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Nutritional Quality of Tree and Understorey Forage in Silvopastoral Systems

J. Brian Lowry and John R. Wilson
CSIRO Tropical Agriculture, Bag No. 3, Indooroopilly, Qld 4068, Australia

Abstract: In silvopastoral systems trees may provide feed directly, and also affect the composition and quality of sub-canopy vegetation. Green leaves may be available as feed from thinning of unwanted trees, from the pruning of trees to obtain good log form, from lopping of larger living trees, and from the canopy at final harvest. Perhaps of more significance is the annual seasonal fall of leaf, flower or pod, the amount and quality of each being a feature of individual tree species. As fallen tree leaf is rarely considered a feed resource, we review published records of its use as feed in a variety of habitats and argue that there are good grounds for considering it to be particularly relevant as feed in the semi-arid tropics. Quality is obviously less than for green leaf, with protein reduced by about 50%. However, higher fragmentability may make it a useful supplement to mature tropical grass. The effect of trees on the quality of sub-canopy pasture is more complex than that of shade alone, which can affect quality in either direction. Water relations are highly dependent on tree species, usually reducing availability for the grass, but some trees utilize water from deeper soil to the benefit of the grass. The most marked effects on quality are when the sub-canopy environment fosters a higher quality species (often *Panicum maximum* var *trichoglume)* than that in the surrounding area. We review the published cases where positive effects on sub-canopy vegetation have been recorded.

Keywords. *Acacia* spp., *Albizia* spp., deciduous, digestibility, hydraulic lift, impact index, leaf phenology, NDF.

Silvopastoral systems are so diverse that the only common factor, apart from trees, would seem to be the animal production component. On the other hand, there are several possible products from the tree component, including timber, pulpwood, fuelwood, fruit, nut or industrial crops, or the trees may provide other benefits such as shelter or salinity control. It is worth pausing to consider the characteristics of a silvopastoral system in relation to pastures and forests. We see it as follows. The system uses large trees rather than shrubs. The trees will often be well separated. This may be planned, or it may be that climate will not sustain trees at high density. There is likely to be plenty of lateral light penetrations. The system contrasts with establishment of browse shrubs, alley cropping, closed forests or dedicated woodlots. However, some plantations and forests may be managed as silvopastoral systems until canopy closure. Also, plants such as leucaena or gliricidia can be managed either as shrubs or as trees. Silvopastoral systems can be found in temperate environments, but the concern of this review is largely with the wet-dry or semi-arid tropics. One must consider these with the recognition that most of the rigorous studies of ecophysiology have been in temperate or subtropical systems.

In a silvopastoral system, animal production will always be based, to varying degrees, on the herbage production of the ground cover. The contribution from the arboreal component may range from nothing, as in palm or eucalypt plantations, to trees with high feed value. Another major variable is the interaction between trees and ground cover. The effect on ground cover may range from its virtual suppression under a closed forest canopy to the islands of fertility seen under some trees in tropical savannah. The review falls somewhat inevitably into two sections: feed from the trees and feed from the pasture. An aspect of the former, which we attempt to cover at some length, is the potential for a forage contribution from the natural fall of edible material, usually leaf, flower or pod. This may be a relatively unfamiliar concept, to landuse planners, if not to village livestock rearers, and be relevant to choice of tree species in a silvopastoral system. The coverage of aspects of pasture is more selective because of a major review on shading effects on grass growth in an accompanying paper. We review pertinent aspects of the nutritive quality of forage available in tree-pasture systems and, where applicable, contrast the quality of understorey forage with that grown in open pasture, including the possibility of toxicity with certain grasses. Finally, we bring together the records of tree species known to have a positive effect on sub-canopy vegetation.

Feed Directly from the Trees

Even if the species concerned is a recognized fodder tree, there may, if it is being grown in a silvopastoral system, be little green leaf available for associated livestock. For most of the growing period trees will be so large that most leaf will be out of reach of the animal. During establishment it will be necessary to prevent the animals from browsing. The circumstances in which some green leaf would be available include:

— Where the trees are being grown for timber, from pruning treatments carried out to obtain good log form. This would be particularly so for open-grown trees, where pruning has to be more drastic because of a greater tendency for lateral branching. The mixed garden system of West Java may include emergent trees of *Albizia falcataria* or *Maesopsis emenii* which are pruned to a height of more than 15 m. This provides a clear log for local timber production, the individual who prunes the trees takes away the branches as feed, and the high shallow tree crown minimizes interference with other crops (Lowry *et al.*, 1992).

— Thinning of unwanted trees when final crop trees are selected. This might involve felling the unwanted trees, coppicing or cutting them back to leave them for browse only.

— Pollarding or harvesting from the standing canopy. In Nepal, harvest of feed from large trees is a normal dry-season practice (Joshi and Singh, 1990). With well-established trees the green crowns would constitute a standing reserve of high-quality feed that could be utilized for drought feeding. This would involve removal of part of the crown by lopping lower branches, without destroying the log form. This might delay eventual log harvest, but contribute strongly to animal production.

— At final harvest for timber the entire green canopy would be available for feed. In some semi-arid systems, whole trees may be pushed over at intervals to supply feed, particularly during severe drought. This applies particularly to mulga (*Acacia aneura*) in Australia (Everist, 1986).

The value of green leaf from trees as feed is covered in numerous publications on fodder trees, a useful source being Gutteridge and Shelton (1994). It is worth noting that green leaf may have high value in relation to its available biomass, if it is fed as a supplement to dry-season grasses. It can have a catalytic effect in enabling rumen microbes to ferment highly fibrous, low protein, material which would otherwise be poorly digested. The relative value would be less if fed in association with green legumes and forbs in a plantation understorey. A major quality-determining variable for tree leaf is its morphology. The amount of cell wall material ranges from about 20% dry matter in membranous deciduous leaves to over 55% in tough sclerophyllous leaves or phyllodes. Although the NDF content is usually considerably lower than in mature tropical grasses it should be noted that the NDF itself is much less digestible than in grasses (Lowry and Kennedy, 1996). In general the green leaf is a good source of protein, but the availability of this protein will depend greatly on tannin activity, which is very variable between species. Quality is also affected by other secondary compounds that may have anti-nutritional or toxic effects (Lowry, 1990) and these compounds vary greatly between taxa. Thus the nutritional value of green tree leaf can not be generalized and must be considered on the basis of each individual species.

Feed from Natural Fall of Leaf, Flower or Pod

Fallen tree leaf as feed for ruminants

All trees drop their leaves eventually. For a tree large enough for the canopy to be inaccessible as browse, most of the biomass in the canopy will sooner or later be on the ground and thus in principle accessible to grazing animals. It is true that there are arboreal foliovores such as monkeys with fermentative digestion, possums, and even fruit bats that can feed in the canopy (Lowry, 1989b), but in general losses to such animals will be very slight. Much larger losses are likely to occur from insects but that will not be discussed here. Losses may occur in total leaf biomass, or in forage quality from the selective feeding on mesophyll tissues by leaf miners. However, in general, most canopy leaf arrives on the ground. There is little published data on production of fallen leaf, and although one can assume it is directly related to the annual biomass increment of the tree species, the proportion going into stem, branch and leaf will vary with each species. Such data are obviously needed where fallen leaf can be utilized by grazing animals. Whether this occurs depends obviously on its composition and acceptability to animals. Perhaps even more it depends on the phenology of leaf fall, which varies enormously between species.

Substrate availability: The commonest pattern of leaf replacement is an annual leaf change. This may involve what is are sometimes moved from Mitchell grass paddocks into *Acacia cambagei* woodland to utilize leaf fall (Dr. David Taylor, Forest Research Institute, Queensland, pers. comm.).

Finally, one can note a series of voluntary intake experiments with penned sheep, in which fallen leaf was provided as a supplement to a basal diet of mature Rhodesia grass. Sheep ate significant amounts of *Cassia brewsteri, Bauhinia variegate, Celts sinners, Melia azedarach, Gmelina arborea, Flindersia schottiana* and *Brachychiton discolor* (Lowry, 1999). The only case of an acceptable browse tree where the fallen leaf was not eaten was *Tipuana tipu*.

Indirect evidence: Recently there has been some indirect evidence for utilization of fallen leaf in northern Australian range lands. In a major study on stocking rates and land condition, Ash *et al.* (1995) used faecal C^{13} measurements to determine the proportion of C_3 and C_4 plants in the diets of grazing cattle. They found that on degraded lands in the dry season cattle had up to 30% C_3 plants in the diet. This was under conditions where no green legumes, other fords, or green browse could be found, and it seems inescapable that a high proportion of the diet was fallen tree leaf, even that of eucalypts. Another relevant recent paper reviews the relation between stocking rate and animal condition (Ash and Stafford Smith, 1996). It highlights and addresses the paradox that animal condition may remain anomalously high when pasture indices suggest animals should be in very poor condition. Again the conclusion is that animals are utilizing feeds in the environment not included in the usual pasture assessments. Fallen tree leaf would be the most obvious candidate.

Overall, it seems likely that utilization of fallen leaf by grazing ruminants occurs to a considerable extent in the dry tropics. The scarcity of published accounts and research may be because it is not a conspicuous behavior and no one has paid much attention to it.

Feed quality of fallen tree leaf

Elementary biology indicates that freshly fallen senescent leaf will be of much lower feed value than green leaf, due to translocation from it of cytoplasmic components, particularly protein. It should, therefore, have lower protein and higher cell wall (neutral detergent fiber; NDF) content. However, there is remarkably little published comparative data relevant to animal nutrition. The concern has been recycling of nutrients in ecological systems. However, a recent review by Killingbeck (1996) gathers nitrogen and phosphorus data for some 77 tree species, none of them tropical. In general, changes in leaf phosphorus follow those in nitrogen, and for nitrogen-fixing trees nitrogen was less resorbed on senescence than for other tree species, thus leaving higher levels of protein in the fallen leaf. Aerts (1996) concluded that, on average, woody perennials resorb 50% of nitrogen and 52% of phosphorus, and that because of higher initial concentrations, nutrient levels in fallen leaves of deciduous species are much higher than in evergreens.

Protein contents of fallen leaf of 7 potential agroforestry species, while about half that of the green leaf, were generally higher than for mature herbage of dry season grasses (Lowry, 1999). Fallen tree leaf had NDF content of 25 to 55%, much less than that of mature grass forage (70 to 80 %). However, it should still be regarded as a low-quality fibrous feed as the NDF itself was much less digestible *in vitro*. The nutritional value of fallen tree leaf is much more dependent on the non-NDF (cell contents, ND-soluble) fraction.

In temperate regions, autumn leaf fall occurs when pasture feed supply is not too low, and most temperate pastures would be expected to be of higher quality than the fallen leaf. There is thus little reason to expect animals to eat it. A quite different situation applies in the wet-dry tropics, where the dry-season loss of feed quality in the grasses makes the comparative feed value much more of an open question. Fallen leaf would be available in the presence of grass that had been dead for months. The grass would have been subject to photochemical bleaching, oxidation, possible leaching, and have extremely low protein and digestibility. With fallen tree leaf the transition from living tissue to being available on the ground would occur within days.

Direct experimental results on the feed value of fallen leaf are very few. Fallen teak leaves were progressively substituted for spear grass as the 70% roughage component in 4 diets for sheep (Reddy and Reddy, 1984a). The diet with the highest level of teak leaf had slightly lower digestibility but, with sheep having a considerably higher voluntary intake of it, actually provided more nutrients. Fallen mango leaf was also fed as 30 and 60% of a complete diet (Reddy and Reddy, 1984b). These experiments, involving pelleted diets containing 30% concentrate, were very different from feeding as the sole diet, fallen leaf of siris (*Albizia lebbeck)* (Lowry, 1989) and *Samanea saman* (Lowry, 1995), but the intake aspect was remarkably similar. Both tree legumes, especially siris, were readily eaten, and intake was high in relation to whole-tract digestibility (43 and 27%, respectively). Consequently, the feed value of the fallen leaf was higher than the dry matter digestibility (DMD) value alone would indicate. It seems reasonable to expect similar effects with other tree species.

These results prompted the comparison of intra-ruminal dacron bag digestibility of fallen leaf from 27 native deciduous trees with that of dry season grasses in North Queensland (Lowry, 1995). These showed that they were in general more digestible than the mature grass forage, some surprisingly so.

Morphologically, dicotyledonous tree leaf is very different from C_4 grass. It has a more reticulate structure and less tensile strength. Under the mechanical process of chewing it should break down more readily and yield less linear particles (Wilson, 1991). It has been shown that this does in fact happen, using an artificial mastication device and separating the particles by wet sieving (Kennedy and Lowry, 1996). *In vitro* experiments (Kennedy and Lowry, 1996; Lowry, 1999) indicate that, compared to mature grasses, tree leaf undergoes more rapid initial fermentation, but digests to a lesser extent. The eventual VFA production from fallen tree leaf is about half that from mature tropical grass, but is often comparable at 24 h. Ultimately, there are more accessible nutrients in the grass. However, to obtain these, the grass would have to stay in the rumen 72 h or more. This would represent a rate of passage so slow that the animal would starve. In fact, feed particles break down and leave the rumen according to size, whether or not they are digested, and there is a trade off between rate of digestion and rate of passage. Thus, although tree leaf has less total available nutrients than the grass, the rapid fragmentation, coupled with rapid initial fermentation of the ND-soluble fraction, suggests that the animal could extract these nutrients quickly and increase its intake. This is what is seen with the few *in vivo* experiments so far conducted.

Associative effects: Given that fallen leaf is very likely to be eaten with dry season pasture, and that they have very different lignocellulose chemistry and morphology, it might be asked if there are any associative effects. When they were co-fermented *in vitro* in a rumen simulation system it was found that the presence of tree leaf could indeed affect the digestibility of the grass. This depended on tree species. Some had a negative effect, but these were not common forages (Lowry and Seebeck, 1997). Positive effects (synergies) were found with, *inter alia*, *Melia azedarach*, *Tipuana tipu* and *Albizia lebbeck*. In the latter case the effect was due to a polar, low-molecular weight, soluble fraction in the fallen leaf (Lowry, 1999; Kennedy and Lowry, to be published).

Fallen leaf must be fresh and apparent: Voluntary intake experiments with several species showed that 'freshness' of fallen leaf was very important to animals. Animals clearly selected for the most recently fallen leaf within a particular batch (Lowry, 1999). This rapid loss of palatability compared with the slow loss of quality of mature grasses may be due to the "enzymic browning" process that makes some fruits unpalatable to humans. As cell membranes break down, leaf phenolics will be exposed to the action of polyphenoloxidases before these are denatured, will then be exposed to aerial oxidation, and there will be opportunity for the remaining protein to become bound with leaf phenolics. Furthermore, the oxidative processes could yield quinonoid products that may be toxic to micro-organisms. This loss of quality is unlikely to be a problem, in that if animals utilize fallen leaves in the field they would be able to do so as it falls. However, it does present a problem with collecting and storing material for feed evaluation. It also indicates a new desirable parameter; that the leaf drop from a particular tree occur quickly enough to be apparent as a definable feed source while still fresh, rather than accumulating slowly.

An obvious consideration is leaf size. Tree legumes with finely divided bipinnate leaves may have leaflets so small that they are lost in the sward. Large membranous leaves or leaflets are likely to be more accessible. A further aspect with pinnate legumes such as siris is that leaflets separate from rachis and rachillae on senescence, and it is really only the leaflets that are likely to be eaten. Loss of quality on senescence will be to some extent offset by the shedding of the more highly fibrous rachis and rachillae. In the case of siris the respective NDF contents of leaflets and stem fractions were 42.9 and 53.6%.

A positive aspect of leaf senescence – loss of toxins?: Many trees are protected against herbivory by defensive secondary compounds, but fortunately many of these can be remetabolized or translocated from the dying leaf. One could thus hypothesise that compounds that made green leaf unpalatable or toxic may be at much lower levels in fallen leaf. The mimosine content of leucaena leaflets decreases markedly with age of the leaflets, from about 45 g kg^{-1} in young leaflets to <5 g kg^{-1} as the leaves are shed (Tangendjaja *et al.*, 1986).

In *Terminalia oblongata*, which is regarded as a useful browse, but which occasionally causes intoxication, the fallen leaf is considered innocuous compared with new growth (Anderson, 1993).

An interesting situation applies with *Cassia brewsteri*, in which freshly fallen leaf is preferred to green leaf. Something similar may happen with *Acacia cambadgei* (gidgee) as noted above. Also the shrub legume *Gliricidia sepium* is known throughout the tropics as a fast growing species suitable for living fences, green manure, soil amelioration – and animal feed of high protein and digestibility. However, animals show strong aversion to leaf of the living or freshly cut plant, which has a somewhat mousy smell. They can, however, be induced to eat leaf after it has been wilted for some time. Once accepted, it is eaten readily. This has led to the strange situation of the tree being regarded as valuable fodder in some regions and not in others (Lowry *et al.*, 1992).

Falling flower and fruit

In contrast to the lack of recognition of fallen leaf as a feed, there is a wider appreciation that trees can drop other edible products, particularly pods. This is probably because of some well-known cases such as *Acacia nilotica,* and *A. tortilis*, where the pods are an important source of protein during the dry season. There seems to be very little data on the production that might be expected, even for such a well-known case as the edible pods from *Samanea saman.* As trees mature, yield of pods is likely to increase and be comparable to the annual leaf production. Some data can be found from the tree crop literature. A useful summary is that of Felker and Bandurski (1979). The yield will, however, vary greatly according to the environment of the plant. In inland Australia, pod yield from *Acacia nilotica* trees located close to flowing artesian water was up to 40 kg m^{-2} basal area and negligible in the immediate area without access to water (Lowry *et al.*, 1993). In general it is not just yield of pods, but fruiting morphology and phenology that determines whether they are utilizable. Thus leucaena pods typically dehisce while on the tree, the seeds become lost in the ground cover and are too hard to utilize, while the empty valves, when they fall, appear unpalatable. In contrast, pods of *Albizia lebbeck* retain seed when they fall, and the intact pods are readily eaten by cattle, and are a good protein supplement (Schlink *et al.*, 1990).

Less obvious is the possibility of significant amounts of fallen flower. The only report we know of where this is recognized as a distinct aspect of browse is that of Onana (1995). However, there are many dry season deciduous trees where flowering follows leaf drop and where significant amounts of flower are shed late in the dry season before the new leaf flush. Some mimosoid tree legumes produce large amounts of fluffy flower, mostly stamens. *Albizia lebbeck* can produce 10 kg from a mature tree, of high palatability, digestibility, and protein content, that falls in the height of the dry season (Lowry, 1989a). Cattle utilize significant amounts of fallen flower, also largely as fluffy stamens, from the unrelated species

Planchonia careya (Lowry, 1992). In contrast, with *Bombax ceiba*, a tree of the monsoon forests of Asia-Australia, most of the biomass is in large fleshy corollas, which fall in considerable amount and are highly palatable (Lowry, 1999). Onana (1995) notes the high palatability of flowers from *Bombax costatum.*

In general, the fall of flower or fruit is very much an attribute of the particular species. Thus, although *Albizia lebbeck* produces significant amounts of flower, the closely related species *A. procera* and *A. canescens* produce negligible amounts. Flowers may fall at a time of year for them to be of little use or at a time when they have high strategic nutritional value. The potential for a contribution of this type has to be considered for each silvopastoral system.

Effect of Trees on Understorey Pasture

The effect of trees on sub-canopy forage growth can be more complex than that of shade alone. A major review of these effects can be found in an accompanying paper (Cruz *et al.*, 1999). Relevant previous accounts are those of Wilson (1997) and Wilson and Ludlow (1991). Given that light interception is not the only important parameter, the net effect of tree canopy on pasture becomes very much a function of the tree species, soil and rainfall regime. It is important to note that there are circumstances when actual grass yield can be increased by shading (Wilson 1990, 1996; Wild *et al.*, 1993). However, this discussion will be largely concerned with effects on forage quality. Before that it is worth noting two ecophysiological effects not previously highlighted.

Hydraulic lift

Trees and grasses are normally in competition for water, but there is a physiological mechanism (hydraulic lift) by which some trees can supply, rather than deny, water to surface herbage. Caldwell and Richards (1989) have shown that the desert shrub *Artemisia tridentata* brings water to its canopy from its deepest roots in two stages, with an intermediate stage in which the water is stored in the surface roots or secreted into the surface soil. The grass *Agropyron desertorum* growing below the canopy was able to "parasitize" this water. A proportion of the deuterated water supplied to the deepest roots of the tree was found to appear in the grass within hours. Subsequently this has been shown to occur in several other species (Emerman and Dawson, 1996; references therein) and may indeed be not uncommon in semi-arid regions (Caldwell *et al.*, 1998). This effect must be considered as possibly contributing to the apparent enhancement of sub-canopy herbage under some tree species in arid environments, and it would obviously be of interest to know if it can occur with the tree species of a particular silvopastoral system. The process would obviously help maintain greenness and quality of the understorey herbage.

Modification of soil pH

An aspect that has only recently become evident is that particular tree species can have a direct effect on soil acidity, either remediating or aggravating it (Noble and Randall, 1999). This effect has two components. One is the efficacy with which divalent cations (calcium and magnesium) are transported from deep in the profile and released via litterfall onto the surface soil, thus raising pH. The other, and contrary effect, is the extent to which organic chelating agents in the litter leachates complex with cations and carry them down through the soil, thus lowering surface pH. Together these give an "impact index" on soil acidity for each species. In the range of species studied, eucalypts and pines tend to increase acidity, while the most beneficial effect was shown by *Melia azedarach*. It seems likely that trees with high ash alkalinity would favor legumes in the sub-canopy vegetation, thus having an indirect effect on protein availability for livestock. Clearly the impact index would be a desirable parameter to know in considering choice of tree species.

Canopy effects on forage quality

Sward morphology: In well-watered situations the shading effect of dense tree canopies promotes stem elongation in most forages and reduces basal tillering, leading to decreased leaf/stem ratio (Wong and Wilson, 1980). This in itself could decrease forage digestibility and quality (Wilson and Wong, 1982), but in the wet-dry tropics this may be overshadowed by other factors increasing palatability. Another important implication of altered morphology is that sub-canopy grass would be more sensitive to grazing and would require closer management.

Tissue composition: Shaded grasses tend to have higher nitrogen, and lower cell wall content, which would increase quality, but also lower soluble carbohydrate, and the cell walls have a higher lignin content, which would decrease quality (Samarakoon *et al.*, 1990b). As these factors work in opposite directions, shade may not have a large net effect on digestibility. In subtropical areas it appears that shaded and unshaded grasses may differ in digestibility by 3 to 5 units in either direction. In the wet-dry tropics the differences can be much greater, with shaded green panic having digestibility 10 units higher, but this would be likely due to delayed maturation (Liano, 1990).

Temperature effects: The marked differences between "warm climate" and "cool climate" grasses, and the effect of growing temperature on digestibility (Wilson, 1982) have led to the suggestion that the sub-canopy micro-environment may increase quality. However, at an effect of about 0.6% DMD per degree Celsius, the air temperature differences of only 1 to 2°C are insignificant. The cooler conditions are likely to be more relevant to grazing livestock than the plants. In contrast to air temperatures, soil surface temperatures are much reduced and this may positively influence nitrogen mineralization (Cruz *et al.*, 1999; Wilson, 1996). This has most animal production significance when it induces a flush of new green growth at the onset of the wet season, at a time of high nutritional value. This can even occur under trees such as eucalypts that have an overall adverse effect on grass production.

Water relations: Although competition from trees will often massively reduce water availability to the understorey, the opposite effect during periods of intermittent good rainfall may be to conserve it; this is very dependent on tree species, rooting pattern and rainfall regime (Cruz *et al.*, 1999). The effects on quality of the grass herbage are several-fold. In long periods of low rainfall, trees which compete strongly for water in surface soil layers (some eucalypts) may curtail the growth and development of understorey grass leading to a higher proportion of leaf to stem, higher soluble carbohydrate and higher digestibility (Wilson, 1983). That is, the natural maturation of forages, especially tropical grasses, normally leading to a continuous decline in digestibility, is arrested. Of course production is affected, and if severe water stress is continued too long, the understorey plants will die. Alternatively, there are the trees where, following good falls of rain, water is conserved in the sub-canopy area, so that grass continues living while maturing in the surrounding area. *Panicum maximum* associated with the *Albizia lebbeck* canopy in North Queensland had digestibility 5-10 units higher than that in the open, and maintained quality for 6-8 weeks longer at the onset of the dry season (Liano, 1990). Several observations on tree canopy effect in India or Africa also refer to grass remaining green for longer into the dry season (Pinney, 1989). This effect on quality may be of greater importance to animal production than dry matter yields, as at optimum stocking rates, it is the low quality rather than supply of dry season feed that limits animal live weight gain.

Species composition: There are various reports of changes of species composition induced by the tree canopy. In plantations the concern has usually been to establish a range of appropriate shade tolerant grasses and legumes and these have been ranked by Shelton *et al.* (1987) and Wong (1990). The shade tolerant grasses most favored in plantations in the wet tropics appear to be *Paspalum conjugatum* and *Axonopus compressus.* In some plantations pasture production will inevitably decline with canopy development. This may be accompanied by a replacement of desirable legumes with lower quality species such as *Mimosa pudica* and *Micania scandens* (Chin, 1993).

Shade tolerance of grasses is discussed elsewhere (Cruz *et al*., 1999; see also Fladung and Hesselbach, 1989; Mullen and Shelton, 1995). An important practical aspect is that in the wet-dry tropics, conditions seem to favor the establishment of *Panicam maximum* var *trichoglume* (green panic) below the canopy, particularly of tree legumes. The grass is both shade-tolerant and highly responsive to nitrogen. In much of northern Australia there have been many observations of green panic becoming spontaneously dominant under the canopy of *Albizia lebbeck* (Prinsen, 1987) and also of *A. procera, A. canescens* and *Tipuana tipu* (Lowry, 1999). This grass is of much higher quality than the native spear grass (*Heteropogon contortus*) likely to predominate in the surrounding open pasture. It seems likely that in a seasonally dry environment the effect on species composition is rather more important than the shaded/unshaded differences in growth for any one particular species. The possibilities for manipulating understorey species composition should be considered along with the tree species in any silvopastoral system. In a plantation the entire ground cover will be modified by the tree component. However, for trees at wide spacings there may be a mosaic of open grassland intercalated with that modified by the tree canopy. It is worth noting that the resulting increased diversity may itself favor animal production.

Possible toxicity: There have been repeated observations of sporadic hepatotoxicity of livestock grazing *Brachiaria decumbens*, the grass often growing as a plantation understorey (Hegarty *et al.*, 1985).This was believed to be due to mycotoxins from saprophytic fungi, but recent results suggest it is associated with grass saponins. In any event, occurrence is linked with a deep damp sward (Low *et al.*, 1994). It appears more likely to occur in shaded pastures, and should be kept in mind. The possibility of toxicity from ferns should also be considered, as many are shade tolerant and some have significant toxicity.

Dry matter digestibilty and intake: There is a voluminous literature detailing DMD and voluntary intake (VI) values for most common forages grown in open (full sunlight) situations in many reviews and in compilations of feed standards (such as SCA, 1990). Studies determining how these values might change when the same forages are grown under tree canopies are relatively few for DMD and very few for VI; the latter requiring large quantities of shade-grown feed for an acceptable test.

Comparisons of *in vivo* or *in vitro* DMD for tropical grasses grown under different levels of light have consistently shown variable influences of shade, with positive, nil or negative effects on DMD (Samarakoon *et al.*, 1990a,b; Senanayake, 1995) but the changes have generally been 3% units in either direction. Slightly larger change in DMD was recorded when shade was down to 30% light or lower, but again results were variable. For example, at 30% light Norton *et al.* (1991) found a decrease of 4% units, whereas in the opposite direction increases of c. 10% units (Fleischer *et al.*, 1984) and 6% units (Deinum *et al.*, 1996) at 11 and 17% light, respectively, have been reported. The DMD of forage under tree canopies compared to the adjacent open pasture has been reported to be slightly (% units) lower (Hawke, 1991; Belsky, 1992), slightly higher (Jackson and Ash, 1998), or variably up or down by 5 to 6% units according to time of year (Ovalle and Avandano, 1987). The above studies indicate that it is not possible to generalize about the direction of influence of shade and tree canopies on DMD, except to say that for decrease in light down to 40 to 50% any change in DMD is likely to be small.

With respect to voluntary intake of forage and the possible effect of tree canopies, Hight *et al.* (1968) reported that forage of the temperate grass, rye grass, when grown under dense shade (22% light) had a 13.8% lower VI than when grown in full sun; resulting in 29% lower live weight gain of sheep fed on it. Again with temperate grasses, Goto *et al.* (1986) reported lower palatability of shade, compared to sun, grown forages which they associated with higher nitrate-N levels under shade. High nitrate in tropical forages is rarely a problem. Studies with a number of tropical grasses have, with one exception, not repeated the above results and do not support any significant effect on VI of growing forage under shade conditions (Samarakoon *et al.*, 1990a; Norton *et al.* (1991). The exception of 30% lower VI for shade-grown kikuyu in Samarakoon *et al.*, 1990a) was believed due to fungal-infected lower leaves in the very tall, dense and wet sward. More comparisons are needed of VI of shade- and sun-grown forages to assess whether this aspect of nutritive quality is altered for forages under tree canopies.

Examples of Positive Tree Effects on Understorey Forage

The pastoral areas of northern Australia are primarily eucalypt woodland with net herbage production, showing an inverse relation with tree basal area over a range of sites and communities (Burrows *et al.*, 1988; Scanlan and Burrows, 1990, and references therein). It may be that this effect has contributed to the strong backlash against the use of eucalypts in plantation forestry that has developed in India and Thailand. Villagers have found diminished forage availability for cut-and-carry feeding that was unexpected in terms of the existing systems. In fact, the situation is much more complex. Even the effect of eucalypts has to be qualified when looking at growing trees for agroforestry rather than comparing long-established woodland or forest communities. Direct monitoring of pasture when *Eucalyptus grandis* was established in an agroforestry trial in south-east Queensland showed that there was a 35% increase in grass yield under 5- to 8-year-old trees (Wilson *et al.*, 1990; Wild, 1995). However, the perception that trees are adverse for grass growth may make it useful to list those individual tree species that have been highlighted in publications for their positive effect on grass or crop growth. Ironically, some of the most positive effects may occur in traditional systems where it is taken for granted and not documented for publication. One notes that most, but not all, are tree legumes. We refer here to large free-standing trees, and not those hedged, coppiced, on in alley cropping systems.

Acacia (Faidherbia) albida (Mimosaceae)

This African species is almost unique for those of semi-arid woodland in that it is deciduous in the wet season. It is highly valued for promoting grass or crop growth, and there are well-established farming systems that utilize the shaded area for maize or sorghum production. Crop yields under the canopy have been recorded as 56% higher than in areas without trees (Poschen, 1986). In Senegal, yields of groundnut and millet increased from 500 to 900 kg ha^{-1} when grown under the tree canopy (Felker, 1978).

Acacia caven (Mimosaceae)

Thinning natural stands in Chile to various densities showed that the tree canopy had a positive effect on the composition and productivity of the herbaceous layer. DM production at 80% cover was 3.97 t ha^{-1} (vs. 2.78 t ha^{-1} at 30% cover), the length of the short growing season was extended by 25 to 35 days (Ovalle and Avendano, 1987; Ovalle *et al.*, 1990).

Acacia spp. *(Mimosaceae)*

In the Sahel of West Africa, productivity of *Pennisetum pedicellatum* under the trees is about twice that in the open (Bille, 1978). For low-rainfall regions he cited a net productivity of 80 g m^{-2} outside the tree canopy, as compared with 160 g m^{-2} below it, and 170 g m^{-2} from the tree itself. Photosynthetic efficiency was 1.45% below the tree compared with 0.3% outside it. The benefits of tree cover were regarded as unequivocal (" . . une strate ligneuse moderee est plutot benefique pour le development herbace."). In Botswana the same applied to *Panicum maximum*; potential evapotranspiration was reduced by 50 to 70% under shade and the grass remained green 6 weeks longer at the beginning of the dry season (Le Houerou, 1978).

Acacia nilotica (Mimosaceae)

Individual trees were found to promote *Panicum maximum* in Kenya (Pinney, 1989). This tree species is a major woody weed in Australia, where it certainly does not enhance the native Mitchell grass. This is not surprising as it is typically found in dense shrubby thickets on cracking clay soils with no ground water available for deep rooting trees.

Acacia tortilis: A. seiberiana (Mimosaceae)

In the Turkana district of Kenya, Weltzin and Coughenour (1990) found marked positive effects due to tree canopy, with total herbaceous biomass 260 g m^{-2} at the bole and 95 g m^{-2} in the space between trees. A major study also in Kenya by Belsky *et al.* (1989) directly compared various parameters under the tree canopy and in the open, including rainfall interception, light transmission, soil temperature and moisture, and herbaceous layer composition and production. Net primary production under the tree was 705 g m^{-2}, as against 361 g m^{-2} in the open.

Adansonia digitata (Bombaceae)

Although not a legume, and of different canopy form, this species was found by Belskey *et al.* (1989) to promote grasses to almost the same extent as *Acacia tortilis*, the main difference being a lower nitrogen content in the herbaceous layer. The dominant sub-canopy grass was *Cynodon nlemfuensis*, with lesser amounts of *Panicum maximum*, noted elsewhere as the characteristic grass of tree legume shade.

Albizia lebbeck (Mimosaceae)

In North Queensland, early wet season yields of grass dry matter were 82% higher under the canopy in grazed areas and 127% higher in an ungrazed area (Lowry *et al.*, 1988). In early dry season there was also a positive effect on production and even more on quality (Liano, 1990). Apart from the question of relative overall dry matter production, it was noted that grass below the canopy remained green and continued growing for up to 2 months after that in the open had died off. Furthermore, at the end of the dry season, there was a more rapid response to the first rain from grass below the canopy. As noted elsewhere, the effect on quality may be more important than that of total grass dry matter production. The positive effect on grass has been noted also at other tropical and near-tropical sites (Prinsen, 1986; Wildin, unpublished data), but does not appear to be conspicuous in southern Queensland. At a site at latitude 25.5° S, 8-year-old trees had little effect on pasture, but this may have been due to a run of very dry years greatly restricting the growth of the siris trees (Wilson, 1998). The only negative indication appears to be from Rajasthan where it has been reported that sub-canopy forage yields were only 83% of those in the open (Anon, 1998), but this may have been with higher tree densities than in a savannah-type system.

Albizia saman; syn Samanea saman (Mimosaceae)

This species is called "rain tree" throughout much of the tropics, and its effect in promoting green grass below the canopy when that in the surroundings has dried off, is said to be one of the reasons for the common name (NFTA, 1987). Jagoe (1949) found difficulty in finding a suitable unshaded control but found the yield of carpet grass (*Axonopus compressus*) under the canopy (20,840 lbs per acre) was considerably greater than grass growing in the open (4180-9380 lbs per acre). Crude protein levels were also higher (14.3% vs. 9.7%).

Combretum molle (Combretaceae)

This tree was found to promote growth of *Panicum maximum* in a Zimbabwe savannah, the yield of pasture under an "open canopy" being 500 g m^{-2}, as against 300 g m^{-2} in the open. Interestingly, this paper gives results also for a "closed canopy", as about 300 g m^{-2}, indicating that only partial shade is beneficial. A variety of other parameters were measured (Kennard and Walker, 1973). Of the dominant tree species in the same savannah, *Terminalia sericea* had similar effects but *Brachystegia speciformis* and *Julbernardia globiflora* did not.

Cordia alliodora (Tiliaceae)

When this timber tree was grown in association with *Cynodon nlemfuensis* in an agroforestry trial in Costa Rica, annual grass yield was 4.09 t ha^{-1}, in comparison to 2.63 t ha^{-1} in the control plots without trees (Pezo *et al.*, 1989).

Erythrina poeppigiana (Papilionaceae)

Yields of African star grass (*Cynodon nlemfuensis*) obtained in association with this tree were 9.31 t ha^{-1}, compared with 2.63 t ha^{-1} in control plots without trees (Pezo *et al.*, 1989).

Prosopis cineraria (Mimosaceae)

This is the tree that is repeatedly highlighted on the Indian subcontinent for its positive effect on grass or crop production. Shankar *et al.* (1976) found grass production increased about 100% within a 3 m radius of the stem compared with the surrounding area. There were marked differences between tree species, with *Prosopis* having the greatest effect. Other aspects of the system are discussed by Singh and Lal (1969) and Mann and Shankarnarayan (1980).

Prosopis juliflora (Mimosaceae)

This species is used with the grass *Leptochloa fusca* to rehabilitate harsh saline sites. Apparently it is almost impossible to establish the grass without the trees being present (Singh, 1995).

Quercus douglasii (Fagaceae)

The effects of blue oak on sub-canopy herbaceous vegetation appear to be adverse in northern California but positive in central California, including in drought years (Frost and McDougald 1989; this paper cites several other references for both areas). Peak standing crop was 700-1000 kg ha^{-1} higher beneath the canopies than in open grassland. Removal of trees led to a reduction in herbage production.

Quercus suber: Q. rotundifolia (Fagaceae)

The Dehasa of southern Spain, although not tropical, is another area of woodland with hot dry summers. In this open woodland the oak trees apparently create a micro-environment favorable to perennial grasses through their effect on soil water relations (Joffre and Rambal, 1988).

Retama sphaerocarpa (Fabaceae)

This is a leguminous shrub common in semi-arid environments of south-east Spain, different from the other species listed in being virtually leafless; photosynthesis takes place in cladodes. It is another species with which enhanced sub-canopy herbage is associated. Moro *et al.* (1997) showed this to be linked to both soil fertility and microclimate.

Terminalia sericea (Combretaceae)

This species was noted by Kennard and Walker (1973) as one of the two that particularly promoted *Panicum maximum* (*Combretum molle*).

Unspecified Species

A study in the Nigerian savannah, reporting higher herbage yields under the tree canopy, provides considerable detail on the relative amounts of 5 grass species but does not state what tree species are involved (Muoghalu and Ischei, 1995).

What are the Silvopastoral Systems Most Favorable for Animal Production?

In developing new land use, or in managing an existing system, it is likely that animal production will be only one component of the returns expected. We hope that this review will provide assistance in indicating the impact that choice of tree and pasture species and management practices will have on the animal production component, and in seeing new possibilities. One example could be the case of *Gmelina arborea.* There is widespread planting of this tree species in the tropics, with its value seen only as that of a fast growing hardwood. In fact it may have considerable forage value which can be incorporated into planning – if not already recognized and utilized at the local level. Assessment of digestibility and intake indicate that nutritive quality of the understorey forage in most instances will not be very different from that of the same forage grown in open pasture. Quality may sometimes be a little lower, at other times a little higher, varying with the often opposing influences of the degree of shade or degree of soil water deficit imposed by different tree species or rainfall regimes.

The aspects that most favor animal production are trees that provide high quality browse, and are managed by pruning, thinning or lopping to make this available at times of nutritional stress. Animal production may also be favored by trees that have a natural drop of edible leaf, flower or pod in the dry season. Also desirable are trees that are nitrogen-fixing and have a canopy that benefits sub-canopy vegetation, if only at certain times. This vegetation should contain forage species that are shade-tolerant, nitrogen-responding and otherwise compatible with the tree species. The tree spacings should be wide enough to allow lateral light penetration and create a mosaic of shaded and unshaded pasture.

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