Invited Review

Tree legumes: an underexploited resource in warm-climate silvopastures

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ABSTRACT - Tree legumes are an underexploited resource in warm-climate silvopastures. Perceived benefits of tree legumes include provisioning (browse/mast, timber, fuel, human food, natural medicines, and ornamentals), regulating (C sequestration, greenhouse gas mitigation, soil erosion control and riparian buffers, shade, windbreaks, and habitat for pollinators), supporting (biological N₂-fixation, nutrient cycling, soil fertility and soil health, photosynthesis, and primary productivity), and cultural ecosystem services. Tree legumes, however, have not been assessed to the same extent as herbaceous legumes. Once tree legumes are established, they are often more persistent than most herbaceous legumes. There are limitations for extended research with tree legume silvopastures, but extensive research has been done in Africa and Australia and recent efforts have been reported in South America. Economic benefits must be demonstrated to land managers to increase adoption. These benefits are apparent in the research and successes already available, but more long-term research, including the livestock component is necessary. Other factors that reduce adoption include paucity of domesticated germplasm, lag in research/technology, challenges of multipurpose trees and management complexity, challenges to mechanization, dangers of invasive weeds, and social and cultural barriers. In the current scenario of climate change and the need to increase food security, tree legumes are a key component for the sustainable intensification of livestock systems in warm-climate regions.

Key Words: biological N₂ fixation, ecosystem services, grassland, nutrient cycling, tropical

Introduction

Tree legumes are an underexploited resource in warm-climate grasslands. Substantial research efforts have been put towards domestication and use of herbaceous legumes, with some failures, but also some success stories (Shelton et al., 2005). Tree legumes, however, have not been assessed to the same extent as herbaceous legumes. There have been successes in Africa (Wambugu et al., 2011; Franzel et al., 2014), Asia (Hasniati and Shelton, 2005), Australia (Virgona et al., 2012), and South America (Xavier et al., 2014; Hernández-Muciño et al., 2015;

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Apolinário et al., 2015), but the extent of their adoption in livestock production systems is still limited. There are several tree legume species with potential for utilization in extensively managed warm-climate areas. The wide adaptation potential of these legumes, ranging from semiarid to humid and sub-humid areas, increases the scope of their utilization. Tree legumes in silvopastoral systems provide different ecosystem services (ES), including, but not limited to, biological N, fixation (BNF), diversification of livestock diets, C sequestration, shade for livestock, flowers for pollinators, biodiversity conservation, and reduction of greenhouse gas (GHG) emissions (Dubeux et al., 2015). Once they are established, tree legumes are often more persistent than most herbaceous legumes. Therefore, there is a need to intensify the research efforts addressing domestication and utilization of tree legumes in warm-climate grasslands.

Increasing human global population in the last century has led to extensive exploitation of natural resources. Land-use changes and excessive fossil fuel use are among the top reasons currently linked to climate change (Whitmee et al., 2015). Nitrogen fertilizers also represent a large C footprint because of natural gas used in the manufacturing

process (Lal, 2004). Therefore, producing more food to sustain growing human population without further harming the environment poses a formidable challenge. Tedeschi et al. (2015) defined sustainable intensification as the production of more output(s) through the more efficient use of resources, while minimizing negative impact on the environment. Incorporation of tree legumes into livestock production systems could be a possible approach to sustainable intensification that has now been recognized as a promising development paradigm (Tedeschi et al., 2015). Compelling reasons for that include the increase in primary productivity, reduction of N fertilizer inputs, and greater C sequestration (above- and below-ground) when introducing a N₂-fixing tree legume in a grassland system. The ultimate goals are to increase livestock production and the provision of other ES at the same time.

Greater diversity of plant species (i.e. species richness) and plant functional groups increases stability and primary productivity of grasslands (Tilman et al., 1996). Greater efficiency in resource utilization, both spatial and temporal, is one of the major gains with increasing biodiversity. Multispecies grasslands also increase their resilience and stability. Tree legumes add N to the system, which sustains the growth of perennial warm-season grasses. Grasses cover the soil, thereby reducing erosion and promoting soil organic matter because of their recalcitrant and extensive root system (George et al., 2013). Nitrogen uptake by grasses also stimulates BNF by legumes (Nyfeler et al., 2011). These mutual benefits of complementary resource use in grass-legume mixtures promote a viable option for sustainable intensification. This review will address major aspects of tree legume incorporation in animal production systems, including the ES provided by tree legumes and their domestication, utilization, and adoption in warmclimate grasslands.

Ecosystem services provided by tree legumes

Trees in silvopastures provide a wide range of products and ES as managers seek to diversify consumables as well as income beyond the herbaceous pasture as means of risk avoidance and income diversification (Brenes, 2004); Frey et al., 2012). These can be broadly divided into the following categories: provisioning, regulating, supporting, and cultural services according to the guidelines of the Millennium Ecosystem Assessment report of the United Nations (MEA, 2005) [MEA (2005) Millennium ecosystem assessment: Ecosystems and human well-being synthesis. Island Press, Washington D.C.].

Provisioning ES

Provisioning ES encompass the products obtained from ecosystems. These include, but are not limited to, food for humans, forage for livestock, fiber, fuel, genetic resources, biochemicals, natural medicines, ornamental resources, and fresh water.

Browse and mast

Browse for direct animal intake, although not obligatory, is perhaps the most common silvopastoral product. Leaves, mast, and seed pods from these trees can be important feed sources (Kneuper et al., 2003). Animals consuming this arboreal forage produce progeny, meat, milk, fiber, hides, and transport (McDowell, 1977). Milk and meat, in particular, are important human dietary components in otherwise cereal-dominated diets (Fanzo, 2014). Especially in drier climates, these animals also contribute indirect socio-economic benefits such as status, economic stability, and buffer against climatic fluctuations (McDowell, 1977; Maxwell et al., 2012; Mlambo and Mapiye, 2015). Although ruminants are most often considered in this formula (Muir and Massaete, 1997; Nguluve and Muir, 1999), monogastrics such as chickens, rabbits, and pigs (Muir et al., 1992; Muir and Massaete, 1995) can also consume browse. Leaves and edible stems can be harvested by the animal (Muir and Massaete, 1997) via the manager as cut-and-carry (Fujisaka et al., 2000), mechanized green chop (Felker et al., 1991), or as litter (Sanchez et al., 2007).

Because of their deep roots that reach sub-surface moisture, the arboreal browse can be particularly important in arid climates during dry seasons or years when herbaceous forage is scarce (Zampaligre et al., 2013; Mlambo and Mapiye, 2015). In addition, because of their ability to fix atmospheric N, these trees are usually considered for silvopasture because of the protein they offer. This not only provides N to the animals directly, but in the case of ruminants, can also contribute to more efficient energy, namely plant fiber, use from herbaceous canopy forages, especially grasses (Singh and Kundu, 2010). Other nutrients directly contributed include soluble energy, dietary fiber as well as numerous minerals and vitamins. Additionally, arboreal browse can contribute nonnutrient plant fractions, such as condensed tannins, which can constrain animal nutrition (D'Mello, 1992; Grainger et al., 2009), but can also be essential for animal health (Muir, 2011). We are not always certain whether these

non-nutrient plant components increase or decrease browse palatability (Adams et al., 2013), especially if the browser has heavy gastrointestinal parasite loads and self-medicates through appetite mechanisms (Provenza et al., 2015).

Timber

Timber is among the most important products in silvopastoral systems (Kuntashula and Mafongoya, 2005). A tradeoff between forage and wood production (Muir, 1998) means that manager or market priorities dictate manipulation favorable to one or the other. The importance of timber is often underestimated, because it is harvested sporadically and used locally. However, in some systems, it provides land managers with renewable income that often exceeds that derived from animal production. This income varies by species in local markets (Apolinário et al., 2015), because wood can exhibit very different fuel and tensile qualities (Erakjrumen, 2009).

These qualities are especially important in tropical regions where insect and microbial attack result in high degradation rates (Stangerlin et al., 2013). Many silvopastoral tree species are selected for their easy establishment and quick growth/regrowth rates, which also mean they are not as useful for timber. As a consequence, some systems specifically integrate non-leguminous hardwood or pine species that do not necessarily provide forage but, rather, are harvested at long intervals for sale. In such systems, forage production is limited to the herbaceous layer. Examples include cork production in southern Europe (Bergmeier et al., 2010) and mahogany in the humid tropics (Quinto et al., 2009). A concerted effort to identify and domesticate leguminous trees with hardwood characteristics could combine the advantages of biological N₂ fixation with timber quality.

Fuel

Bioenergy is often thought of as a novel silvopasture use. In reality, it is already historically important as heat and for cooking. Silvopastures, including managed rangelands, provide fuel as wood or charcoal in numerous parts of the world (Arevalo, 2016; Iiyama et al., 2014), many of them informal and undocumented. In some regions, overuse of native leguminous trees for fuel has created the need for introduced species with greater wood growing rates, including *Leucaena* spp., *Acacia* spp., and *Prosopis* spp. (Froughbakhch et al., 2001). Cultivating wood fuel in silvopastoral and agroforestry systems is widely

recommended as a more sustainable bioenergy source (Arevalo, 2016). These trees can also provide material for charcoal manufacture, useful in transporting and marketing over long distances because of its greater BTU:mass ratios vis-à-vis wood. Silvopastoral production could be particularly important where indiscriminate native-forest charcoal production is discouraged, but market demand is strong (Russell and Franzel, 2004). Biochar and activated carbon are additional products that have been proposed from agroforestry and silvopastoral systems (Ntuli and Hapazari, 2013; Fagbenro et al., 2015).

More recently, leguminous trees have been proposed for biogas and electricity production (Biswas et al., 2011; Chen et al., 2015). If they occupy marginal land and fix their own N, this would constitute very sustainable systems that do not compete with other agricultural needs. Biodiesel from Pongamia pinnata, for example, has been proposed because of its large seeds (Biswas et al., 2011). The legume tree option is particularly attractive in cases, such as with Prosopis glandulosa, in which the tree is an aggressive invasive with otherwise limited browse utility (Cho et al., 2014). For example, mesquite (*P. glandulosa*) rangeland silvopastures in southern North America make particularly attractive sources of renewable bioenergy, because such systems are self-regenerating, favor greater herbaceous forage production, and save current economic and environmental costs of brush control.

Human food

Most commonly, humans consume tree products indirectly through herbivore animal products. There are documented cases, however, in which leguminous tree components in agroforestry or silvopastoral systems can be consumed directly by humans. These include leaves, pods (*P. glandulosa*), or seeds (*L. leucocephala* and *Prosopis* spp.) as starch, protein, or sucrose sources (Zolfaghari et al., 1986; Giovannetti et al., 2008). This is an area that merits additional germplasm collection and evaluation, since arboreal legumes could provide nutritionally important protein directly to humans, much as domesticated herbaceous pulse legumes already do (Boye et al., 2010).

Other provisioning ES

Tree legumes can also provide other provisioning ES such as natural medicines and ornamentals. García-Mateos et al. (2001) indicated that *Erythrina americana*

Miller, a tree legume in Mexico, is used as an ornamental tree and the flowers are frequently eaten, used to make tea, and used as a sedative. The seeds are toxic because of alkaloids; they are applied in folk medicine as laxative, diuretic, expectorant, anti-asthmatic, and antimalarial. Further biochemical studies isolated compounds with properties that support the applications in popular medicine. In addition, Erythrina americana is also used to provide shade for cocoa (Theobroma cacao L.) and coffee (Coffea Arabica L.) and as a support tree, as live fence, green manure, and animal feed. Hastings (1990) also reported medicinal use of different Erythrina species. This example shows the versatility and multiple ES provided by this single genus. Numerous other tree legumes still lack preliminary evaluation for these different ES, reflecting the underexploited nature of this resource.

Supporting ES

Biological N, fixation

The legume family (Leguminosae or Fabaceae) is the third largest family of flowering plants, with approximately 650 genera and nearly 20,000 species (Doyle, 1994). Legumes are generally treated as a single family with three subfamilies: Mimosoideae, Papilionoideae (also known as Faboideae), and Caesalpinoideae. Biological N₂ fixation is perhaps one of the most desired traits in legumes. Many, but not all, legume trees can form symbiosis with N₂-fixing bacteria (Faria et al., 1989). The origin of this complex symbiosis is still not very well elucidated. Although over 90% of Papilionoideae and Mimosoideae presumably are capable of forming symbioses with rhizobia, very few members of Caesalpinoideae do so (Faria et al., 1989; Doyle, 1994). Mimosoideae includes important tree legumes from genera such as *Leucaena*, *Mimosa*, *Acacia*, *Calliandra*,

and *Prosopis*. Papilionoideae (Faboideae) are represented by *Gliricidia*, *Sesbania*, *Cratylia*, and *Cajanus*, among others. *Bauhinia* is a genus representing tree legumes in the Caesalpinoideae subfamily and, although important in some livestock systems (Santos et al., 2010), the literature indicates that *Bauhinia cheilantha* (Bong.) Steud. does not fix atmospheric-N₂ (Freitas et al., 2010).

Franco and Faria (1997) surveyed 616 tree legume species for nodulation in different regions of Brazil. They found that 387 out of 616 species nodulated. Proportion of nodulating species was lower for the Caesalpinoideae subfamily (25%) compared with the sub-families Mimosoideae (76%) and Papilionoideae (80%). Wurzburguer and Hedin (2016) concluded that fixation is determined by biodiversity, evolutionary history, and species-specific traits (tree growth rate, canopy stature, and response to disturbance) in the tropical biome. Biological N, fixation varies with species, environment, and management. Montoya and Tejeda (1989) screened tree legumes with potential use for agroforestry systems in Mexico. Their results indicated that Acacia pennatula, Gliricidia sepium, Albizia lebbek, and Piscidia piscipula (syn. P. communis) presented potential for BNF, forage, and firewood. Dubeux et al. (2015) reported BNF by tree legumes ranging from 24 to 304 kg N ha⁻¹ year⁻¹ for different species and locations; however, the typical range is from 50 to 150 kg N ha⁻¹ year⁻¹ (Table 1).

Nutrient cycling

Tree legumes in silvopastoral systems have potential to improve nutrient cycling in grassland ecosystems by adding BNF, taking up nutrients from deeper soil layers and recycling to surface layers, modifying the soil environment under the tree canopy and rhizosphere, and providing more uniform shade across the pasture and improving spatial distribution of cattle excreta. Nitrogen-

Table 1 - N₂-fixation by tree legumes in different locations

Tree legume species	Location	N Fixed (kg N ha ⁻¹ year ⁻¹)	Source
L. leucocephala	Tanzania	110	Hogberg and Kvarnstrom (1982)
	Nigeria	304	Danso et al. (1992)
Sesbania sesban	Senegal ¹	43-102	Ndoye and Dreyfus (1988)
	Kenya	52	Gathumbi et al. (2002)
Gliricidia sepium	Nigeria	108	Danso et al. (1992)
	Brazil	110^{2}	Apolinário et al. (2015)
Cajanus cajan	Kenya	91	Gathumbi et al. (2002)
Calliandra calothyrsus	Kenya	24	Gathumbi et al. (2002)
Mimosa caesalpiniifolia	Brazil	163 ²	Apolinário et al. (2015)

¹ Greenhous

² From February 2012 to September 2013. Source: Dubeux et al. (2015).

fixing tree legumes can be used to reclaim degraded areas (Franco and Faria, 1997; Macedo et al., 2008). Recycling of BNF by tree legumes in a silvopasture occurs mainly by litter deposition/decomposition and animal excreta. In silvopastoral systems where trees are at a height where the foliage is not reached by browsers, litter is a major pathway of nutrient return/addition. Apolinário et al. (2015) reported leaf N concentration in gliricidia [Gliricidia sepium (Jacq.) Kunthel ranging from 33.6 to 38.0 g kg⁻¹, while sabiá (Mimosa caesalpiniifolia Benth.) leaf N ranged from 26.9 to 38.5 g kg⁻¹. Biologically fixed N in leaves ranged from 30 to 121 kg ha⁻¹. Considering that these leaves will be deposited as leaf litter, there is a significant contribution of N using this pathway. In the same study site, Apolinário et al. (2016) measured the litter deposition for two consecutive years. Litter fall was produced throughout the year, but concentrated in the dry season. Sabiá produced greater litter fall amounts in the two cycles than gliricidia (10.8 vs. 10.4 Mg ha⁻¹, respectively), but the overall average N concentration of gliricidia was greater than that of sabiá (21.5 and 18.8 g kg⁻¹, respectively). Thus, N amount cycled through litter was greater for gliricidia in both cycles (105 and 109 kg N ha⁻¹) than for sabiá (87 and 98 kg N ha⁻¹). The proportion of the N in the litter that was derived from the atmosphere by symbiotic fixation was similar in both species (55%) and varied little along the two cycles (Apolinário et al., 2016).

Excreta is another pathway of legume nutrient return, when browsers have access to legume foliage or even litter on the ground (Mlambo and Mapiye, 2015). The contribution of legume-tree N in these cycles can be particularly important in infertile soils (Catchpoole and Blair, 1990). This N can be cycled back to humans via forage and then animal protein, or more directly as cereal and pulse fertilizer if animals are kept in confinement where nutrients can be gathered and applied to crops. Introduction of tree legumes has long been recognized as a viable strategy to improve and diversify livestock diets in the tropics (Tuwei et al., 2003).

Tree legumes, however, often present condensed tannins (CT) and if present at levels greater than 55 g total CT kg⁻¹ dry matter (DM) (Jackson et al., 1996), they may present dietary constraints to livestock. Greater levels of CT increase fecal NDF-N and reduce N and fiber digestibility, because CT binds to protein and fiber, rendering them less available for digestion (Merkel et al., 1999; Jackson et al., 1996). Grainger et al. (2009) tested two CT levels (163 and 326 g CT d⁻¹) extracted from *Acacia mearnsii* bark on diets of lactating dairy cows. Addition of CT at these levels reduced methane emission; however, it also reduced

voluntary intake, digestibility, and milk production. This is important not only for ruminant performance, but also for N cycling. Cattle return N via urine and dung, but the proportion of returned N varies according to dietary N. Greater available N in the diet leads to greater return via urine, where losses are greater than via feces (Dubeux et al., 2007). An increase in NDF-N as a result of CT will likely reduce N losses from grassland systems because of the shift in the pathway of N return (feces vs. urine). Jackson et al. (1996) reported that Acacia boliviana, Senna velutina, and Gliricidia sepium presented <55 g CT kg⁻¹ DM, Leucaena species and Calliandra calothyrsus contained intermediate leaf CT concentrations (60 to 90 g CT kg⁻¹ DM), and Flemingia and Desmodium species presented total CT>90 g kg⁻¹ DM. Greater fecal NDF-N might explain slower decomposition of feces from cattle browsing tree legumes compared with a grass-only diet. Lima et al. (2016) studied the decay of feces originated from cattle grazing/browsing signalgrass (Brachiaria decumbens Stapf.) pastures, silvopastoral system with signalgrass and Sabia (Mimosa caesalpiniifolia Benth), and silvopastoral system with signalgrass and gliricidia [Gliricidia sepium Benth (Jacq.) Walp Kunthex.] and found faster decomposition from cattle grazing signalgrass pastures ($k = 0.00284 \text{ g g}^{-1} \text{ d}^{-1}$), followed by signalgrass/ sabia ($k = 0.00233 \text{ g g}^{-1} \text{ d}^{-1}$), and signalgrass/gliricidia $(k = 0.00200 \text{ g g}^{-1} \text{ d}^{-1})$. In a temperate silvopastoral system, cattle used significant time budget for browsing on temperate ryegrass pasture, with significant differences in browsing time among seasons of the year (Vandermeulen et al., 2016). Similar behavior likely occurs in warm-season silvopastoral systems using tree legumes.

Cattle spend time under the shade during the warm season, concentrating dung and urine return in these areas (Dubeux et al., 2014). Tree legumes provide shade for grazing livestock and that may improve spatial dung distribution. Lira (2013) monitored animal behavior in silvopastoral systems (sabia-signalgrass and gliricidiasignalgrass) and contrasted them with signalgrass monocultures. They concluded that tree legumes did not improve dung distribution compared with the grass monoculture. A reason for this might be the small paddock size, where cattle stayed for a short period of time. Xavier et al. (2014) observed greater livestock performance in silvopastoral systems planted with tree legumes (Acacia mangium and Mimosa artemisiana) and eucalyptus (Eucalyptus grandis) with signalgrass in the understory compared with signalgrass in monoculture. They concluded that shade provided by the trees was advantageous for the cattle, improving their performance.

Deep-rooted tree legumes may intercept and take up nutrients from deep soil layers and recycle them back to the surface soil, improving soil fertility for companion/ following crops. In Zambia, Leucaena leucocephala and Gliricidia sepium rooted to at least a 2-m depth (Chintu et al., 2004). Introducing ¹⁵N-labelled fertilizer at various soil depths down to 2 m, these authors concluded that there was less subsoil nitrate-N beneath planted legume trees than beneath mono-cropped maize plots, indicating that trees probably retrieved subsoil N. Maize (Zea mays L.) yields subsequent to coppicing tree fallows were at least 170% greater than unfertilized controls, demonstrating improved soil fertility status in the tree systems. Chikowo et al. (2003) also observed less nitrates under fallows of Acacia angustissima, Sesbania sesban, and Cajanus cajan, compared with maize monculture. The same authors also observed a flush of nitrates in the S. sesban and A. angustissima plots with the first rainfalls of the season, which might pose a problem, because these nitrate levels are ahead of the peak N demand by crops. These results reflect the role tree legumes play in recycling nutrients from deep soil layers and improving soil fertility in the surface soil layers. Management strategies must be put in place to capture the N available at the beginning of the rainy season, rendering it available later for growing crops when the N demand increases, improving synchrony between nutrient release and nutrient uptake.

Soil fertility and soil health

Arboreal legumes can contribute to soil conservation and enrichment in numerous ways, including increased organic matter and acidity mitigation (Chintu et al., 2005). The most documented, however, is biologically fixed N from litter, root, and nodule decay (Catchpoole and Blair, 1990; Sanchez et al., 2007; Apolinário et al., 2015). Quantities and rates of this contribution vary considerably among species with a strong correlation between these factors and nutritive value to browsers (Wardle et al., 2002). In high-rainfall regions where soil is prone to erosion on hillsides or in dry regions with few topographic barriers such as windy plains, soil stabilization can be important. These include contour plantings on hillsides (Niang et al., 1998) and wind breaks on open plains (Udawatta and Jose, 2012). Soil microclimate caused by shade and litter, especially A horizon temperatures and moisture retention, can also be a key factor affecting soil fertility buildup (Gea-Izquierdo et al., 2009).

Photosynthesis and primary productivity

Primary productivity is affected by vegetation, management, climate, and environment. Increasing efficiency of resource utilization, both in time and space, provides opportunity to increase primary productivity. One way to increase efficiency of resource utilization is to increase the diversity of plant functional groups and species richness (Tilman et al., 1996). In Europe, where biodiversity is a socially supported goal, trees in silvopastures are encouraged, because they provide an additional canopy to hemi-arboreal and arboreal systems (Bergmeier et al., 2010). Biodiversity may eventually become a similar universal value, increasing interest in arboreal legumes adapted to warmer climates.

Introduction of tree legumes in silvopastoral systems is one option to increase primary productivity. Tree legumes are often deep-rooted (Chintu et al., 2004), exploring deeper soil layers, different than the ones explored by shallow-rooted grasses. Seasonal differences in growth of tree legumes and companion grasses might increase primary productivity as a result of the complementary nature of resource utilization in time. Thus, spatial and time complementarity in the use of available resources leads to greater ecosystem productivity. As a result, there is a greater potential to increase C sequestration under tree legume-grass mixtures compared with grass monocultures. Different functional groups also improve nutrient cycling efficiency. Pan et al. (2015) observed lower leaf N and leaf N:P ratio in grasses than in shrubs and trees, greater leaf N in trees than in shrubs, and greater leaf N and N:P ratios in legumes than in non-legumes. These differences directly affect nutrient cycling and primary ecosystem productivity. In some cases, primary productivity might increase, but the biomass that is produced may not always be used by grazers and browsers. This is the case in the Brazilian Caatinga, where in many cases, only 10% of produced biomass is grazeable by livestock. The remaining is mainly composed by thorns, branches, and lignified stems (Santos et al., 2010). This biomass, however, might be used for timber, fuel, and nutrient cycling.

Regulating ES

Carbon sequestration and GHG mitigation

Agroforestry systems with the use of tree legumes can sequester C in vegetation and below ground, reducing GHG from atmosphere. Mutuo et al. (2005) reported average

above-ground C stocks up to 60 Mg C ha⁻¹, depending on the rotation age of the land-use system. The potential for C sequestration in the soil (top 20 cm) was less (25 Mg C ha⁻¹) than in the above-ground vegetation. Establishment of tree legumes associated with no-till practices increased top soil C stocks between 0.5 and 1.6 Mg C ha⁻¹ year⁻¹, with values above the ones observed for annual cropping systems. These authors also observed that agroforestry systems can mitigate N₂O and CO₂ emissions from soils compared with high-input cropping systems. They observed, however, that addition of high-quality legume residues would increase N₂O and CO₂ emissions. Thus, a balance must be reached when adopting tree legumes, considering the benefits of these systems in terms of C sequestration and the potential emissions from residues used as organic amendments. Macedo et al. (2008) also concluded that the combined use of tree legumes, N-fixing bacteria, and arbuscular mycorrhizal fungi was able to reclaim degraded land after 13 years of establishment and to re-establish the nutrient cycling process within the system. Legumes added an average of 1.73 Mg C ha⁻¹ year⁻¹ and 0.13 Mg N ha⁻¹ year⁻¹, during the 13-year period.

Litter deposition is a key aspect of this process. Franco and Faria (1997) reported annual litter deposition by tree legumes of up to 12 Mg DM ha⁻¹ and 190 kg ha⁻¹. Carbon deposited via litter will be later incorporated into soil organic C (SOC). Nyamadzawo et al. (2008) studied the effect of tree legume fallows followed by maize cropping on SOC. They compared the tree legume fallows with natural fallows and continuous maize systems. Fallows maintained greater SOC than continuous maize. *Acacia angustissima* was the best fallow for SOC sequestration when compared with *S. sesban* or natural fallow.

Tree legumes might reduce the use of industrial N fertilizer because of BNF. Lal (2004) indicated that C emission for production, transportation, storage, and distribution of N fertilizer is 0.9 to 1.8 kg C equivalent per kg N (or 3.3-6.6 kg CO₂eq per kg N). Thus, addition of N₂-fixing tree legumes has potential to reduce N fertilizer inputs and offset GHG emissions from the industrial process of manufacturing N fertilizers. Tree legumes containing CT also have potential to mitigate methane emissions from livestock. Puchala et al. (2011) compared methane emissions from goats fed sericea lespedeza (Lespedeza cuneata) or a mixture of crabgrass (Digitaria ischaemum) and Kentucky 31 tall fescue (Festuca arundinacea). They observed lower methane emissions from goats fed lespedeza, both expressed as quantity per day or relative to DM intake, suggesting that CT decreased methane emission. Several tree legume species are rich in CT, presenting potential to mitigate methane

emission from livestock. Further research needs to be done in this area, clarifying the role of CT on ruminal fermentation, forage digestibility, and animal performance.

Soil erosion control and riparian buffers

Soil erosion is a problem on overgrazed pastures. Intercropping tree legumes might be an option to mitigate soil erosion. Nichols et al. (2001) established N-fixing tree legumes (*Inga edulis*) intercropped with native timber trees (Terminalia amazonia) on eroded tropical pasture in Costa Rica. They observed that tree legumes rapidly restored the area and there was no need to use N fertilizer. It is important to mention that tree legumes should be combined with grasses and herbaceous legumes in the understory to improve soil cover. Benefits of tree legumes would be mainly towards BNF and reestablishment of nutrient cycling process (Macedo et al., 2008), improving primary productivity of the entire system. Sun et al. (2004) recommended the use of tree hedge legume species along contours to prevent soil erosion on sloping lands in China. Guo et al. (2008), however, indicated that trees might compete with the intercropped species for water and nutrients. Agroforestry combined with grass can be used as buffers to improve water quality in a watershed. Udawatta et al. (2010) tested two agroforestry buffers, two grass buffers, and two controls (no buffers) on water quality of grazed pastures. They observed that on pasture watersheds, the agroforestry and grass buffers reduced runoff and reduced non-point source pollution compared with the control.

Shade and windbreaks

The importance of tree shade influences on silvopastoral micro-environment is challenging to quantify. Competition between upper story and herbaceous canopies for sunlight can be a negative factor, especially where soil moisture is not limited and non-forage crops are included (Fujisaka et al., 2000; Gea-Izquierdo et al., 2009). The use of heavy pruning (Bacab et al., 2012) or deciduous trees in silvopastoral systems with reverse phenology that drop their leaves during the growing season, as in the case of *Faidherbia albida* (Roupsard et al., 1999), could circumvent this negative effect of tree shade in silvopastures.

Many benefits also arise from shade, some of them often imperceptible to the manager. Tree shade, for example, can benefit soil bioactivity (Vallejo et al., 2010). Many herbaceous forages thrive in shaded environments because of decreased temperature stress and evapotranspiration (Feldhake, 2009; Gea-Izquierdo et al., 2009). These include

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grasses such as *Panicum maximum* (Muir and Jank, 2004) and most legumes, for example *Galactia elliottii* (Muir and Pitman, 1989). Shade can also mitigate heat stress in animals, especially in critically warm climates, times of the day, or seasons (Karki and Goodman, 2010). These stress reductions can foster better gains and greater reproductive rates (Bussoni et al., 2015). Because animals favor shade, trees can be strategically planted to manipulate herd activity and distribution in the silvopastoral landscape. Other animals, such as wildlife, can also benefit from the tree component in silvopastures for habitat, protection, and feed; these range from insects (Fonte et al., 2012) to large ungulates (Nixon and Mankin, 2011). The case for avifauna, including migratory species, is especially strong in neotropical regions (McDermott and Rodewald, 2014).

Additional indirect benefits from an arboreal component within pastures include windbreaks. Benefits include slowing soil erosion and plant transpiration (Lynch et al., 1980), noise mitigation, odor dispersal, and security (Workman et al., 2003). In windy regions where temperatures can be extreme, trees also provide protection to animals (Lynch and Donnelly, 1980). Living fences are another use for arboreal legumes in silvopastures (Nahed-Toral et al., 2013), although establishment of palatable species in grazed pastures can be challenging (Love et al., 2009).

Forage for pollinators

Pollinator insects are key to sustain food production. More than 80% of wild plant species and almost 75% of cultivated plant species rely on insects, particularly wild bees, for fruit and seed production (Potts et al., 2010). Pollinator richness and density, however, have been declining in recent years on a global scale (Thomann et al., 2013). Pollinator decline threatens not only food security, but also might lead to the extinction of pollinator-dependent plants. Intensification of livestock production, including the use of N fertilizer and frequent intensive defoliation, has been attributed as a cause of pollinator population. These practices result in grasslands with degraded species pool and structurally homogeneous sward (Tallowin et al., 2005). Potts et al. (2009) observed greater diversity and species richness of pollinators in pastures sown with legumes compared with fertilized grass monocultures. The legumes used in this research, however, were herbaceous species, including Trifolium pretense, T. repens, Lotus corniculatus, Vicia sativa, and Medicago lupulina. The pollinator population was driven by floral abundance, floral richness, availability of nectar resources, and sward

structure. This evidence indicates that adding tree legumes and grass-legume mixtures to the understory coupled with lenient grazing would improve grassland characteristics, supporting greater presence of pollinators. Studies linking pollinators and tree legumes are scarce in the literature and should be pursued in warm-climate regions.

Cultural ES

Cultural ES include recreational, aesthetic, and spiritual values provided by ecosystems. Among recreational values, game farming is perhaps the most popular in regions of USA (Chitwood et al., 2015) and Africa (Merwe and Saayman, 2003). Piasentier et al. (2007) studied the grazing behavior of fallow deer (Dama dama) on mixtures with different proportions of fescue (F. arundinacea) and clover (T. repens L. var. hollandicum cv. Huia). Deer preferred legume over grass and spent more time grazing on clover. Legumes presenting CT might also reduce internal parasites in deer. Hoskin et al. (2000) reported that diets with the CT-containing legume sulla (Hedysarum coronarium) reduced the impact of internal parasites on red deer (Cervus elaphus), reducing the dependence on anthelmintic treatment. Tomkins et al. (1991) demonstrated the use of leucaena (Leucaena leucocephala) replacing Pangola digitgrass (Digitaria eriantha) on forage intake and digestibility by red deer. Inclusion of leucaena increased total dry matter intake and DM and N digestibilities. Rico-Gray et al. (1991) also reported the importance of tree legumes (Caesalpinia violacea) in deer diet in Yucatan, Mexico. Deer are browsers and prefer woody species (Ismail and Jiwan, 2015). Therefore, introduction of N₂-fixing palatable tree legumes is a viable way to increase sustainability of game farming operations. Benefits include financial return for the land manager as well as preservation of wildlife and desirable legume species.

Biodiversity is a desirable characteristic in grasslands. Greater species richness and plant functional groups not only have potential to increase primary productivity as stated earlier, but also enhance the capacity of grasslands to provide environmental and aesthetic services for humans (Sanderson et al., 2004). Spiritual and aesthetic values are ecosystem services often neglected, compared with other ES provided by trees. Laband (2013), discussing possible reasons for this, argued that these ES are deeply personal and not transferable within the society; nevertheless, they are extremely important for the welfare of human beings. Valuation of these ES is not trivial, but is possible (Sander and Haight, 2012).

Adoption challenges

Silvopastoral techniques have been widely adopted locally in some regions such as Central America (Nahed-Toral et al., 2013) and northern Australia (Mullen et al., 2005) and efforts to introduce leguminous tree species in pastures have been ongoing for decades in some parts of the tropics (Nair et al., 1984; Cameron et al., 1991; Argel et al., 1998). Despite this history, they have not been as widely adopted in areas where they were not traditionally practiced (Dagang and Nair, 2003). According to Clavero and Suarez (2006), this arises mostly from socio-cultural barriers that encompass everything from lack of experience to a paucity of technical information from extension services. We discuss below some of the tangible reasons for this widespread failure, with particular focus on arboreal legumes.

Paucity of domesticated germplasm

At the international level, there is a paucity of diverse, widely available legume-tree germplasm for warmclimate silvopastoral systems compared with what has been domesticated for herbaceous legumes. As a result, most new systems depend on a few widely used arboreal or semi-arboreal legumes that have become pantropic. These include Leucaena spp., Sesbania sesban, Gliricidia sepium, Acacia spp., Callliandra spp., Mimosa spp., and Chaecystisus palmensis among a few others (Argel et al., 1998). However, compared with the vast array of locally and pan-tropically available germplasm that has not received attention outside their areas of origin, for example numerous native species in Mexico (Nahed-Toral et al., 2013), these are a tiny fraction of what is available. This very limited genetic range in currently available germplasm can bottleneck edapho-climatic adaptation to newly introduced systems and, consequently, application to the myriad warm-climate production systems that could benefit from arboreal tree legumes for silvopasture.

Commercial seed production of warm-season arboreal legumes for silvopastures is even more severely limited. Although small quantities can be obtained from national and CGIAR research institutes such as Centro Internacional de Agricultura Tropical (CIAT, 2016), International Livestock Research Institute (ILRI, 2016), or World Agroforestry Centre (ICRAF, 2016), very few (*L. leucocephala* is one exception) are commercially available in large quantities on the international market. Because they are trees, seed production from new local plantings may take years, thereby

slowing adoption rates in the absence of commercial seed sources.

Lag in research/technology

Where nursery transplants are used, legume tree establishment is rarely considered a limitation (Fujisaka et al., 2000). This technique, however, can be constrained by cost and labor in large plantings. In these extensive systems, trees established directly from seed may suffer from weak seedling vigor, predation, and competition with weeds (Cobbina, 1994; Chintu et al., 2004). The need for rhizobial inoculation adds a further challenge in warm climates where such inoculants are unstable (Bala and Giller, 2001). Additional research is needed to develop techniques that lower the cost and shorten the establishment period in which animals must be excluded, for example, identifying species such as sabia (Mimosa caesalpiniifolia) that are unpalatable to ruminants relative to the herbaceous pasture component and, therefore, do not require elaborate protection during establishment (Lehmkuhler et al., 2003: Apolinário et al., 2015). Species preferred by grazers/browsers must be fully developed before grazing commences. In Australia, it is a recommended practice to let the trees grow, increase trunk diameter, and develop the root system before animals are turned in. As a result, long-lived (>40 year) productive Leucaena stands have been reported by Radrizzani et al. (2010) in Australia. Selecting species that are more promiscuous rhizobial hosts and do not require soil pH adjustment or P application would further simplify and reduce establishment cost.

Once established, legume-tree persistence, especially as it relates to pruning tolerance (Wencomo and Ortiz, 2011), can be problematic. When grazing herbaceous forage legumes in mixtures, management for persistence must focus on the most preferred species (Kretschmer, Jr., 1989). If the tree legume is the most preferred forage, stocking rate or resting period should be adjusted based on that. This may lead to sub-utilization of other forage components, but would preserve the preferred species. An alternative is the use of protein banks in a separate paddock, where the grazing management would be easier to adjust based on the target species.

Challenges of multi-purpose trees

Multi-purpose systems that include dual-purpose understory crops can suffer from sunlight and soil moisture competition with tree legume over-story (Fujisaka et al., 2000). Determining ideal pruning pressure to allow sunlight penetration and maximum soil moisture availability to the herbaceous component might further productivity of the system, while maintaining tree persistence (Bacab et al., 2012). If wood is a primary goal, however, management must favor the tree (Muir, 1998) to the detriment of herbaceous species. If tree browse or soil amendments are a priority, then these may have to be pruned more often, taking care to maintain carbohydrate reserves and rhizobium viability (and consequent biologically fixed N levels) (Kadiata et al., 1997; Latt et al., 2000).

Management complexity

Managing cattle, herbaceous vegetation, and trees together is indeed more complex than typical grass monocultures, reducing the interest in investigating and adopting these systems. Research that presents animal performance and pasture data is limited for silvopastoral systems with tree legumes, although a few are available (Mello et al., 2014; Xavier et al., 2014). Land, labor, and animal costs associated with this type of research reduce its feasibility. Complexity includes interactions among soil, herbaceous vegetation, trees, grazing animals, and the environment. Perceived benefits from these systems, however, are leading to greater research interest and adoption by land managers (Mullen et al., 2005; Shelton et al., 2005).

Challenges to mechanization

Introducing trees into an herbaceous landscape is not only biologically challenging but also logistically difficult. The presence of trees, especially in mechanized systems, can complicate extant mechanized management such as haying. Land managers are not always willing to add that complexity without a clear return on investment and additional work (Bussoni et al., 2015). Sacrificing grazing during establishment, balancing tree productivity with herbaceous forage needs, knowing when to prune for wood or browse productivity are examples of questions future silvopastoral managers want answered before they invest.

Dangers of invasive weeds

Arboreal legumes, due to their competitiveness in N-deficient environments, can quickly become invasive weeds. Examples include *L. leucocephala, Acacia* spp., and *Prosopis glandulosa* (Wise et al., 2012; Chiou et al., 2013;

Thompson et al., 2015). Repeatedly around the world, these and similar species were originally introduced as browse species, only to escape into surrounding environments where they out-compete native vegetation. In ideal growing conditions with few natural enemies, the challenge is to introduce these trees responsibly such that they do not become nuisances in adjacent ecosystems where they are not wanted.

Social and cultural barriers

Introducing new techniques or expanding their use into established pastoral systems is challenging but not impossible. The additional labor and investment in establishing, maintaining, and profiting from arboreal legumes in silvopastures require more active management than currently involved, especially in natural silvopastures (Cubbage et al., 2012). Understanding research, extension, and land manager perceptions and expectations is an essential first step (Workman et al., 2003; Bussoni et al., 2015). Proving its economic viability is likewise important to land managers interested in diversification and income enhancement (Cubbage et al., 2012; Frey et al., 2012). If there is openness to introducing arboreal legumes, bridging the gap between research and application can be more successfully achieved when extension services are present, trained, and motivated (Workman et al., 2003). Involving the land manager in participatory testing and disseminating arboreal legumes in silvopasture may also increase the chances for long-term changes (Peters et al., 2003; Kuntashula and Mafongova, 2005).

Conclusions

Tree legumes are an underexploited resource in warm-climate silvopastures. Perceived benefits from tree legumes include provisioning, regulating, supporting, and cultural ecosystem services. There are limitations for extended research with tree legume silvopastures, but extensive research has been done in Africa and Australia and recent efforts have been reported in South America. Economic benefits must be demonstrated to land managers to increase adoption. These benefits are apparent in the research and successes are already available, but more long-term research, including the livestock component, is necessary. Tree legumes are a key component for the sustainable intensification of livestock systems in warm-climate regions.

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