livestock, and improvement of crop quality and quantity), but at a scale and magnitude corresponding to the prevailing social and economic conditions. Furthermore, added emphasis is placed on environmental benefits such as water qual-

ity in the temperate regions. Management practices to attain these objectives have included enhancement of microclimatic conditions; improved utilization and recycling of soil nutrients; control of subsurface water levels; improved soil and water quality; provision of favorable habitats for plant, insect or animal species; soil stabilization; and protection from wind and snow, among others (Williams et al. 1997; Garrett and McGraw 2000).

As an association of woody and herbaceous plant communities, often with domesticated or semiwild animals, agroforestry systems are deliberately designed to optimize the use of spatial, temporal, and physical resources, by maximizing positive interactions (facilitation) and minimizing negative ones (competition) among the components (Jose et al. 2000a). An understanding of the biophysical processes and mechanisms involved in the allocation of these re-

sources is essential for the development of ecologically sound agroforestry systems that are economically viable and socially acceptable (Ong et al. 1996; Rao et al. 1998). These complex biophysical interactions, which have received much recent attention in temperate agroforestry, will be the focus of this paper; companion chapters on this topic from simultaneous agroforestry systems in the tropics by Garcia-Barrios and Ong (2004) and north temperate agroforestry systems by Thevathasan and Gordon (2004) complement this chapter.

Interaction: the ecological basics

The interactions that occur among individual organisms can be grouped into four broad categories: (a) eating or being eaten, (b) competing for resources, (c) cooperating, and (d) no direct interaction (Perry 1994). Terminologies such as predation, parasitism, competition, amensalism, mutualism, commensalism, and neutralism have also been used extensively to define the relationship between two species. All of these are applicable in an agroforestry context as well (Table 1). When interaction is positive or synergistic, complementarity between system components can be expected; when interaction is negative or antagonistic, it becomes competitive. Interactions can also be classified as occurring in above- and belowground compartments, as commonly referred to in the agroforestry literature (Singh et al. 1989; Ong et al. 1991).

Similar to natural systems, productivity of an agroforestry system is ultimately the net result of positive and negative interactions among the components. Interactions occur as component species exploit growth resources above- and belowground (Ong et al. 1996). The likelihood and intensity of interspecific (as well as intraspecific) interactions decline with decreases in organism density until a maximum yield is reached. Beyond any maximum-yield density, interactions among plants occur when two or more organisms attempt to capture resources from the same location or at the same time (spatial or temporal). The Armstrong and McGehee model illustrates this mechanism of coexistence and competition (Armstrong and McGehee 1980). In this model, a single resource R, is consumed by two species, A and B. Species A has a linear growth response, whereas species B has a nonlinear response (Figure 1). For each species, the two species equilibrium with only that species and the resource present is the point at which the growth rate is equal to zero (R_A
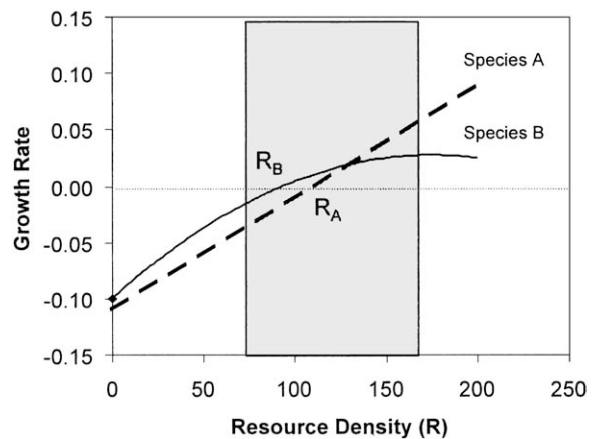

Figure 1. Population growth rates of species A and B as functions of the resource density, R, according to the Armstrong and McGhee (1980) model. R_A, and R_B are the equilibrium densities of species A and B, respectively, when grown alone. Shaded region shows the range of resource densities over which the two species can coexist Source: Adapted from Murdoch et al. (2003).

is the equilibrium density with species A alone and R_B is the equilibrium density with species B alone; see Figure 1). If the resource pool is low, the species with the lowest R value (i.e., the species that reduces the equilibrium density of the resource to the lowest level) will win in competition. In the example shown in Figure 1, species B will be the winner. If the resource pool is sufficiently large, however, species A and B will be able to coexist over a range of resource densities (shaded region in Figure 1). This rather simplistic explanation of what spurs interactions, while true in agroforestry systems, is somewhat better suited for systems where component species have very similar root distributions, such as when herbaceous weeds invade an agronomic monoculture system. This is because all organisms in a single-species system can be expected to have fairly similar physiological needs and to respond to fulfill those needs in a similar manner. Species in agroforestry systems can have different physiological needs for particular resources in certain amounts, at certain times, and possess different structural or biological means to obtain them. This idea can be easily considered in terms of niche separation. The utilization of the environment by any species includes three main components: space, resources, and time. Any species utilizing the same exact combination of these resources as another will be in direct competition, eventually resulting in competitive exclusion. However, if one species differs in utilization of even one of the components, for example light saturation of

Table 1. Interactions between two species as commonly depicted in ecological literature.

Type of interaction	Effect of the interaction[1]		Nature of the interaction	Agroforestry example
	Species 1	Species 2		
Amensalism	–	0	One species is inhibited and the other unaffected	Allelopathy; black walnut inhibiting growth of tomato
Commensalism	+	0	One species is benefited and the other one is unaffected	Improved fallows
Competition	–	–	Both species are negatively affected as a result of each other's use of growth resources	Poorly managed alley cropping or silvopasture
Mutualism (or synergism)	+	+	Both species are positively affected	Mycorrhizae, *Rhizobium* in leguminous plants
Neutralism	0	0	Neither species affects the other	Scattered trees; winter wheat in a temperate deciduous tree alley cropping
Predation and Parasitism	+	–	One species benefits at the expense of another. Predators tend to take large bites and parasites small bites. Parasites frequently invade the body of their hosts and eat from within; predators eat from outside	Pests and diseases

[1] 0 = no effect; + = positive; – = negative.
Source: Modified from Perry, 1994.

C3 vs. C4 plants, an equilibrium species mixture may be established.

The *resource-ratio hypothesis*, proposed by Tilman (1982, 1985, 1990), has been used to explain coexistence and competitive exclusion in an agroforestry context as well. According to this hypothesis, coexistence occurs where resource requirements differ among the species. Greater capture of a limiting resource would be accompanied by an increased ability to utilize nonlimiting resources, which, by definition, are available but underutilized. Thus, based on the differences in physical or phenological characteristics of component species, the interactions between tree and crop species may lead to an increased capture of a limiting growth resource (Ong et al. 1996; Ashton 2000; Garcia-Barrios and Ong 2004). The system as a whole could then accrue greater total biomass than the cumulative production of those species if they were grown separately on an equivalent land area (Cannell et al. 1996). Production possibility curves have been widely used in agroforestry literature to explain this concept. For example, Figure 2a provides a graphical representation of complementarity in resource use. The line from A1 to B1 represents the total yield of A and B as the proportion of each species in sole systems on a given area varies. The curve described by A+B represents over-yielding (compared to either of the sole crop yields) of one possible mixture of species A and B.

Figure 2a, however, ignores the fact that agroforestry systems are dynamic and temporal changes can be expected over the life of the system. A hypothetical scenario of how interactions can change over time is depicted in Figure 2b. Although complementarity in sharing resources can be expected, very often there is an overlap between the needs and physical structures of two or more agroforestry component species. When this occurs, species will compete for resources. In agroforestry systems, this is more the rule than the exception. Complementarity may result in overyielding early on in agroforestry systems, but competition intensifies with time and results in under-yielding in several temperate agroforestry systems (Figure 2b). Thus, agroforestry systems may experience a complex series of inter- and intra-specific interactions guided by modification and utilization of light, water, and nutrients. The following sections discuss important above- and belowground interactions occurring between component species in temperate agroforestry systems.

Aboveground interactions

Microclimatic modification

The presence of trees modifies site microclimate in terms of temperature, water vapor content or par-

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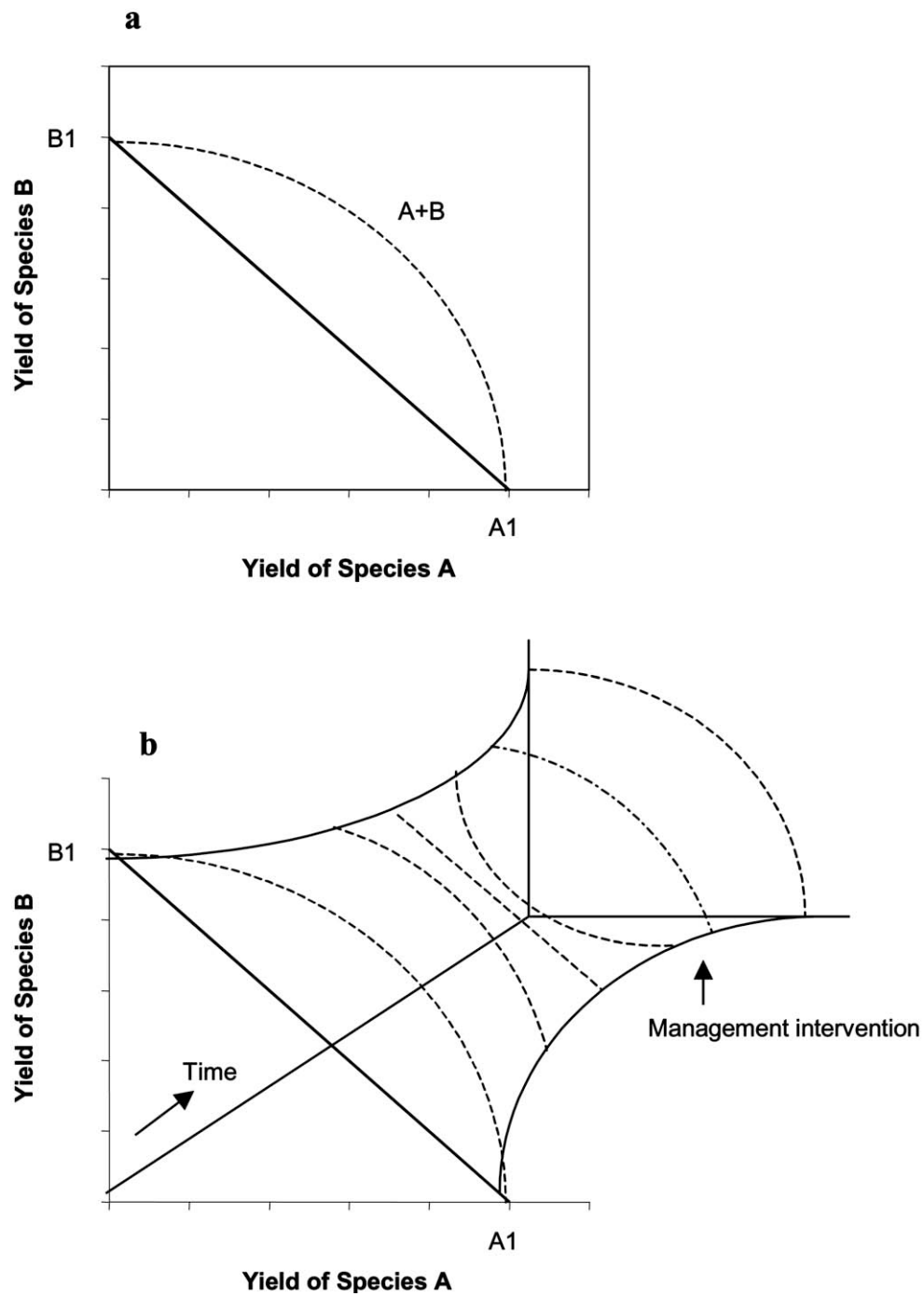
Figure 2. The production possibility curves for two species, A and B. (a) Points A1 and B1 represent the maximum production potential if species A and B were grown in monocultures. Line A1 to B1 represents the proportional yield of species A and B when grown in mixtures. The curve described by A+B represents overyielding (compared to either monoculture yields) of one possible mixture of species A and B. (b) A hypothetical temporal production possibility surface for species A and B (modified from Wojtkowski 1998). As time progresses overyielding gives away to underyielding, but a timely management intervention (e.g., root pruning of trees) alleviates competitive interactions, thereby resulting in overyielding again.

tial pressure, and wind speed, among other factors. Serving as windbreaks, trees slow the movement of air and thus in general reduce evaporative stress. Wind speed was substantially reduced under a radiata pine (*Pinus radiata*) silvopastoral system in New Zealand due to increased tree stocking (Hawke and Wedderburn 1994). Windbreaks are known to improve the distribution and utilization of irrigation water, reduce evapotranspiration, and improve crop water use efficiency (Davis and Norman 1988). Planting windbreaks or shelterbelts in crop fields provides wind protection as well as changes in microclimate; improved crop quality and yield within the sheltered area (10 to 15H, where H is the height of the windbreak) have also been reported (Kort 1988; Brandle et al. 2000; Brandle et al. 2004).

Temperature reductions can help reduce heat stress of crops and/or animals in agroforestry systems. Crops such as cotton (*Gossypium hirsutum*) and soybean (*Glycine max*) have been observed to have higher rates of field emergence when grown at moderate temperatures. For example, Ramsey and Jose (unpublished), in their study of a pecan (*Carya illinoensis*)–cotton alleycropping system in the southern United States, observed earlier germination and higher survival rates of cotton under pecan canopy cover due to cooler and moister soil conditions than in sole system. Similarly, a study in Nebraska, Midwestern United States, showed earlier germination, accelerated growth and increased yields of tomato (*Lycopersicon esculentum*) and snap bean (*Phaseolus vulgaris*) under simulated narrow alleys compared to wider alleys (Bagley 1964; Garrett and McGraw 2000). In addition, studies on *Paulownia* – wheat (*Triticum aestivum*) intercropping in temperate China have shown increased wheat quality due to enhanced microclimatic conditions (Wang and Shogren 1992).

Heat stress has been identified as a major constraint to cattle production in the tropical and temperate regions of the world (Payne 1990; Mitlohner et al. 2001). At high temperatures, evaporative cooling is the principal mechanism for heat dissipation in cattle. It is influenced by humidity and wind speed and by physiological factors such as respiration rate and density and activity of sweat glands. The failure of homeostasis at high temperatures may lead to reduced productivity or even death (Blackshaw and Blackshaw 1994). Providing shade, however, can reduce the energy expended for thermoregulation, which in turn can lead to higher feed conversion and weight gain. In a recent study in Texas, southern United States, Mitlohner

et al. (2001) found that cattle provided with shade reached their target body weight 20 days earlier than those not afforded shade. These authors concluded that cattle without shade had a physiological (i.e., higher respiration rate) and behavioral (i.e., less active) stress response to heat that negatively affected productivity.

The location of shade for livestock in the landscape may have very negative impacts on other communities. For example, trees used for shade along streams in riparian pastures concentrate livestock along the bank and could create major negative impacts on the banks and the stream.

Shading: Is it competition or facilitation?

When plant growth is not limited by water or nutrients, production is limited by the amount of radiant energy that the foliage can intercept (Monteith et al. 1991; Monteith 1994). A number of studies have examined the mechanism of competition for light between perennial woody species and annual crops (Monteith et al. 1991; Knowles et. al. 1999; Gillespie et al. 2000). Biomass growth is dependent upon the fraction of incident photosynthetically active radiation (PAR, 400 to 700 nm wavelength) that each species intercepts, and the efficiency with which the intercepted radiation is converted by photosynthesis (Ong et al. 1996). These factors, in turn, are influenced by time of day, aspect, temperature, CO_2 level, species combination, photosynthetic pathway (C3 vs. C4), canopy structure, plant age and height, leaf area and angle, and transmission and reflectance traits of the canopy, (Brenner 1996; Kozlowski and Pallardy 1997).

Shading by associated tree species has been shown to be a factor in reducing yield in temperate agroforestry systems. For example, low PAR levels resulting from overhead shading significantly reduced yield of winter wheat near tree rows in a *Paulownia* – winter wheat temperate alleycropping system in China (Chirko et al. 1996). Nissen et al. (1999) also reported that both shading and belowground competition decreased the yield of cabbage (*Brassica oleracea.*) in a *Eucalyptus* alleycropping system in the Philippines. Maize (*Zea mays*) and soybean yields were reduced to 75% and 79% of the sole crop yield, respectively, when grown in alleycropping configurations involving poplar (*Populus deltoides* x *nigra* DN-177) and silver maple (*Acer saccharinum.*) in Ontario, Canada (Simpson and Gordon, Personal Communication). Similar results have also been reported for temperate silvopastoral systems. For example, Lin et al. (1999)

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observed significant decreases in mean dry weight of warm season grasses as the amount of light declined.

A few studies have investigated the physiological basis of observed yield reduction in response to shading in agroforestry systems (Jose and Gillespie 1995; Gillespie et al. 2000; Miller and Pallardy 2001). Shading is known to change quality of light reaching the understory canopy: overhead canopies absorb mostly the red and blue portions of the solar spectrum so that diffuse radiation will be richer in orange, yellow, and green wavelengths (Krueger 1981). The phytochrome system of plants interacts with red and infrared wavelengths to influence the amount of growth regulating hormones and thereby growth (Baraldi et al. 1995). Lack of adequate red light is known to influence tillering in grasses (Davis and Simmons 1994a), stem production in clover (*Trifolium* spp.) (Robin et al. 1994), flowering (Davis and Simmons 1994b), and other basic plant growth processes (Sharrow 1999).

As stated earlier, the response to shading may also depend on the differences in carbon fixation pathways of the associated crop species. It is well known that photosynthetic rate (P_{net}) of C3 plants increases sharply as PAR increases from deep shade up to approximately 25% to 50% of full sunlight, then peaks and remains constant as light is increased further (Figure 3). In contrast, the photosynthetic apparatus of C4 plants does not become light-saturated and continues to increase P_{net} up to full sunlight. This difference is related to the respective abilities of C3 and C4 species to use CO_2 (Kozlowski and Pallardy 1997; Lambers et al. 1998). Theoretically, C3 plants planted under shade should be able to perform better than C4 plants and could be better suited for agroforestry practices. Wanvestraut et al. (2004) showed no effect, however, of moderate shading on cotton (C3 species) growth and yield in temperate alleycropping with pecan.

Contrary to an expected yield decrease in maize (a C4 species) in response to shading, Gillespie et al. (2000) reported no effect in two alleycropping systems in the Midwestern United States. This happened despite a strong positive correlation between PAR and P_{net}. These researchers found that, in general, the eastern-most row of maize in a black walnut (*Juglans nigra*) alleycropping system received 11% lower PAR than the middle row (Figure 4). Shading was greater in a red oak (*Quercus rubra*) alleycropping system due to higher canopy leaf area, where a 41% reduction in PAR was observed for the eastern row. Similarly, western rows were receiving 17% and 41% lower PAR in comparison to the middle rows in the black walnut and
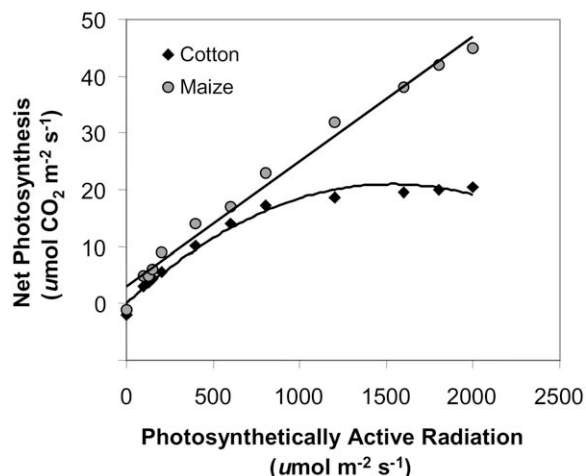

Figure 3. Net photosynthesis as a function of photon flux density in the PAR range in maize (C4 plant) and cotton (C3 plant) (Jose, unpublished data).
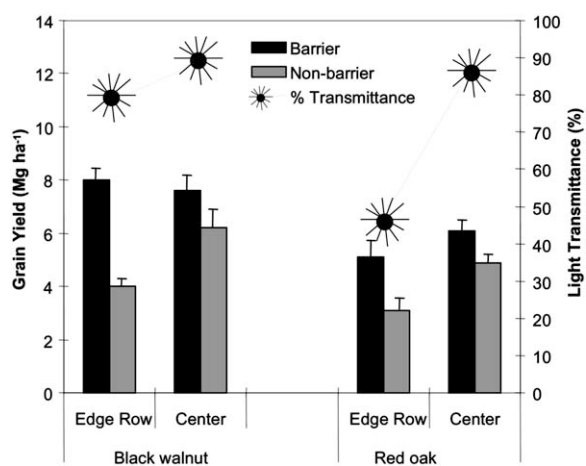

Figure 4. Grain yield of alleycropped maize at the edge (average of eastern and western rows closest to tree row) and alley center in two alley cropping systems involving black walnut and red oak in southern Indiana, United States. Percent light transmittance (as a fraction of full sunlight) reaching the top of edge and center row plants is also shown (Based on data given in Gillespie et al. 2000).

red oak systems, respectively. Irrespective of the shading, no apparent yield reduction was observed when belowground competition for nutrients and water was eliminated through trenching and polyethylene barriers. Leihner et al. (1996) also reported similar findings in maize and concluded that shading played only a minor role in competition at the tree-crop interface.

Positive effects (facilitation) of moderate shading on crop growth have been reported in some cases. Lin et al. (1999) found that two native warm-season legumes, *Desmodium canescens* and *D. paniculatum*,

Table 2. Crude protein and total crude protein of selected grasses and legumes when grown under three levels of shade during 1994 and 1995 at New Franklin, Missouri, USA.

Species	Crude protein (%)			Total crude protein (g pot^{-1})		
	Full Sun	50% Shade	80% Shade	Full Sun	50% Shade	80% Shade
Introduced cool-season grasses						
Kentucky bluegrass	20.3 b	20.7 b	22.7 a	2.45 A	2.58 A	1.57 B
Orchardgrass 'Benchmark'	12.6 c	15.7 b	19.6 a	1.80 A	1.84 A	1.19 B
Orchardgrass 'Justus'	19.8 a	16.7 a	18.5 a	1.60 A	1.92 A	1.79 A
Ryegrass 'Manhattan II'	15.3 b	16.0 b	18.5 a	1.74 A	2.06 A	1.62 A
Smooth bromegrass	16.7 c	18.1 b	20.2 a	1.64 A	2.25 A	1.94 AB
Tall Fescue 'KY31'	14.0 b	15.0 b	18.1 a	1.83 B	2.43 A	1.43 C
Tall Fescue 'Martin'	14.3 b	15.5 b	18.5 a	1.75 A	1.84 A	1.12 B
Timothy	15.4 c	17.6 b	20.4 a	1.60 A	1.59 A	1.12 A
Introduced cool-season legumes						
Alfalfa 'Cody'	19.4 a	19.9 a	19.4 a	1.49 A	1.48 A	1.00 A
White clover	20.1 a	20.6 a	19.9 a	2.49 A	2.03 A	1.23 B
Introduced warm-season legumes						
Striate lespedeza 'Kobe'	13.2 a	13.0 a	12.5 a	3.34 A	2.65 B	1.56 C
Native warm-season legumes						
Slender lespedeza	11.0 a	10.5 a	10.8 a	2.04 A	2.04 A	1.04 A
Desmodium paniculatum	11.6 b	11.7 b	12.9 a	2.57 B	3.53 A	3.38 A
Desmodium canescens	13.0 a	13.2 a	12.8 a	2.19 B	2.98 A	2.88 A
Hog peanut	9.1 ab	8.7 b	9.7 a	0.80 B	2.51 A	2.97 A

Means followed by the same letter within a row do not differ significantly from each other (Tukey's studentized range test, $\alpha = 0.05$).
Adapted from Lin et al. (1999).

exhibited shade tolerance and had significantly higher dry weight at 50% and 80% shade than in full sunlight. These authors also reported that total crude protein content of some of the forage species was greater under 50% and 80% shade than in full sun (Table 2). Burner (2003) reported that orchardgrass (*Dactylis glomerata*) yield across six harvests did not differ among loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) silvopastures compared to yield in open pastures. In addition, orchardgrass persistence was greater in the loblolly pine system (72% stand occupancy) than the open (44% stand occupancy). In another study of a loblolly pine-mixed grass/forb silvopasture, Burner and Brauer (2003) showed that herbage yield was unaffected at alley widths of 4.9 m and above. Light transmittance was as high as 90% at this spacing. Alley widths below 4.9 m had a profound influence on light transmittance. For example, light transmittance was as low as 43% at a spacing of 2.4 m. Herbage yield increased as light transmittance increased from 43% to 92% (Figure 5a). These authors also observed a general increase in herbage

quality (crude protein and digestibility) under silvopasture compared to open grown pasture (Figures 5b and 5c).

Insect density and diversity

Plant–insect interactions are another important factor in the design of agroforestry systems, as variations in tree–crop combinations, and spatial arrangements have been shown to have an effect on insect population density (Vandermeer 1989). According to Stamps and Linit (1998), agroforestry is a potentially useful technology for reducing pest problems because tree-crop combinations provide greater niche diversity and complexity than polycultural systems of annual crops. This effect may be explained in one or more of the following ways: (1) wide spacing of host plants in the intercropping scheme may make the plants more difficult for herbivores to find; (2) one plant species may serve as a trap-crop to prevent herbivores from finding the other crop; (3) one plant species may serve as a repellent to the pest; (4) one plant species may serve to disrupt the ability of the pest to efficiently attack
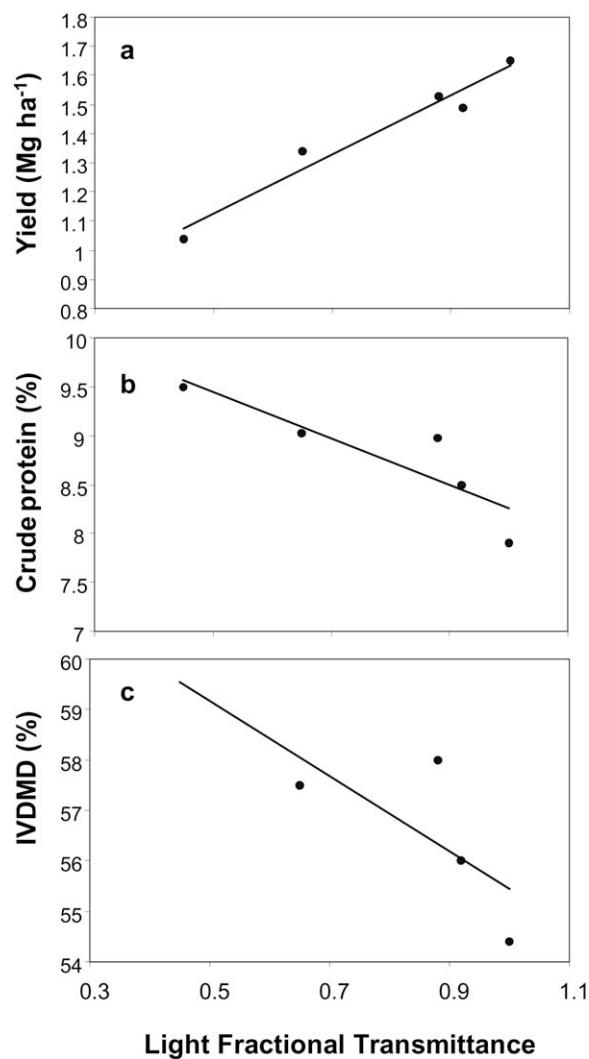
Figure 5. Forage yield, crude protein content, and in vitro dry matter digestibility (IVDMD) as a function of light transmittance in a mixed grass-forb (Bermuda grass and tall fescue being dominant grass) – loblolly pine silvopasture near Booneville, Arkansas, USA. (Based on data given in Burner and Brauer 2003).

its intended host; and (5) the intercropping situation may attract more predators and parasites than monocultures, thus reducing pest density through predation and parasitism (Root 1973; Vandermeer 1989).

The theory of "three trophic level terrestrial interactions" (Price et al. 1980), which states that the addition of a predator to a system of herbivores will lower the density of the herbivores, explains the basis of the predator-prey interactions and related biological pest control observed in agroforestry settings. Studies with pecan, for example, have looked at the influence of ground covers on arthropod densities in tree-crop sys-

tems (Bugg et al. 1991; Smith et al. 1996). Bugg et al. (1991) observed that cover crops (e.g. annual legumes and grasses) sustained lady beetles (Coleoptera: Coccinellidae) and other arthropods that may be useful in the biological control of pests in pecan. Stamps et al. (2002) observed similar results in a black walnut-based alleycropping system in Missouri in Central United States. Alleycropped forages (*Medicago sativa* and *Bromis inermis*) supported a more diverse and even arthropod fauna than adjacent monocropped forages (Table 3). In another alleycropping trial with peas (*Pisum sativum*) and four tree species (*Juglans*, *Platanus*, *Fraxinus* and *Prunus* sp.), Peng et al. (1993) found an increase in insect diversity and improved natural-enemy abundance compared to monocultured peas. The greater diversity of birds that are found in agroforestry systems compared to monoculture agronomic systems (Gillespie et al. 1995; Schultz et al. 2000) could also provide the beneficial service of pest reduction to adjacent crops. Although beyond the scope of this discussion, the competitive activity of belowground pests is another important consideration in agroforestry (Ong et al. 1991).

Belowground interactions

Competition for water and/or nutrients

Belowground competition is most likely to occur when two or more species have developed a specialized root system that directs them to explore the same soil strata for resources (van Noordwijk et al. 1996). This interaction can be problematic even in mixed-species systems. Researchers in the temperate zone, humid tropics, and semiarid tropics have reported observing the greatest concentration of tree-root density within the top 30 cm of soil, the region predominantly explored by crop root systems (Itimu 1997; Lehmannn et al. 1998; Imo and Timmer 2000; Jose et al. 2000b). For example, the root systems of all component species in two temperate alleycropping systems, consisting of maize and black walnut or red oak, were found to most heavily occupy the top 30 cm of soil and to decrease in density with depth. Consequently, maize yields were reduced by 35% and 33% for black walnut and red oak systems, respectively (Jose et al. 2000b).

Although it is difficult to separate the belowground competition for water from that for nutrients, it is widely recognized that crop production in agroforestry systems in semiarid regions is likely to be limited by

Table 3. Shannon diversity indices and evenness for arthropods found in alley cropped and monoculture alfalfa over two years of sampling in Missouri, USA.

Year	Alfalfa	Herbivores		Predators		Parasitic Hymenoptera	
		Shannon Index	Evenness	Shannon Index	Evenness	Shannon Index	Evenness
1997	Alley cropped	1.04 (0.33)	0.56 (0.17)	**0.42 (0.25)**[a]	**0.31 (0.18)**	**0.15 (0.15)**	**0.12 (0.16)**
	Monocropped	1.16 (0.36)	0.58 (0.13)	**0.17 (0.12)**	**0.13 (0.08)**	**0.04 (0.05)**	**0.05 (0.06)**
1998	Alley cropped	1.30 (0.31)	0.59 (0.15)	**0.29 (0.16)**	**0.23 (0.17)**	0.03 (0.04)	0.02 (0.05)
	Monocropped	1.23 (0.37)	0.54 (0.16)	**0.16 (0.09)**	**0.11 (0.10)**	0.03 (0.04)	0.02 (0.03)
Total	Alley cropped	1.17 (0.35)	0.57 (0.16)	**0.36 (0.22)**	**0.27 (0.18)**	**0.09 (0.12)**	**0.07 (0.13)**
	Monocropped	1.19 (0.36)	0.56 (0.14)	**0.17 (0.11)**	**0.12 (0.09)**	**0.04 (0.04)**	**0.03 (0.05)**

[a]Bold face indicates significant differences between treatments (i.e., alleycropped vs.monocropped) within a given year or for the total study period. Values in parentheses indicate SE.
Source: Adapted from Stamps et al. (2002).

competition for water. When considering alleycropping systems in the temperate regions, it is not clear as to which competitive vector will limit productivity, although competition for water has been reported to limit system productivity. In Indiana, United States, Gillespie et al. (2000) observed reductions in alley-grown maize yield, between rows of black walnut, when compared to alley-grown maize where a polyethylene root barrier separated interspecific belowground interactions. In the barrier-separated treatments, maize yield from plants grown adjacent to the tree-row were comparable to the yield of maize grown in the alley center, despite shading from the tree-row. Jose et al. (2000a), in a companion study to Gillespie et al. (2000), quantified competition for water in that system and concluded that severe interspecific competition for water was occurring.

In another temperate-zone alleycropping system with silver maple and maize in northeastern Missouri, United States, Miller and Pallardy (2001) also found competition for water to reduce crop yields by 22% to 27%. The presence of a root barrier increased soil water availability in the crop alley, a result reported from other temperate trials as well (Jose et al. 2000a; Hou et al. 2003). These authors further observed significantly higher predawn leaf water potential for maize grown at the tree–crop interface with the root barrier compared to plants without the root barrier (Figure 6). In a similar trial using belowground root barriers in Ohio, United States, Ssekabembe et al. (1994) showed that soil water was higher within the alley in the barrier treatment than the nonbarrier treatment where black locust (*Robinia pseudoacacia*) hedgerows depleted soil water.

Competition for water was also the primary determinant of cotton productivity in a pecan-cotton alleycropping system in the southern United States (Wanvestraut et al. 2004). Cotton lint yield was 26% lower in the nonbarrier treatment compared to one in which a trenched barrier was present. Plants in the barrier treatment outperformed those in the nonbarrier treatment beginning early in the growing season and were 26% taller than non-barrier plants by the end of the growing season. A difference in leaf area development was noticeable by week 5 and led to a 47.3% difference by the end of the growing season. Jose et al. (2000a) also reported a 21% increase in maize leaf area in the barrier treatment of the previously mentioned black walnut – maize alleycropping system. Water stress has been found to cause large reductions in plant height (NeSmith and Ritchie 1992a; Robertson 1994), and leaf area (Gavloski et al. 1992; NeSmith and Ritchie 1992b) in crop plants. Since leaf elongation is the first process inhibited by water stress (Hsiao 1973; Taiz and Zeiger 1991), it is plausible that plants without barrier in these examples were experiencing severe water stress. It should be noted, however, that the competitive interactions involving water become more intense as soil water gets depleted (Miller and Pallardy 2001). As a result, the degree to which competition for water limits productivity will ultimately depend on the precipitation pattern of a given area, especially in the absence of irrigation.

Research reports on competition for nutrients in temperate agroforestry are rather limited (Jose et al. 2000b; Miller and Pallardy 2001; Allen 2003). Many of the reported agroforestry systems were fertilized at the conventional agronomic level as needed for the crop component. In their silver maple–maize alleycropping trial, Miller and Pallardy (2001) applied the standard rate of N fertilization (179 kg N ha^{-1}) and a supplemental rate (standard + 89.6 kg ha^{-1})
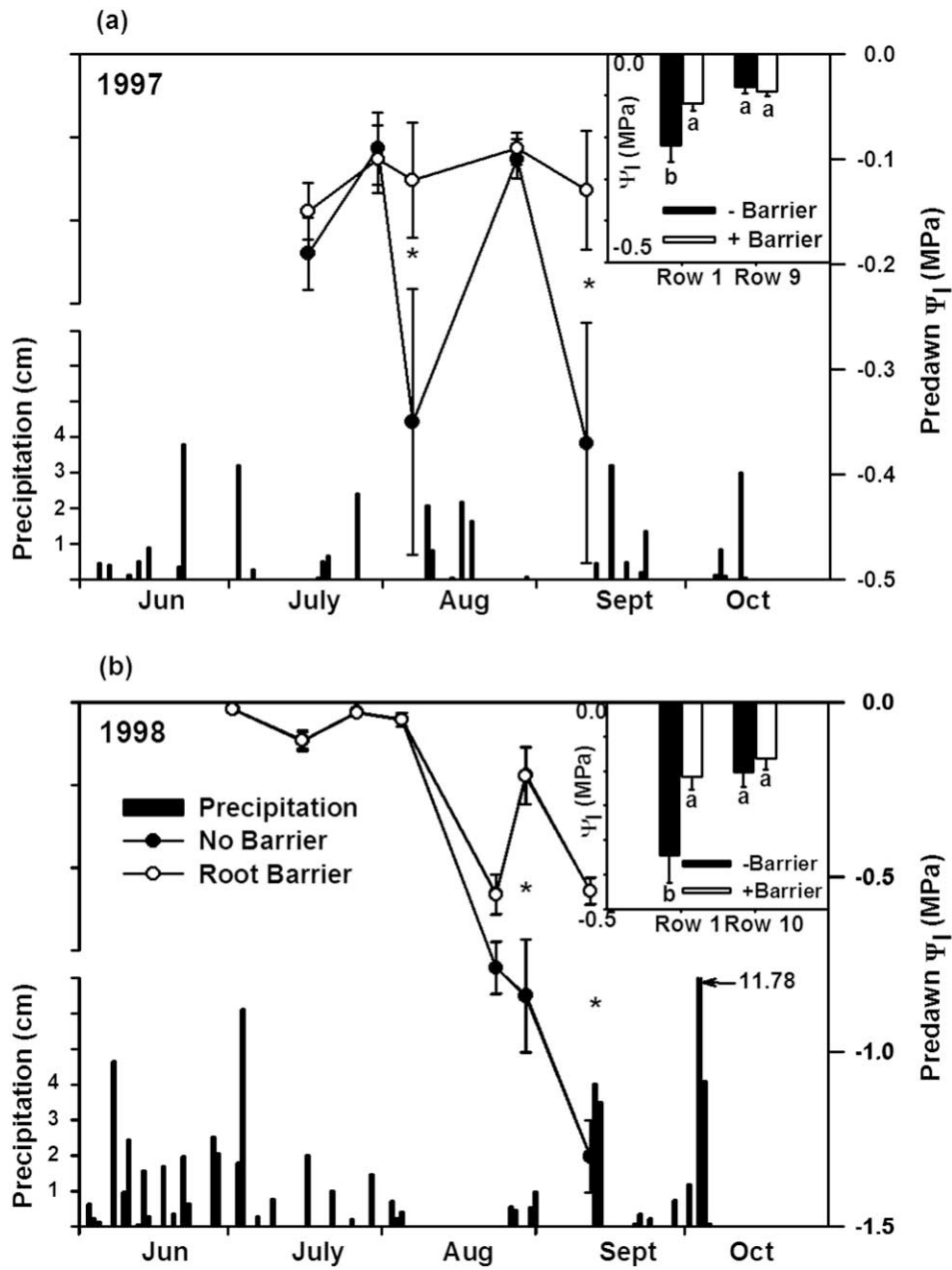
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Figure 6. Seasonal patterns of predawn leaf water potential (Ψ_l) for the first row of maize adjacent to the tree row (line graphs) and seasonal means for adjacent and center rows of maize (insets) during 1997 (a) and 1998 (b) in a maize-silver maple alley cropping practice in north-central Missouri, United States. Significant treatment and row differences ($P < 0.05$) indicated by * or different letters; error bars indicate ± 1 SE (Reprinted from Miller and Pallardy) 2001).

and concluded that soil nitrogen status had little effect on maize physiology and yield. Jose et al. (2000b) reported that competition for fertilizer nitrogen was minimal in their black walnut–maize alleycropping system, since nutrient acquisition was not simultaneous among the system's components. Water availability, however, was a factor in nutrient competition, as competition for water by tree roots was responsible for reduction in biomass in intercropped maize, resulting in decreased efficiency of fertilizer use (Jose et al. 2000b). Similarly, in a poplar (*Populus* sp.) – barley (*Hordeum vulgare*) system in southern Ontario, associated trees and crops utilized different sets of soil nutrient resource horizons (Williams et al. 1997; Thevathasan and Gordon 2004). Significant competition and resultant yield decrease eventually can be expected in the absence of fertilization in most temperate agroforestry systems.

Allelopathy

Allelochemicals are present in many types of plants and are released into the rhizosphere by a variety of mechanisms, including decomposition of residues, volatilization, and root exudation. Allelochemicals are known to affect germination, growth, development, distribution, and reproduction of a number of plant species (Inderjit and Malik 2002). The degree to which these allelopathic chemicals inhibit growth depends upon their production rates and residence times as well as the combinations in which they are released into the ecosystem. While there are many unanswered questions and concerns about allelopathy in agroforestry, there are a few examples from temperate systems where allelopathy could be reducing crop yield. Two of the most widely used examples are those of black walnut and pecan, two commonly used tree species in temperate agroforestry. It has long been recognized that the principal chemical responsible for walnut and pecan allelopathy is a phenolic compound called juglone (5-hydroxy-1,4-naphthoquinone) (Davis 1928).

Several reported studies using known concentrations of juglone (ranging from 10^{-6} to 10^{-3} M) applied either in hydroponic or soil culture have shown inhibitory effects on survival and growth of several herbaceous and woody plants (Table 4). For example, Rietveld (1983) investigated the sensitivity of 16 species of herbs, shrubs, and trees to juglone in solution culture with juglone concentrations varying from 10^{-3} M to 10^{-6} M. Although seed germination and radicle elongation were not affected in all species,

shoot elongation and dry weight accumulation were affected. Many species were sensitive to juglone concentrations as low as 10^{-6} M. Seedlings of all species were severely wilted and eventually killed by 10^{-3} M juglone.

Interest in quantifying the effects of juglone on field crops has resulted in recent hydroponic experiments using corn and soybean (Jose and Gillespie 1998a), the two major field crops planted in black walnut-based alleycropping systems of North America. Three different concentrations of juglone (10^{-4}, 10^{-5}, and 10^{-6} M) along with a juglone-free control treatment were applied to maize and soybean in solution culture. Within three days, juglone induced significant inhibition of shoot and root relative growth rates. In general, soybean was more sensitive to juglone than was maize. Root relative growth rate was the most inhibited variable for both species, and reductions of 86.5% and 99% in this variable were observed in maize and soybean, respectively, at 10^{-4} M juglone concentration.

Actual juglone concentrations in the field may not be as high as 10^{-4} M (Jose and Gillespie 1998b; Thevathasan et al. 1998; Thevathasan and Gordon 2004). Also, under certain soil conditions, juglone may be oxidized to non-toxic forms. For example, Fisher (1978) found that the inhibitory activity of juglone disappeared under low soil water regimes. Although reduced growth of maize in the field under black walnut has been attributed to competition for water (Jose et al. 2000b), the results of Jose and Gillespie (1998a) indicate a possibility of juglone phytotoxicity. Similarly, soybean yield reduction under black walnut (Seifert 1991) may also be partly explained by the toxic effects of juglone. Interestingly, certain annual species may induce allelopathic effects on trees as well. For example, Smith et al. (2001) administered allelochemical-containing leachates to container-grown pecan trees, and found that tall fescue (*Festuca arundinacea*), bermudagrass (*Cynodon dactylon*) and cutleaf evening primrose (*Oenothera laciniata*) leachate decreased pecan trunk weight by 22%, root weight by 17%, and total tree dry weight by 19%, compared to the control treatment.

Reports of tropical tree species providing allelochemicals through leaf litter, and in turn, providing pest control for associated agronomic species are common in the agroforestry literature (Rizvi et al. 1999). Similar complementary examples are yet to be reported from temperate systems.

Table 4. Percent change in shoot and root dry weights of seedlings grown at different juglone concentrations in hydroponic cultures. A negative change means growth was reduced whereas a positive change means growth was enhanced compared to control seedlings.

Species	Shoot dry weight (%)			Root dry weight (%)		
	Concentration of juglone (M)					
	10^{-6}	10^{-5}	10^{-4}	10^{-6}	10^{-5}	10^{-4}
Herbs[a]						
Crimson clover (*Trifolium incanatum*)	−15	−50	−81	11	−50	−78
Crown vetch (*Coronilla varia*)	2	−83	−94	−1	−82	−97
Hairy vetch (*Vicia villosa*)	2	−29	−67	−10	−10	−57
Korean lespedeza (*Lespedeza stipulacea*)	−9	−47	−27	14	−29	−14
Sericea lespedeza (*L. cuneata*)	−30	−72	−92	−6	−63	−88
Shrubs[a]						
Ginnala maple (*Acer ginnala*)	67	64	−35	−35	−28	−83
Siberian peashrub (*Caragana arborescens*)	24	−46	−83	−14	−72	−91
Russian olive (*Elaeagnus angustifolia*)	−16	32	−92	8	99	−75
Autumn olive (*E. umbellata*)	−45	−65	−94	−18	−41	−88
Amur honeysuckle (*Lonicera maackii*)	−41	−61	−91	−55	−61	−94
Trees [b]						
White pine (*Pinus strobus*)	−7	−3	−31	−33	−29	−50
Scotch pine (*P. sylvestris*)	−38	0	−63	−50	0	−25
Japanese larch (*Larix leptolepis*)	−36	−14	−71	−20	0	−60
Norway spruce (*Picea abies*)	20	−20	−20	17	−17	−16
White oak (*Quercus alba*)	−23	−41	−53	−21	−27	−20
White ash (*Fraxinus americana*)	−20	−58	−83	−7	−31	−71
European black alder (*Alnus glutinosa*)	−33	−86	−94	−26	−87	−94
Yellow poplar (*Liriodendron tulipifera*)	19	8	−72	4	−20	−77
Row crops [c]						
Corn (*Zea mays*)	4	−29	−56	6	−39	−61
Soybean (*Glycine max*)	−11	−37	−33	−9	−48	−56

[a]Seedlings were grown for 4 to 6 weeks; source: Rietveld (1983).
[b]Seedlings were grown for 8 to 10 weeks for white pine, scotch pine, Japanese larch, and Norway spruce; source: Funk et al.(1979); the rest of the tree seedlings were grown for 4 to 6 weeks; source: Rietveld (1983).
[c] Seedlings were grown for 3 days; source: Jose (1997).

Safety net role

Intensive agricultural practices have led to inefficient use of applied nitrogen and to contamination of surface and subsurface water through nitrate leaching (Bonilla et al. 1999; Ng et al. 2000). The "safety net" hypothesis of nutrient capture assumes that the deep roots of trees are capable of retrieving nitrate-N and other nutrients that have leached below the rooting zone of associated agronomic crops, and of eventually recycling these nutrients as litterfall and root turnover in the cropping zone. Also, the longer temporal activity of tree roots, even at the same strata, help capture nutrients before and after a crop is planted and harvested. This would essentially increase the total resource-use efficiency of the system (van Noordwijk et al. 1996). The vertical distribution of a given species' root system in its native habitat may often exhibit a signature pattern. This can lead to overlapping vertical root distributions if two or more species have evolved in similar environments. The result is often less than optimum (biologically) growth for one or more of the species involved. Many plant species, however, have shown some degree of plasticity (ability to respond to changes in local nutrient supplies or impervious soil layers) in their vertical (as well as lateral) distribution. Plants also exploit plasticity to avoid competition (Ong et al. 1996; Schroth 1999).

Spatial separation of root architectures can be induced under certain circumstances leading to a more complementary situation. In the previously mentioned alleycropping system consisting of cotton and pecan, Wanvestraut et al. (2004) observed that cotton roots exhibited a degree of plasticity, being limited to shallower soil strata and avoiding a region of high pecan root density deeper in the soil. From the same study site, Allen (2003) reported a 34% reduction in nitrate nitrogen concentration in the soil solution at 0.9 m depth when pecan and cotton roots were not separated by a root barrier compared to the root barrier treatment, potentially indicating the safety net role of pecan roots.

The safety net concept can also be applied in explaining the sediment and nutrient capture functions of riparian buffers. Riparian buffers are widely recommended as a tool for removing non-point source pollutants from agricultural areas (Addy et al. 1999; Bharati et al. 2002; Lee et al. 2003; Schultz et al. 2004). In a recent study of a riparian buffer strip in central Iowa, Midwestern United States, Lee et al. (2003) compared the efficiency of a switchgrass (*Panicum virgatum*) buffer, a switchgrass/woody buffer, and a no buffer treatment located at the lower end of agronomic field plots. The switchgrass buffer removed 95% of the sediment, 80% of the total N, 62% of the nitrate-N, 78% of the total P, and 58% of the phosphate-P. The switch grass/woody buffer removed 97% of the sediment, 94% of the total N, 85% of the nitrate-N, 91% of the total-P, and 80% of the phosphate-P in the runoff. While the switchgrass buffer was effective in removing sediment and sediment-bound nutrients, addition of woody species increased the removal efficiency of soluble nutrients by over 20%. The 'nutrient-capture' functions of trees and other plants are also being exploited in phytoremediation of contaminated sites (Rockwood et al. 2004) and explored in the rehabilitation of heavily fertilized agricultural systems in North America (Nair and Graetz 2004).

Hydraulic lift

Hydraulic lift, the process in which some deep-rooted plants take in water from lower soil layers and release that water into upper, drier soil layers, has been reported to be an appreciable water source for neighboring plants (Corak et al. 1987; Caldwell and Richards 1989). Recent evidence shows that this phenomenon can help promote greater plant growth, and could have important implications for net primary productivity, as well as ecosystem nutrient cycling and water balance (Horton and Hart 1998).

In an agroforestry context, trees can benefit associated crop plants through the mechanism of hydraulic lift, thus providing more water during dry periods (Dawson 1993; van Noordwijk et al. 1996; Burgess et al. 1998; Ong et al. 1999). Although hydraulic lift has been reported in such genera as *Quercus*, and *Pinus* with potential for agroforestry (Ishikawa and Bledsoe 2000; Penuelas and Filella 2003), direct beneficial evidence is not yet available from temperate agroforestry systems.

N_2-fixation and sharing

Biological nitrogen fixation by tree, crop, or both components of agroforestry systems has received a lot of attention in the tropics (Nair et al. 1999). Despite its biological importance, such reports are rare in the temperate agroforestry literature. Although there are 650 woody species belonging to nine families that are capable of fixing atmospheric nitrogen, relatively few occur in the temperate regions of the world. Temperate-zone nitrogen fixing trees and shrubs with potential for agroforestry include *Robinia, Prosopis*, and *Alnus* (Table 5). Some evidence exists from a temperate alleycropping system where significant transfer of fixed nitrogen to associated crop species has been reported. Seiter et al. (1995) using ^{15}N injection technique demonstrated that 32% to 58% of the total nitrogen in maize was derived from nitrogen fixed by associated *Alnus rubra* in an alleycropping system, and that nitrogen transfer decreased with increasing distance from trees, in Oregon, United States.

Herbaceous legumes in alleycropping and silvopastoral systems are capable of fixing substantial amounts of atmospheric nitrogen as well (Table 5). Annual nitrogen fixation rates exceeding 350 kg N ha^{-1} have been reported in temperate pastures (Sharrow 1999). Although direct transfer of fixed nitrogen from legumes to associated tree species is possible, this can be a slow process, which requires several years for sufficient enrichment of soil nitrogen levels to benefit tree growth. One of the best-known examples from temperate silvopasture is that reported by Waring and Snowdon (1985), who observed decreased growth of *Pinus radiata* for the initial three years in a silvopasture with subclover. At the end of the seventh growing season, however, soil nitrogen was increased by 36% and tree diameters by 14% in

Table 5. Nitrogen fixation potential of selected tree and crop species suitable for temperate agroforestry systems.

Species	Typical levels of N_2-fixation (kg ha^{-1} yr^{-1})	Source
Leguminous		
Trees/shrubs		
Black locust (*Robinia pseudoacacia*)	30–35	Boring and Swank (1984)
Leucaena (*Leucaena leucocephala*)	100–500	Sanginga et al. (1995)
Mesquite (*Prosopis glandulosa*)	20–50	Sharifi et al. (1982)
Silk tree (*Albizia julibrissin*)	60–70[a]	Rhoades et al. (1997)
Herbaceous species		
Alfalfa (*Medicago sativa*)	148	Butler and Evers (2003[b])
Clover (*Trifolium* spp.)	42–400	Butler and Evers (2003)
Hairy vetch (*Vicia villosa*)	90–100	Butler and Evers (2003)
Soybeans (*Glycine max*)	60	Troeh and Thompson (1993)
Non-leguminous trees and shrubs Alder (*Alnus* spp.)	48–185	Daniere et al. (1986)
Autumn olive (*Elaeagnus umbellata*)	236	Paschke et al. (1989)
Snowbrush (*Ceanothus velutinus*)	24–101	McNabb and Cromack (1985)

[a]Estimated based on data given in Rhoades et al. (1997).
[b] Butler and Evers, Pers. Comm.

silvopasture compared to *P. radiata* monoculture. Van Sambeek et al. (1986) and Dupraz et al. (1999) have also reported similar growth increases in black walnut when interplanted with leguminous forage crops in the Midwestern United States and southern France, respectively.

Modeling interactions

Models help synthesize experimental and empirical evidence on how different components of an agroforestry system interact in space and time. They also help extrapolate research results to new suite of climate, soil, species and management, which are too numerous to be studied with field experiments. Earlier modeling efforts focused on integrating separately developed crop and tree models into agroforestry models and were not very successful (van Noordwijk and Lusiana 1999). Recent models, however, integrates the principles of above- and belowground resource capture and utilization in mixed cropping systems (van Noordwijk and Lusiana 1999). A variety of computer-based models (e.g., HyPAR; SBELTS; WaNuLCAS) with application to agroforestry have been developed in recent years (Mobbs et al. 1998; van Noordwijk and Lusiana 1999; Qi et al. 2000). Many of them fail to

allow for the role of animal production and the associated interactions and management challenges. A recent model (ALWAYS; Alternative Land-use With Agroforestry Systems) offers promise in simulating the complex biophysical functioning of silvopastoral systems (Balandier et al. 2003). Although we have made considerable progress in modeling interactions, many models oversimplify the biophysical processes that are central to predicting the component yields. Considerable improvement is needed in making models a viable tool for selecting site-specific agroforestry combinations and making yield predictions. Since the topic is so advanced a detailed discussion is neither warranted nor feasible here.

Lessons learned

Although certain temperate agroforestry systems such as alleycropping, silvopasture, and windbreaks are well researched for their ecological viability and suitability, many other systems have received little attention. For example, forest farming is gaining popularity among landowners in temperate North America; but has received little or no research attention in this area. Similarly, design considerations and environmental benefits of riparian buffers have received considerable attention (e.g., Schultz et al. 2004), but the complex

ecological interactions among its components still remain to be explored. In spite of these deficiencies, the following generalizations can be drawn based on the available literature on interspecific interactions in temperate agroforestry systems.

1. Aboveground competition for light is minor in several of the reported alleycropping systems. Shading, however, has been shown to decrease yield of associated forage species in silvopastoral systems. But, competition for light can be managed in design or maintenance of agroforestry systems.

2. Shading has generally been favored for higher quality forage and better cattle performance and production in a few of the available silvopastoral examples.

3. Competition for nutrients is minimal as most of the temperate agroforestry systems are managed with high input of inorganic or organic nutrient supplements.

4. Some evidence exists for the safety net role of trees from temperate alleycropping and riparian buffer strips. It is likely that this concept can be incorporated into the design of other agroforestry systems.

5. Competitive interactions involving water seem to be the most influential driving force of productivity in both alleycropping and silvopastoral trials.

6. The role of allelopathy in temperate agroforestry is still ambiguous, despite the widespread use of such potentially allelopathic species as black walnut and pecan in alleycropping and silvopastoral systems.

7. Evidence of increased insect diversity exists in certain specific alleycropping examples. Some beneficial arthropods are reported to be controlling pests in pecan-clover or black walnut-alfalfa alleycropping. Riparian forest buffers may also provide a refuge for beneficial insects and birds.

8. Although a few N_2-fixing trees and shrubs have potential to be incorporated into temperate agroforestry practices, their use is limited as revealed by the literature. N_2-fixing herbaceous plants have been widely used in silvopastoral examples and soil enrichment and tree growth enhancement have been reported.

Research needs

A thorough understanding of the interactions among trees, crops, animals, and their associated fauna is necessary to determine the sustainability and profitability of agroforestry systems. Although considerable progress has been made in our understanding of the complex interactions, it is limited to only a few practices in certain regions. For example, many of the examples used in this review come from alleycropping systems in the Midwestern United States involving black walnut. Since many other systems are in the formative stages of research and adoption, much more baseline information is needed in order to establish guidelines for tree–crop interactions of specific systems. To optimize production and sustainability of these systems, major research initiatives are needed in a number of areas. These include:

1. Testing of other tree and herbaceous species for different temperate agroforestry systems.

2. Study of cultural practices that would minimize competition and maximize niche separation (e.g., repeated trenching to train trees to root deeply over the lifespan of alleycropping systems, simple agronomic disking on a periodic basis, knifing of fertilizer, etc.).

3. Genetic modification of components to increase productivity and reduce competition. For example, (a) genetic selection for vertical root morphology in both tree and crop components, (b) selection for greater tolerance of shade in the crop component.

4. Continued use of modeling component interactions: modeling provides a means for integrating different positive and negative interacting vectors so that resource allocation and yield can be predicted.

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