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Effects of Shade on the Growth and Mineral Nutrition of Tropical Grasses in Silvopastoral Systems

Pablo Cruz[1], Jorge Sierra[2], John R. Wilson[3], Maguy Dulormne[2] and Régis Tournebize[2]
1*Station d'Agronomie, INRA. BP 27, 31326 Castanet-Tolosan, France*
[2]*Station Agropédoclimatique de la Zone Caraïbe, INRA. BP 515, 97165 Pointe-à-Pitre, France*
[3]*CSIRO Tropical Agriculture, 306 Carmody Road, St. Lucia, Queensland 4067, Australia*

Abstract: Interactions between tree and grass strata in silvopastoral systems have been studied for a large number of species and environmental conditions. In tropical environment the increase of growth and/or mineral nutrition of the grass stratum due to tree shade has been very often reported. This effect has been observed even for non-leguminous tree component and under artificial shading, and occurs most frequently when water and nitrogen are limiting factors for grass growth. This paper reviews the literature on morphogenetic and trophic responses of tropical C_4 grasses to shading, as well as on the ecological, physiological and physical mechanisms involved in these responses. It is concluded that shade enhances the availability of nutrients in the soil, which concerns the chemical and/or physical fertility. The principal processes involved are: (i) recycling of nitrogen fixed by legume trees via leaf-root-nodules decomposition and/or animal excreta, (ii) changes in microclimatic conditions by shade, favoring the biological activity of the soil, and (iii) transfer of nutrients absorbed by trees from the deeper layers of the soil to the surface via leaf drop and/or animal excreta. The needs and perspectives for future research are discussed.

Key words: Tree-grass interactions, nutrient cycling, morphogenesis, CO_2 assimilation, light-use efficiency.

Production systems based on the combination of one tree (frequently leguminous) species and grass stands have been described for (i) tropical (Botero and Russo, 1998) and temperate (Sibbald *et al.*, 1991) regions, (ii) under humid (Benavides *et al.*, 1989) and dry (Jeltsch *et al.*, 1998) conditions, and (iii) as part of the natural (Belsky *et al.*, 1993) or artificial (Nygren and Cruz, 1998) systems. Interactions between shrubs and grasses have been studied in a range of environments, using species as diverse as the systems employed. When studying interactions between shrub and grass components, particular emphasis has been laid upon competition (Jacquard, 1968) or facilitation (Vandermeer, 1989) between strata for resources like light, water and nutrients.

Because of the diverse conditions under which these studies were performed, the results were sometimes contradictory. The frequency of certain effects is sufficiently high to merit closer scrutiny, as for example, increase in the growth and nutrient uptake, particularly N, of the grasses due to shade. This effect was observed in numerous field trials of silvopastoral systems, even with non-leguminous trees and artificial shade (Benavides *et al.*, 1989; Belsky,1992; Belsky

et al., 1989, 1993; Cruz, 1997a; Lowry *et al.*, 1988; Ovalle and Avendaño, 1988; Stuart-Hill and Tainton, 1989; Weltzin and Coughenour, 1990; Wilson *et al.*,1990).

The benefits of shade on the growth of grassland species are controversial and some results, obtained under a wide range of environmental conditions, have reported the lower production under shade (Somarriba, 1988; Cavagnaro and Passera, 1991; Robinson, 1991; Scanlan and Burrows, 1990; Sibbald *et al.*, 1991; Mordelet and Menaut, 1995). In all these cases, the result was a reduction in the production of grassland biomass and not a reduction in its radiation-use efficiency (RUE). Thus, a reduction in the growth of understorey grass could easily be interpreted as a negative or undesirable effect, when in fact the entire shrub-grass system may have improved in terms of overall efficiency (Hubert and Boglio, 1989) or have shown specific efficiency of the underlying stratum (Wilson and Ludlow, 1991; Cruz, 1997a).

As a general rule, it is possible to highlight competitive or facilitation phenomena in certain well-defined silvopastoral systems. Thus, amongst naturally-occurring isolated trees, typical of the African savannah, an improvement in the growth of understorey grass can be related to an increase in the availability of the nutrients provided by the trees. This has frequently been explained in terms of processes independent of the direct effect of shade. Amongst these processes, mention should be made of nutrient recycling through mamalian and bird excreta and/or recycling of the nutrients by shrub leaf litter (du Preez *et al.*, 1983; Joffre *et al.*, 1988; Belsky *et al.*, 1989; Welzin and Coughenour, 1990; Isichei and Muoghalu, 1992; Belsky, 1994; Campbell *et al.*, 1994). During this recycling, the role of the tree "pump", absorbing nutrients at considerable depth and restoring them to the surface through leaf fall has been demonstrated by Sharma *et al.* (1990), under the conditions of arid rangelands. However, this recycling mechanism does not seem to provide an explanation for systems where root depth of tree and grass is not different. In the humid savannah, Mordelet *et al.* (1997) have shown that tree and grass root distributions are overlapped and are located mostly in the top 20 cm of the soil.

Under open grazing systems, nutrients undergo internal recycling through the action of livestock. Animals consume the foliage of the tree/shrub and thus improve the mineral nutrition of grass through their excreta. Another example is that of associations where the tree/shrub component is made up of a legume which fixes atmospheric nitrogen (Catchpoole and Blair, 1990b). Consumption and excretion by animals of the nitrogen contained in the tree legume has been reported as the principal route for transferring nitrogen fixed by the legume towards the associated grass (Catchpoole and Blair,1990a).

At a given degree of shade, water availability appears to be a key factor determining the level of grass production. The availability of water to the grass understorey, under given conditions of moisture, is strongly dependent upon the density (Eastham *et al.*, 1990) and age of the shrub layer (Wilson, 1998). Consequently, the complexity of controlling soil water availability and its interaction with a range of shrub densities is such that highly variable results may be anticipated.

In assessing the results described and anticipated from tree-grass relationships, Belsky (1994) pointed out that: (i) in both tropical and temperate climates, trees reduce understorey plant productivity through competition for light, water and nutrients; (ii) understorey productivity may be improved in the case of isolated trees (or low tree density), as is often observed in the tropics and subtropics with low rainfall and moderate soil fertility; (iii) high density communities of trees combined with high rainfall or extremely nutrient-poor soils, reduce the understorey productivity. However, numerous exceptions to these rules may be cited. For example, under moderate or high tree or shrub densities, improvements in understorey productivity have been reported in humid tropical regions (Lowry *et al.*, 1988; Benavides *et al.*, 1989; Cruz *et al.*, 1995) and the subtropics (Wilson *et al.*, 1990; Carvalho, 1997). These positive shade effects are noticed on relatively nitrogen-deficient soils, and have usually been observed when the open grassland is subjected to a moderate degree of water stress.

Under conditions where water is not limiting and soil mineral status is not affected by shade, a reduction in grass understorey productivity due to lower irradiance is logical, when compared to full-sun conditions. Such results have been reported by Wilson and Wild (1991), Gaudichau (1992), Wild (1995) and Cruz (1996; 1997a). The innovative study performed by Philippart (1995) demonstrated the relationship between the degree of shade and understorey growth, independent of any water factor.

Undeniably, in silvopastoral systems there are likely to be complex interactions between tree density, tree species (principally if species are legumes or not), rooting depth of tree and grass species, and water and nutrient availability (particularly nitrogen), which should determine the degree of pasture growth. It is necessary to clarify the different components of such complex interactions, through the use of experimental systems and appropriate methodologies. This has given rise to the hypothesis that the beneficial effects of shade on grass growth may be due to its positive influence on soil nitrogen (N) availability (Wilson *et al.*, 1986; Wilson, 1990). This idea was put forward in the light of the results obtained under artificial shade, which enabled separation of the shade effects to the grass understorey from other effects arising from the presence of trees, such as root competition and litter fall.

In this paper we propose to examine the effects of shade on the microclimate of the grass understorey, the consequences regarding the growth of perennial tropical grasses and the mechanisms governing these effects. The need for further research and its field of application will also be discussed.

Microclimatic Environment Under Trees

Irradiance

Under certain conditions, light constitutes the principal environmental resource in competition with trees and understorey species (Riege *et al.*, 1995). When studying these conditions, as pointed out by Wilson (1997), characterising a shade as the percentage radiation transmitted to the grass storey may give rise to erroneous evaluations. Indeed, the growth capability of a canopy is determined by the quantity of photosynthetic irradiance (PI) received daily, which may vary greatly with latitude, season and climatic conditions. If we assume that

Table 1. Average daily values for incident photosynthetic irradiance ($MJ.m^{-2}$) in wet tropical, subtropical and Mediterranean regions

Zone	Location	Summer	Autumn	Winter	Spring
Wet Tropics	Kuala Lumpur[1] (3.1°N)	8.9	9.7	8.9	8.7
	Singapore[2] (1.18°N)	9.1	8.6	8.1	8.3
Subtropics	Samford[1] (27.3°S)	10.8	7.8	6.8	10.3
	Rockhampton[2] (23.24°S)	10.8	8.6	8.1	11.6
Mediterranean	Fresno (California)[1] (36.5°N)	14.0	7.9	4.4	11.3

[1] From Wilson (1997) and [2] estimated by P. Cruz from data published by Cooper and Tainton (1968).

perennial C_4 grasses are exclusively found in tropical or subtropical regions, then variations due to latitude and seasonal changes are less marked. However, climate-related differences may be observed in the intertropical zone (Table 1).

A second source of error when studying the growth of the grass understorey is the use of short-wave (SW) solar radiation values, especially when growth is analysed in terms of RUE. This latter expression of growth, little employed in this research area, should be preferred as the explanatory variable concerning biomass accumulation under different degrees of shade. It is preferably expressed as the cumulative amount of photosynthetically active radiation (photosynthetic irradiance, PI) absorbed by the grass stand, rather than the SW radiation incident during the regrowth period. However, its use requires detailed knowledge of the possible sources of bias inherent in the method, particularly when it is applied to tree/pasture situations. The tree storey absorbs solar radiation selectively, thus depleting the radiation transmitted to the grass in the 400 to 700 µm wave band as a consequence of chlorophyllous absorption. Thus, the proportion of PI to SW incident on the herbaceous understorey differs from that found in full sunlight. Above the tree canopy, this proportion may be considered as being stable, at a level of 0.5 to 0.48, as reported by Szeicz (1974) and Varlet-Grancher *et al.* (1981). At the herbaceous layer, this ratio may be drastically reduced (0.27), as determined by Baldocchi *et al.* (1984). This chlorophyllous selective absorption of SW radiation is shown in Fig. 1, where the relative spectral distribution of the light transmitted to the soil under a canopy is represented for shaded and sunlight areas. This source of error, due to the selective absorption by foliage, may be considered to be negligible if the shade is provided by the use of neutral shade cloths (Wilson, 1988). In this case, the radiation balance can be determined by measuring SW solar radiation with solarimetric tubes, as described by Rigueiro *et al.* (1998). A change in the PI/SW ratio is not the sole effect of chlorophyllous absorption on spectral composition. The proportion of blue light (Holmes and Smith, 1977), and the ratio of red to far-red (R/FR), are also affected by shading (Fig. 2). An example of the influence of different trees on reducing R/FR at understorey level is given in Wilson (1997).

The distribution of shaded and full-sun zones of the grass storey depends on the density and structure of tree planting (isolated, in rows, etc.), their orientation and the position

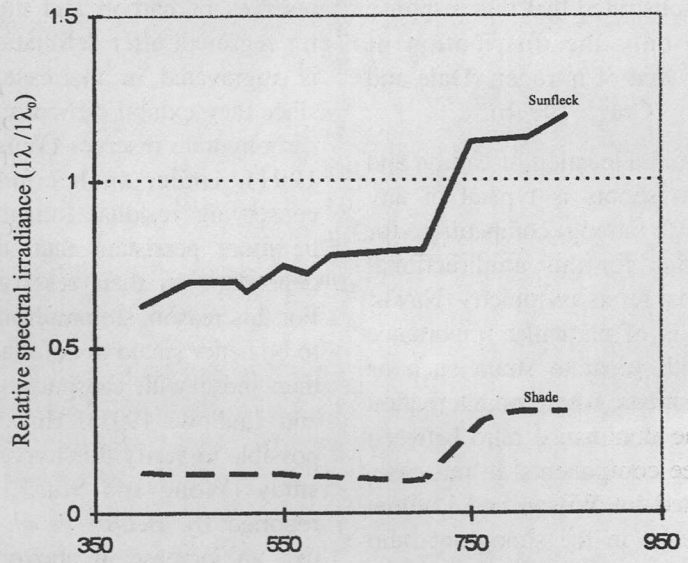

Fig. 1. Special energy distribution of light at ground level (1λ) and above the canopy (Iλo) (from Varlet-Grancher et al., 1993).

of the sun. The amount of energy received by the grass storey differs considerably at different sites, even in the case of densely planted areas and in case of daily integration of transmitted PI beneath the shrubs. Fig. 3 shows this heterogeneity in PI distribution under cultivated rows of *Gliricidia sepium,* planted at a distance of 2 m. These data illustrate the difficulty in clearly determining the terms of mean radiation within a grass-tree association. Use of a model to simulate radiative transfer in mixed inter-cropping systems (Sinoquet and Bonhome, 1992) may enable a satisfactory description of the light microclimate at the herbaceous layer (Tournebize and Sinoquet, 1995).

Morphogenetic and trophic response of understorey grasses

A range of morphogenetic responses by forage species to lower R/FR ratios has been quoted or described: promotion of leaf and stolon elongation or stolon curvature (Willemoës *et al.*, 1987), inhibition of tillering (Deregibus *et al.*, 1983; Casal *et al.*, 1985; Simon and Lemaire, 1987), inhibition of branching (Simon *et al.*, 1989) and an increase in leaf/stem ratio in grass species (Wilson and Ludlow, 1991; Cruz, 1997b).

The most important morphogenetic response to low PI level is a change in the partitioning coefficient of photo-synthates between above-ground and under-ground biomass. An increase in the shoot/root ratio under shade has been reported by numerous authors (Wong *et al.*, 1985; Samarakoon *et al.*, 1990; Dale and Causton, 1992a; Olff, 1992; Cruz, 1995). It corresponds to a growth strategy which enables the plant (or sward) to increase its light uptake to compensate for lower levels of irradiance (Ludlow, 1978).

It has been demonstrated that this response influences not only the distribution of carbon, but also that of nitrogen (Dale and Causton, 1992b; Cruz, 1997b).

The preferential allocation of carbon and nitrogen towards shoots is typical of any plant subjected to strong competition for light. Competition for this unidirectional resource is peculiar for its asymmetry (Navas, 1998), and this is of particular importance in a system with separate strata such as tree-grass associations, where no alternation is possible in the dominance ratio between the grass and tree components. In this case, and as highlighted by Wilson and Ludlow (1991), an increase in the shoot/root ratio in perennial forage species under grazing may pose considerable threat to their survival. Always dominated by the shrub storey, grass growth cycles follow one another under conditions inappropriate to maintaining the reserves of carbon and nitrogen necessary for regrowth after defoliation. The situation is aggravated in the case of C_4 grasses, since they exhibit difficulty in accumulating carbohydrate reserves (Wilson and Ludlow, 1991). Under such conditions, species conserving residual foliage in shade may be more persistent than those which are dependent on their reserves for regrowth. For this reason, stoloniferous species appear to be better suited to defoliation under shade than those with caespitose growth (Wilson and Ludlow, 1991). However, it was not possible to verify this hypothesis in a recent study (Wong and Stür, 1996). The data reported by Belsky *et al.* (1993) showed that an increase in above-ground biomass in the grass storey (25 to 46%) could not be explained solely by changes in the distribution coefficient between shoots and roots, since the reduction in root biomass

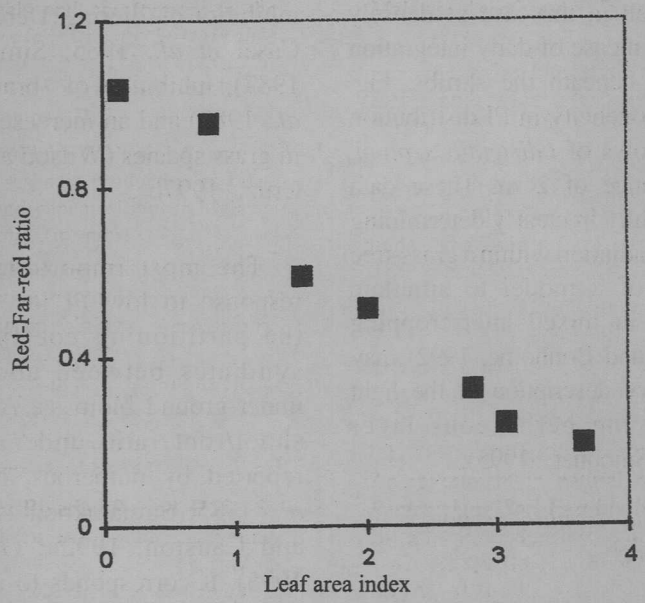

Fig. 2. Relation between red:far red ratio at ground level and leaf area index of the canopy (from Holmes and Smith, 1977).

Table 2. Radiation-use efficiency (g MJ^{-1}) of C_4 perennial grass species under full sunlight and artificial shade conditions

Light level (% full sun)	*Panicum maximum*[a]	*Dichanthium aristatum*[b]	*P. maximum* (seeding year)[c]	*P. maximum* (2nd year)[c]
100	2.0	2.3	2.7	1.9
75			3.2	
70	2.5			
56		3.1		
50			4.5	2.8
40				2.5
30	3.4			
20			5.3	

Data from Sophanodora (1989)[a], Cruz (1996)[b] and Schwenke (1996)[c].

was only some 10%, with absolute values lower than the increase found in shoots.

The preferential distribution of biomass towards shoots poses a methodological problem when estimating the RUE of stands subject to different degrees of shade. In perennial species, this variable is nearly always calculated using above-ground biomass only, and any increase in the shoot/root ratio may cause over-estimation of the RUE under shade. Cruz (1996) and Schwenke (1996) estimated RUE values which were higher than that considered to be the potential value, 2.5 g MJ^{-1} (Cruz, 1995), for a tropical grassland. Similarly, the preferential allocation of nitrogen towards the aerial organs may result in an over-estimation of the nitrogen level of the stand when using the nutrition index method described below.

Table 2 shows estimated RUE values (based on PI) for species adapted to sunlight environment, but growing under shade conditions with optimum nitrogen nutrition. It can be seen that the values are higher than 2.5 g MJ^{-1} under shade. The small increase in the RUE for *Panicum maximum* in the second year (Schwenke, 1996) could be due to lower level of nitrogen than during the seeding year. In *Dichanthium aristatum*, the value corresponding to shading of approximately 33% was not given because of the high tiller mortality. This was interpreted as being a consequence of the lack of carbon reserves during previous regrowth cycles.

Effects on the composition of understorey vegetation

There is a clear contradiction between the characteristics of a forage species which is required to produce a specific quantity of biomass for livestock consumption, and those adapted to grow in shade. The assessment of forage species for use in silvopastoral systems is confronted with the problem of selecting suitable material with two properties which are, to a considerable extent, antagonistic: productivity and perenniality. The compromize, which must be found between these two functional strategies, depends to a great extent upon the silvopastoral system under consideration, as discussed below.

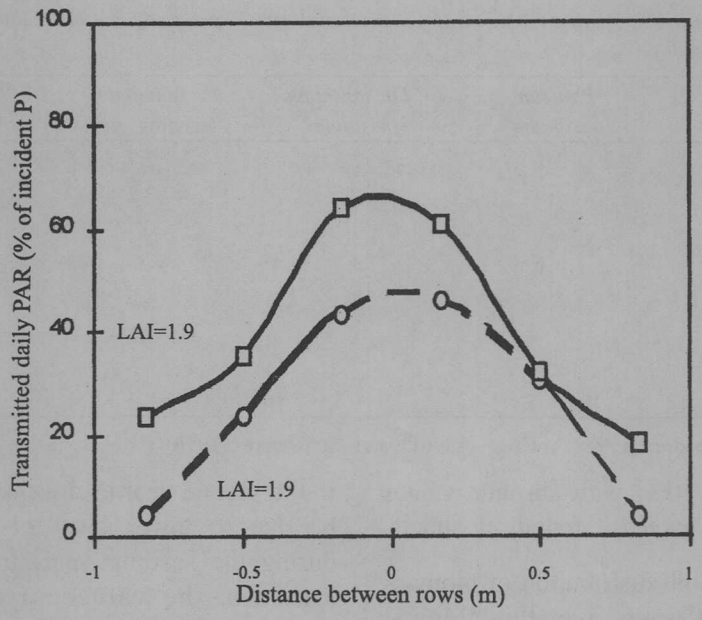

Fig. 3. Spatial distribution of daily PAR between two rows of Gliricidia sepium having different LAIs (from Tourenebize and Sinoquet, 1995). 0 = midway between rows; -1 and 1 = position of rows.

- In systems where isolated trees are present in grasslands, such as the African savannah (Amundson *et al.*, 1995) or humid tropical regions (Guevara *et al.*, 1992), the distribution of species suited to each type of habitat (below-crown species and open grassland species) occurs naturally without the need for human intervention. These adaptation mechanisms were studied by Kinyamario *et al.* (1995) in species occurring in a Kenya savannah.

- In plantations, the shade environment changes gradually with the age of the tree crop. At maturity, levels of PI transmitted to the herbaceous layer may be very low (10% in rubber and oil palm plantations, as reported by Chen, 1989), or moderately high (more than 50% in a coconut plantation, according to Rika *et al.*, 1991). Such systems do not permit the management of shade levels, and breeding programmes for species suited to each situation can be undertaken (Sanchez and Ibrahim, 1991; Kaligis and Sumolang, 1991; Ng, 1991).

- In tropical systems involving legumes such as *Leucaena leucocephala* (Shelton and Brewbaker, 1994), *Gliricidia sepium* (Nygren *et al.*, 1999), *Calliandra calothyrus* (Palmer *et al.*, 1994) and *Erythrina poeppigiana* (Benavides *et al.*,1989) as a shrub component, the intensity of competition for light can be managed. The specificity of these species consists of their adaptation to regular defoliation, whether through pruning or direct removal by livestock. This defoliation en-

ables regulation of the shade level over the grass storey, thus making it possible to use high-productivity forage grasses which are not necessarily adapted to low levels of irradiance.

Some studies have demonstrated that shade thresholds higher than 50% of IR have highly deleterious effects upon the perenniality of forage species (Cruz, 1996; Rigueiro *et al.*, 1998) particularly under regular defoliations. However, broad variations in this attribute have been observed between species, and even within the same genus or accessions of the same species (Stür, 1991). Finally, turf grasses are available which are particularly well-suited to shade, where persistence, rather than productivity, should be sought in breeding programmes (Wilson,1997).

Temperature

A reduction in the light level under trees or shrubs also lowers air, leaf, canopy and soil surface temperature. As a general rule, it is the extreme temperatures which are modified, i.e., the maxima are reduced and the minima are raised, by comparison with those prevailing in open grasslands (Tournebize *et al.*,1996).

Some authors have calculated values for these modifications. Ovalle and Avendaño (1988) observed that cutting the shrub storey increases the maximum surface soil temperature by 8°C in the summer. Belsky *et al.* (1989, 1993) reported reductions in maximum soil temperature of about 5 to 12°C under isolated trees in savannah regions. Finally, under artificial shade, Wilson *et al.* (1986) and Wong and Stür (1996) achieved reductions of between 2 and 6°C in soil temperature levels, depending on the time of the year. Greater reductions (up to 10°C) have been recorded by Wilson and Wild (1995) on litter and in surface soil (top 2 cm). These temperature reductions should play an important role in conserving surface moisture and may influence soil fauna/earthworms, which are effective in litter breakdown and nutrient cycling.

Reductions in the temperature of foliage or the grassland canopy are smaller, and some 1 to 2°C less in the shade, as found by Wong and Stür (1996) and Wilson and Wild (1995). These minor differences will have a very slight effect on sward growth.

Water Status

Soil water status depends on the source of shade, or more precisely, whether it is natural (trees and shrubs) or artificial (shade cloths). In both the cases, the lower surface temperatures found in shade, accompanied by higher air humidity (Wild, 1995) and a reduction in wind speed (Tournebize *et al.*, 1996), potentially enables a lower level of evapotranspiration (Wilson, 1997). The presence of a tree with a large canopy may create the opposite effect because of its water consumption, and therefore, higher humidity levels in the shade are not observed (Belsky *et al.*, 1993; Tournebize *et al.*, 1996). Mordelet and Menaut (1995) showed a lack of relation between rainfall and enhancement or depletion of grass production in savannah formations.

It is important to distinguish between different levels of water status. According to Briones *et al.* (1998), the intensity of inter-species competition for moisture seems to depend on its level in the soil. In a very dry environment, competition for moisture is absent below a threshold level.

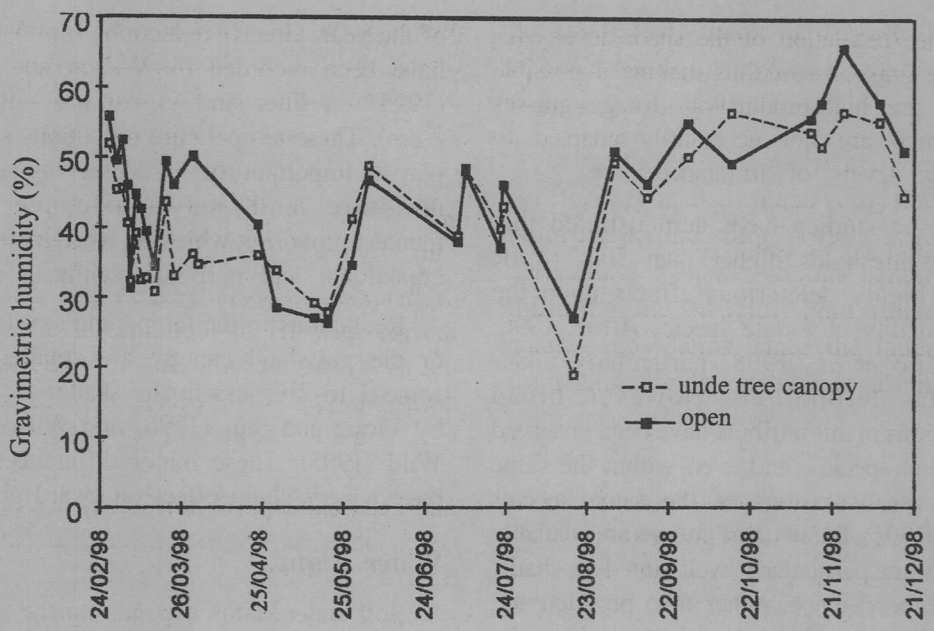

Fig. 4. Annual trend of gravimetric humidity (%) in the top 10 cm of soil under the canopy of Gliricidia sepium and in the open (M. Dulormne and J. Sierra, unpublished data).

In contrast, competition may be very intense when the soil moisture level rises. The extent of competition may depend on the abundance of water and the duration of competition.

In humid tropical climates, higher evapotranspiration in a tree/grass system (Tournebize *et al.*, 1996) does not influence productivity of grass understorey productivity, probably because of the lack of competition for water (Gaudichau, 1992; Cruz *et al.* 1993; Cruz, 1997a). Tournebize *et al.* (1996) measured at the beginning of the humid season, the soil moisture values in these systems, at a depth of 10 cm beneath the trees and in the open. The values were almost similar. However, during the dry season (January-April), the top 10 cm of soil under trees were found to be drier (Fig. 4). In a subtropical environment (S.E. Queensland, Australia), Wild (1995) showed that soil under tree shade was, to a large extent, drier than soil under open grassland or shade-cloths, and that this difference was more marked at a depth of 40 cm than at the surface soil. In the dry zones, particularly in arid areas, the positive effects of shade on the growth of grasses is strongly dependent on rainfall. These effects are short-lived and benefit the development of annual (Frost and McDougald, 1989) or ephemeral (Patten, 1978) plants.

CO_2 Fixation Under Shade

At leaf level

When considering the uptake of CO_2, a low PI level has morphological and physiological effects on leaves. The marked morphological changes include a decrease

in leaf thickness (Smith and Martin, 1987a), specific leaf area (SLA) and dry matter content, and an increase in blade proportion (Wong *et al.*, 1985; Samarakoon *et al.*, 1990). These morphological adaptations correspond to efficient capture of irradiation, which should enable the plant to maximize light interception under shade with the lowest expenditure of energy (Wilson, 1997). At low levels of irradiance, leaves develop a lower specific leaf weight (or higher SLA), so that a unit of leaf area is less "expensive" in terms of carbon.

An increase in the N concentration of blades is another consequence of shading (Deinum *et al.*, 1996). However, because of the lower SLA, the N content, in terms of area, may be lower under shade (Evans, 1989). This constitutes an important factor in the expression of leaf CO_2 uptake. In studies on tropical grass species, Wong and Wilson (1980) and Cruz (1997a) demonstrated that the uptake values expressed by unit of leaf surface area were higher in shade, but this difference was not seen if net uptake was expressed per unit of leaf nitrogen content (Fig. 5).

Physiological adaptations also occur which enable maximisation of the CO_2 fixation. Working on C_4 grasses, Smith and Martin (1987b) demonstrated an increase in the chlorophyll concentration and a fall in the chlorophyll a/b ratio under shade. These species apparently adjusted chlorophyll concentrations and ratios in response to different levels of photosynthetic photon flux density (PPFD). These authors showed that a higher chlorophyll concentration and a lower chlorophyll a/b ratio in shaded plants resulted in an increase in both light-harvesting ability and the size of the light-harvesting complex, respectively. Other physiological adaptations,

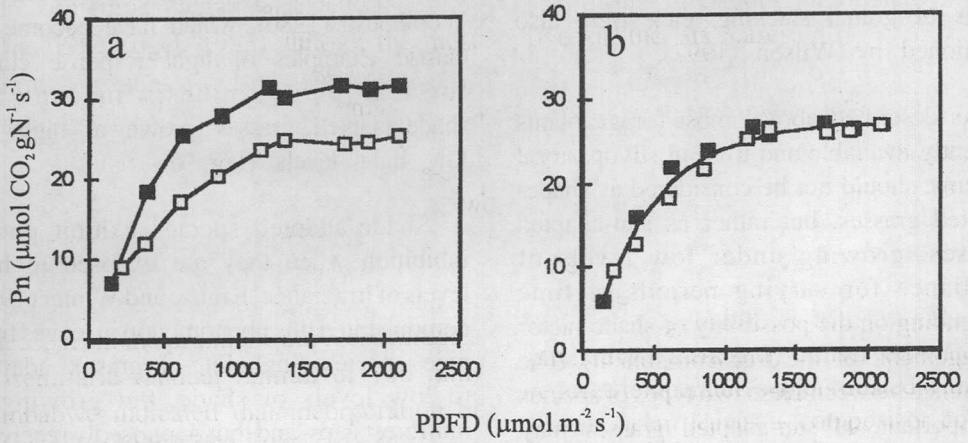

Fig. 5. Light response curves for net CO_2 assimilation (Pn) over a range of photosynthetic photon flux densities (PPFD) for leaves of Dichanthium aristatum grown in open (full sun □) or shade (■) expressed on (a) leaf area basis or on (b) leaf N amount basis (from Cruz, 1997a).

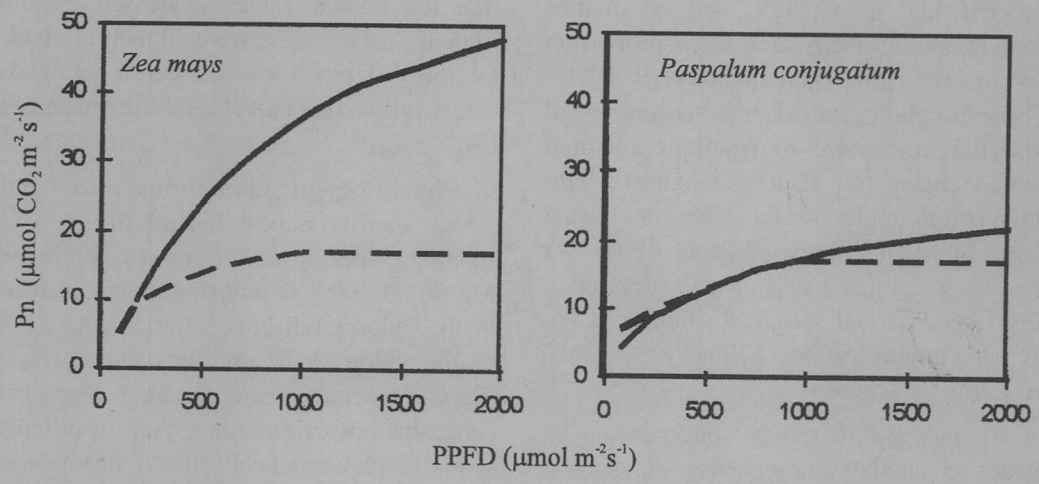

Fig. 6. Light response curves for net leaf photosynthesis (Pn) of a "sun plant" (Zea mays) and a "shade plant" (Paspalum conjugatum) grown at low (---) and high (—) light levels (adapted from Ward and Woolhouse, 1986).

such as an increase in the photosystem II/I ratio, changes in pigment composition, higher levels of granal stacking, etc., were also mentioned by Wilson (1997).

As described above, most forage plants currently available and used in silvopastoral systems, should not be considered as shade-adapted grasses, but rather as sun-adapted grasses, growing under low levels of irradiance for varying periods of time (depending on the possibility of shade factor management, or the tree component). The difference between these two types of species is important, as sun-adapted grasses may be capable of adjusting satisfactorily to moderately low light levels (depending on the species and the duration of shade). In contrast, shade-adapted grasses which can tolerate very low light levels (<2% of sunlight), are unable to achieve high rates of photosynthesis at high light levels. This was illustrated in results obtained by Ward and Woolhouse (1986), which have become the classic examples of light response curves for leaf photosynthesis in sun- and shade-adapted grasses grown at high and low light levels (Fig. 6).

Shade-adapted species exhibit photo-inhibition when they are exposed to high levels of irradiance. Krause and Winter (1996) demonstrated this phenomenon in leaves from nine species (including a grass), adapted to low levels of shade, but growing in rainforest gaps, and thus supposedly receiving high levels of PPFD at mid-day on cloudless days. In contrast, in tropical grasses adapted to high and moderate light levels, Ludlow *et al.* (1988) (quoted by Wilson, 1997) were unable to demonstrate any photo-inhibition when leaves of plants grown at a low light

level were suddenly exposed to full sunlight, even when they were markedly N-deficient. Smith and Martin (1987b) showed that three forest understorey species of the C_4 grass, genus *Muhlenbergia*, grew optimally under high PPFD levels.

Whatever the type of canopy (isolated trees, shrub in rows, regular plantations, etc.), the grass understorey never receives uniform level of shade. On the contrary, it is subjected to an ever-changing light environment, with alternating periods of shade and sunlight of varying lengths, ranging from a few seconds to several minutes or even hours, as may be the case in the central region of an inter-row. The dynamics of the response to changes in irradiance intensity (sunflecks) are sometimes the factor determining the CO_2 uptake of the species in shade (Pearcy, 1989). This response depends on the type of species under consideration, and most studies have been performed on shade-adapted (or shade-tolerant) species.

An example of the incidence and distribution of sunflecks in a *Gliricidia sepium/Digitaria decumbens* association, where trees were planted in rows, 3 metres apart, with a global LAI of 1.7, is illustrated in Figs. 7 and 8 (Dulormne, 1997). These results showed that 80% of the sunflecks duration was lower than 5s and mainly distributed just below the canopy area. In this study, a sunfleck was defined as any change from a low light level ($\leq$360% µmol m^{-2} s^{-1}) to a high light level ($\geq$800% µmol m^{-2} s^{-1}). The duration of a sunfleck was defined as the time during which irradiance was $\geq$800% µmol m^{-2} s^{-1}, with a minimum threshold of 0.6 second. Study of the response of leaves of *Digitaria decumbens,* cultivated in shade (33% of sunlight), to changes in the light level lasting for 60 or 120 seconds, showed that CO_2 uptake in this C_4 forage species was not dependent upon the level of light under which it grew, but was on the light level received on an alternating basis during measurements, i.e., from 350% µmol m^{-2} s^{-1} at low levels to 1000% µmol m^{-2} s^{-1} at a saturating level of PPFD (Dulormne, 1997). These results are illustrated in Fig. 9.

At canopy level

The effects of shade on the morphology of the entire plant, as described previously, may have consequences for canopy photosynthesis because of changes to canopy structure and thus to the interception of light.

From a functional point of view, an important effect with consequences upon the net photosynthesis of the stand is the decrease in the rate of dark respiration at low PI levels (Givnish, 1988). In whole plants of *Panicum maximum*, a sunlight-adapted species, Ludlow *et al.* (1974) demonstrated that the reduction in respiration was proportionally smaller than the reduction in CO_2 uptake. This mechanism seems to be one of the key factors in plant adaptation to low light levels amongst true shade plants (Boardman, 1977).

A difference exists between the light response curve at canopy level and that at leaf level. As shown in Fig. 5, the leaf response of a C_4 grass to changes in unidirectional light reaches a plateau at PPFD levels higher than 1000% µmol m^{-2} s^{-1}. In the canopy, this response is virtually linear, because of the random orientation of leaves in this stratum. Consequently, the reduction in CO_2 uptake of a tropical grassland would usually be proportionally in line with the

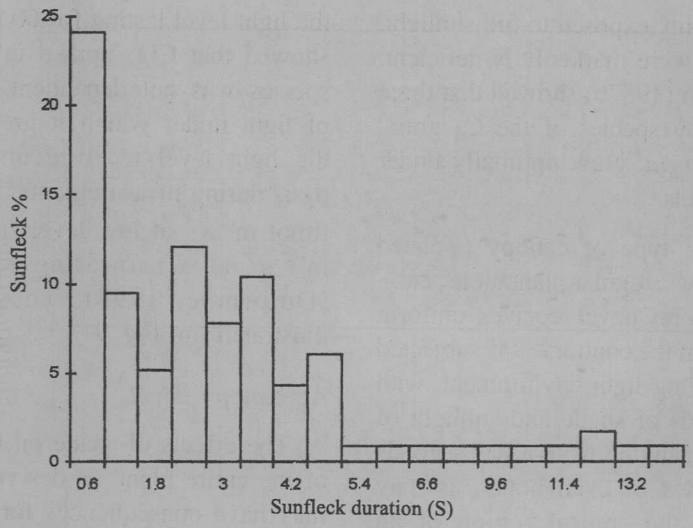

Fig. 7. Daily proportion for the most frequent sunfleck durations between two rows of Gliricidia sepium. Row spacing = 3 m. Global LAI = 1.7 (from Dulormne, 1997).

reduction in the level of incident PI. However, under dense shade the light response curve may be more curvilinear, almost like that of a single leaf, because of the low leaf area index of the canopy (Wilson, 1997). In this case, photosynthesis of the sward will benefit from any improvement in nitrogen nutrition provided by shade, as was demonstrated for leaves by Wilson and Wild (1991). Thus, an improvement in nitrogen availability to the grass understorey is a critical factor in increasing the overall productivity of silvopastoral systems.

Nutrient Availability

Most silvopastoral systems in a subhumid environment favorably influence soil fertility (the availability of nutrients) and/or physical (aeration, drainage, compaction, erosion) conditions (Kass *et al.*, 1997; Sadeghian *et al.*, 1998). Studies also show that the degree and type of effect (chemical or physical), the nutrient involved and the mechanisms responsible for the improvement may vary considerably as a function of the type of pasture system (directly grazed, cut-and-carry), the tree species (legumes or non-legumes) and soil type.

Several mechanisms may be involved in governing nutrient availability: (i) recycling of nitrogen fixed by a NFT (Mazzarino *et al.*, 1991; Dulormne *et al.*, 1999); (ii) mobilisation of soil P via the presence of mycorrhizas (Danso *et al.*, 1992); (iii) changes to microclimatic conditions within the tree/pasture association, favoring the biological activity of the soil (mineralization of organic matter, as reviewed by Cruz *et al.*, 1997); (iv) transfer of nutrients (Ca, Mg, K, P) absorbed by the tree at considerable depths in the soil to the surface

via tree leaf drop and/or animal excreta (Sadeghian *et al.*, 1998). The latter process also includes the safety-net mechanism (Imbach *et al.*, 1989) which involves the uptake by tree roots of nutrients initially released in upper layers of the soil and leached below the root depth of the herbaceous species growing in association. The existence of this effect has been confirmed only in non-silvopastoral agro-ecosystems (legume tree/cocoa or coffee; Babbar and Zak, 1995). It is possible that the safety mechanism may not be of importance in the case of grass swards with a high root density, occupying most of the soil volume.

The processes described above may occur simultaneously and result in improvement in soil fertility, or at least that of the upper soil strata. In the dry Chaco silvopastoral system in Argentine, Mazzarino *et al.* (1991) observed an accumulation of N and P in the surface soil layers, associated with recycling of NFT-fixed N and recycling of absorbed P (Table 3).

Differences in soil N content between the tree/grass association and grass alone become marginal, but are still evident, at deeper soil depths. Increased soil phosphorous level under the tree is evident only at the soil surface. This indicates that P has been transferred from deep in the soil to the upper few centimetres, rather than there being greater release of the nutrient in upper soil layers. Similar results were obtained in the dry tropical forest of Colombia, especially in silvopastoral systems using N-fixing trees *Gliricidia sepium* (Sadeghian *et al.*, 1998) and *Erythrina edulis* (Gómez, 1997). In these cases, gains in Ca, K and Mg content were also observed in the surface layers of the soil, and the increase in extractable P was

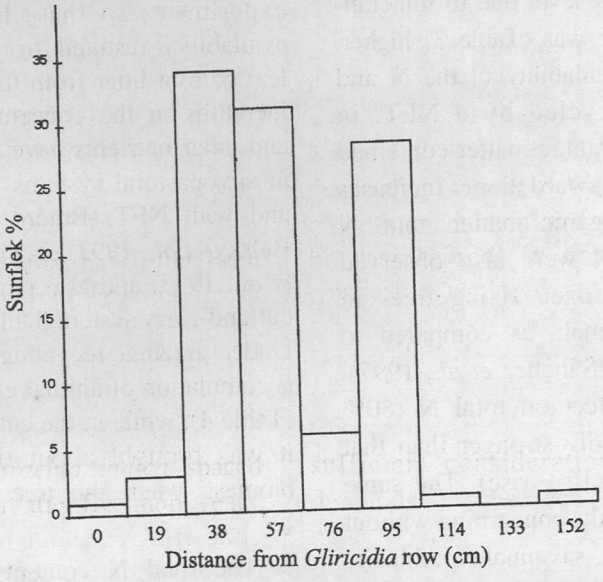

Fig. 8. Spatial distribution of sunfleks between two rows of Gliricidia sepium. Distance between rows = 3 m, IAF = 1.7 (from Dulormne, 1997). Sunfleck = irradiance ≥800 µmol m^{-2} s^{-1} for >0.6 s.

Table 3. Some soil properties in a natural silvopastoral system in the Dry Chaco of Argentina. Soil samples were taken under grassland (Papophorum spp.) in the open or under the tree canopy (Prosopis spp.)

Soil depth (cm)	Total N (g kg^{-1})	Extractable P (mg kg^{-1})	N mineralization			Soil bulk density (g cm^{-3})
			Dry season	Wet season (mg kg^{-1} y^{-1})	Total	
Under tree canopy						
0-10	1.82	39	5	147	152	1.11
10-25	0.97	17				
25-45	0.73	10				
In open grassland						
0-10	1.45	29	19	49	68	1.20
10-25	1.08	20				
25-45	0.68	17				

particularly marked, viz., 71 mg kg^{-1} under *Erythrina edulis* as against 11 mg kg^{-1} under the grassland alone. Part of this increase in extractable P may have been due to mobilisation induced by the presence of mycorrhizas (Sadeghian *et al.*, 1998).

The increase in N level due to mineralization under the tree was (Table 3) higher, indicating greater availability of the N and organic matter recycled by a NFT, in comparison to the organic matter contained in the soil beneath a sward alone. Increases in the levels of organic matter, total N and mineralizable N were also observed beneath the non-nitrogen fixing trees in a Venezuelan savannah, as compared to those beneath grass (Sánchez *et al.*, 1997). In this case, the effect on total N (80% increase) was markedly stronger than that on mineralizable N (16% rise). The same trend was seen in results concerning without NFT in the African savannahs (Abbadie and Lensi, 1990; Mordelet *et al.*, 1993). Bernhard-Reversat (1986) compared a natural, dense savannah of *Acacia seyal* with a plantation of *Eucalyptus camaldulensis*, and demonstrated the important role played by natural shrub storey in enhancing the nutrient content of superficial soil strata.

These results concern systems where grazing had been excluded during the experiment, so that changes in nutrient availability resulted from the recycling of leaf or root litter from the plants. However, increases in the concentrations of total N and other nutrients have also been observed in silvopastoral systems with direct grazing and with NFT (Botero and Russo, 1998; Belsky *et al.*, 1993) or without NFT (Belsky *et al.*, 1993) and also under the tree/pasture cut-and-carry system (Dulormne *et al.*, 1999). Under grazing, recycling occurred through accumulation of animal excreta near the tree (Table 4), while in the cut-and-carry system, it was brought about through dead root biomass when the tree was pruned.

The total N content in soil of a 20 m wide plot of pure grass (*Dichanthium* spp.), situated between other plots of the same grass associated with the NFT *Gliricidia*

sepium in a subhumid zone of the Caribbean region showed 20% increase (Fig. 10). The increase in soil N under grass was maximum near the tree row. This plot had never received any fertilizer N input, and that all tree prunings and grass cuttings were removed from the plot. The reduction in concentration towards the middle of the plot indicated smaller contribution of NFT roots to recycling the N fixed in the soil. In view of the N concentrations observed under a silvopastoral system (0.32%), and the uptake of N by the tree and grass, the authors estimated that N fixation by the NFT reached 650 kg N ha^{-1} y^{-1}, of which, at least one third was recycled in the soil.

Several authors have observed an improvement in N nutrition in tropical grasses growing with non-nitrogen fixing trees or beneath artificial shade in subhumid regions (Wilson, 1990; Wild *et al.*, 1993; Wilson, 1996). These results suggest an increase in the availability of mineral N in the soil due to favorable soil moisture conditions under the shade of tree canopies that favor mineralization (Wilson, 1990). Although Wilson (1996) observed increased water content in top 5 cm soil (a zone of high microbial activity) under the shade, other authors have not reported such difference in soil moisture under the trees or the grasses in silvopastoral systems (Mazzarino *et al.*, 1991; Belsky *et al.*, 1993). In natural systems with isolated trees, where the distance between trees is greater, it is possible that effects on biological activity in the soil may be less important than the amount of substrate available for this activity. In conditions with

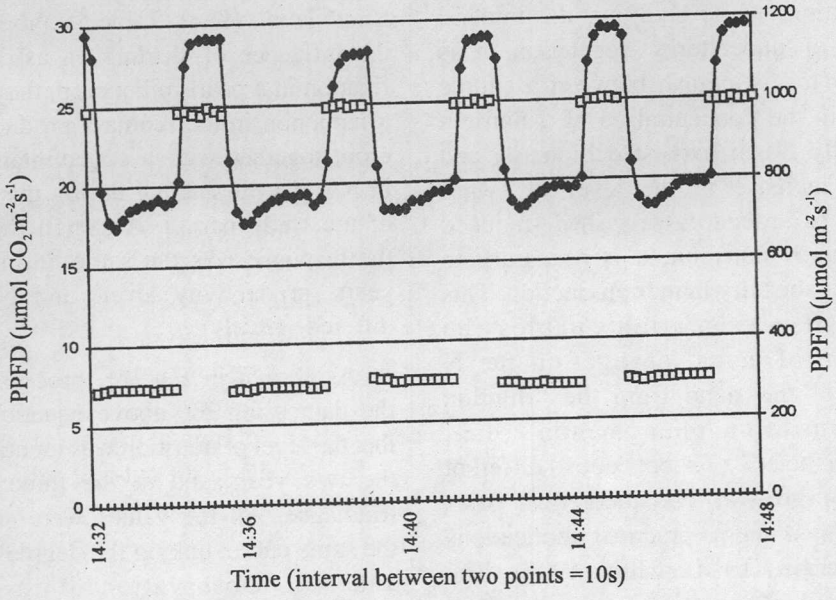

Fig. 9. Net CO_2 assimilation (Pn) of leaves of Digitaria decumbens grown under shade (33% sunlight) exposed alternately to low and high (sunflecks) levels of PPFD (—) (from Dulormne, 1997).

Table 4. Nutrient content of the manure of animals grazing a grassland (Cynodon spp.) or a silvopastoral system (Erythrine fusca + Cynodon spp.)

Type of vegetation	Nutrient content (% dry matter)				
	N	P	K	Ca	Mg
Grassland only	1.13	0.36	0.82	0.6	0.4
Silvopastoral system	1.46	0.42	1.17	0.9	0.5

dense tree canopy with no competition for moisture or artificial shading, this hypothesis may be considered as a possibility. Direct measurements of mineralization are necessary to test the effect of soil moisture on N availability, by comparing natural and artificial systems. As shown in the experiments conducted by Wild (1995), methodological problems need to be resolved in order to demonstrate higher soil N mineralization under shade using *in-situ* core incubation.

To avoid too many errors of interpretation, while studying the mineral nutrition of understorey vegetation, it is necessary to distinguish between a simple increase in the concentration of a nutrient (principally N) in harvested biomass, and the true increase in the level of sward nutrition. In order to assess shade-induced changes in N nutrition, it is necessary to plot N% against dry matter production. This method of presentation enables the separation of actual changes in the N nutrition of the stand from the "dilution or concentration phenomenon", i.e., changes in the N% of shoots due to different degrees of growth. The theoretical basis of this method and its practical implications were described by Lemaire (1997). The N nutrition level of a stand may be described using the function:

$$N\% = \alpha(DM)^{-\beta}$$

where,

DM (dry matter) is expressed in t ha^{-1}, α is the N% for the first ton of biomass and ß is the coefficient of dilution during DM accumulation. When calculating the optimal N nutrition of C_4 stands, the values for α and ß were 3.6 and -0.34, respectively (Cruz and Lemaire, 1996; Lemaire, 1997). The same relationship may be established using N uptake by the stand instead of the N% of the biomass (Cruz, 1997a).

To illustrate the use of this interpretative tool, we may employ the data reported by Smith *et al.* (1984) (Table 5). When studying the influence of shading on associative N_2 fixation in a pearl millet crop, they observed a reduction in the biomass produced by the crop, together with a concomitant increase in N% due to shading during the two years of the study period. Although the trend of the response was the same during the two years, productivity levels and N% values differed greatly.

As shown in Fig. 11, processing of all the data using the above equation showed that the level of nutrition was identical during the two years and at the three levels of irradiance. All the values were situated on the same curve, linking the degree of growth and N%. Observation of this unique relationship makes it possible to affirm that any change to associative N_2 fixation caused by shade did not have any effect on the use of N by the crop.

In addition to its effect on nutrients, the trees also improve the soil physical characteristics like reduction in soil bulk density (Table 3, Mazzarino *et al.*, 1991; Belsky *et al.*, 1993), and increase in porosity (Gómez, 1997), probably through the tree root system or an effect on organic matter in soil. In contrast, tree-grass competition for available nutrients has been cited as an example of a negative effect of the presence of trees on grass nutrition (Kass *et al.*, 1997). This is particularly important during the period after tree pruning, when N fixation in NFTs fall because of the total or partial mortality of nodules in the tree, depending on soil N for its nutrition (Nygren and Ramírez, 1995). Mazzarino *et al.* (1991) suggested that, in natural silvopastoral systems most tree-grass competition occurs in the spaces between the trees, because of the lower concentrations in total and mineralizable N as compared to levels seen in soils directly under the tree canopy.

Conclusions and Perspectives

Silvopastoral systems play a vital role in raising animal productivity and increasing the sustainability of agricultural systems, particularly in the subhumid tropics. The introduction of trees in grassland regions can improve the physical environment of the grass understorey, as long as the tree and grass species are partially complementary. Increasing interest is now being shown in these systems, and agronomic research has clearly demonstrated the positive effects of

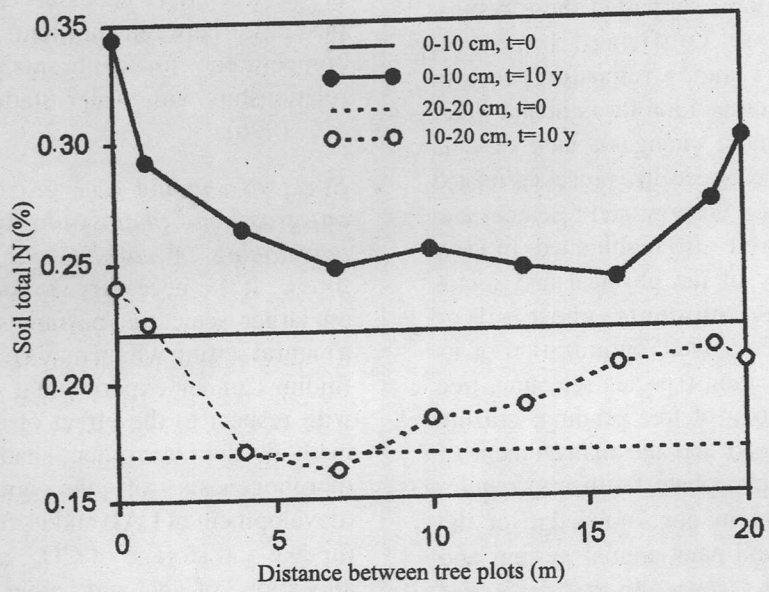

Fig. 10. Concentration of soil nitrogen in a grass plot (Dichanthium spp.) placed between two silvopastoral plots (Gliricidia sepium, NFT). The tree rows correspond to distances 0 and 20 m; t = 0 and t = 10 y correspond to nitrogen concentration at the time of tree planting and 10 y afterwards, respectively (adapted from Dulormne et al., 1999); soil depth sampled: 0-10 cm, 10-20 cm.

Table 5. Effect of shading (% sunlight) on dry matter (DM) production and N (%) in plant tissue of pearl millet, Pennisetum americamum

Shade (%)	Year 1978		Year 1979	
	DM (t ha^{-1})	N (%)	DM (t ha^{-1})	N (%)
0	4.33	0.82	9.29	0.38
50	2.32	1.62	6.96	0.57
75	1.56	2.01	4.27	0.95

silvopastoral systems. Studies performed in recent years have, in particular, been aimed at gaining an understanding of the plant and animal responses to different associated grassland management techniques, and at assessing effects on the physical environment, with particular emphasis on soil fertility. Discussions at two recent symposia on "Ecophysiology of Tropical Intercropping" (Sinoquet and Cruz, 1995) and "Tree-Crop Interactions: a physiological approach" (Ong and Huxley, 1996) supported these results. Although these confirmed important conceptual advances regarding certain mechanisms (competition for light and water and microclimatic changes), lack of data concerning some aspects like processes related to competition for underground resources and root recycling were also highlighted. In view of the diversity of the physical and socio-economic environments where silvo-pastoralism is employed, optimization of its technical application (species selection, tree density, frequency of tree pruning, grazing pressure on grass) and the management of inputs (N and phosphate fertilizers) require an improvement in our knowledge of the entire climate-soil-plant-animal system and of interactions between its different components.

In our opinion, three themes constitute priorities for future research, so as to enable a distinction between the "shade effect" (photosynthesis, morphogenesis, micro-climate) and the "tree effect" (nutrient recycling, underground competition). These are as follows:

- *Spatial and time-based estimations of root recycling*: Although in general terms this concerns both trees and grasses, the recycling of roots and the nutrients they contain constitute a key factor in the cut-and-carry system after pruning of the tree. It is necessary to evaluate the ratio between nutrient input and competition for nutrients, and its relationship with water status (Ong *et al.*, 1996).

- *Effect of shading and grazing system on grassland photosynthesis and the partitioning of carbon and N in the grass:* It is necessary to obtain data on larger scale tree/pasture systems in a natural setting which may be set against findings under experimental conditions with respect to the effect of defoliation methods and intermittent shading on the morphogenesis of the grass layer (development of LAI) and its functioning (uptake and storage of CO_2, uptake and allocation of N and other nutritive elements).

- *Effect of microclimatic conditions on the biological activity of the soil:* It is necessary to discriminate between the direct effect of the tree on potential

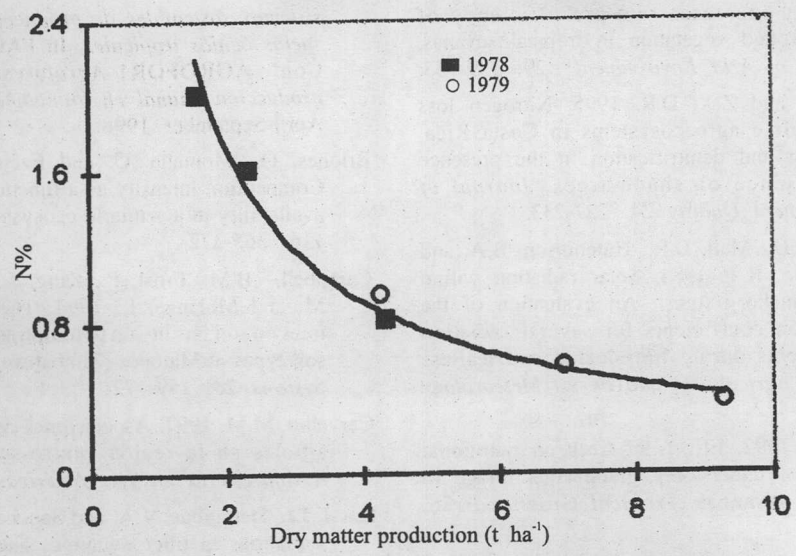

Fig. 11. N concentration of Pennisetum americanum herbage grown under different shade levels, as a function of grass dry matter accumulation in two consecutive years.

fertility (total quantity of a nutrient) and its indirect effect on the immediate availability of nutrients (shade effect). As regards N, this distinction concerns the effect of changes in soil temperature and moisture within the association on the rate of mineralization/immobilization, and its interaction with the labile N provided by NFT.

Other priorities could be proposed for specific systems. It may be valuable to analyse P as a nutrient in systems on acid soils, where a change to the climatic parameters within the tree/pasture association constitutes an essential factor in the semi-arid zones. The selection of grass species or accessions which can tolerate very low levels of irradiance is of fundamental importance in systems where the degree of shading may be considerable (rubber plantations) and cannot be modified, or even in the specific cases of turf grasses. This will be less crucial in systems involving legume forage trees and shrubs, where pruning can regulate the percentage of PI reaching the grass undesrtorey. Research should be directed towards the management of the tree or shrub component.

Finally, when organising our research programmes, we must always remember the views of Ong *et al.* (1996, p. 14): "researchers should not ignore the extensive knowledge and wisdom of farmers and pastoralists, who may not fully understand the principles of resource capture, but are well aware of which tree species are compatible with crops and which are not".

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