Architecture, seasonal growth and interference in three grass species with different flowering phenologies in a tropical savanna

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Abstract

In a field experiment we studied the relationships between architecture, seasonal aerial biomass growth and interference from neighbours in three savanna grass species differing in time of flowering: a precocious species (*Elyonurus adustus*), an early species (*Leptocoryphium lanatum*) and a late species (*Andropogon semiberbis*). To detect the neighbour interference upon architecture and seasonal regrowth, we measured the leaf interception of a plane at different heights, when the species grew alone, in pairs and in groups of three. Although the three species differed widely in the spatial and temporal patterns of occupation of above-ground space, important levels of interference among neighbouring plants were detected. The species differ in: a) the pattern of space occupation when growing alone; b) the magnitude of the interference effect by the companion species; c) the change in pattern as a consequence of interference; d) their reaction to fire.

The interference is not symmetric and it is not related to phenological similarities based on flowering season. *L. lanatum* was both the most impaired and the least impairing of the three species and the opposite is valid for *A. semiberbis*. The basal species (*E. adustus* and *L. lanatum*) showed a higher potential to produce leaf surface during the growth season than the tall species (*A. semiberbis*), but the stronger interference from the latter tended to equate their growth when the species grew in mixtures.

In all three species interference led to a reduction of the growing period. Based on the analysis of growth at the various heights and the architectural peculiarities of the species we concluded that neighbour interference is probably reducing both tillering and leafing in the basal species but only culm elongation and leafing in the erect species.

The species also differed in their reaction to fire. *A. semiberbis* and *E. adustus* showed a pulse of regrowth after the passing of fire which is missing in *L. lanatum*. In all cases the neighbour interference affected both the intensity of growth and the length of the growing period, but it did not affect either the height of the plants nor the reproductive phenology of these three grass species.

Introduction

Neotropical savanna communities are characterized by a rather high specific and functional diversity (Sarmiento 1983; Monasterio & Sarmiento 1976). Sarmiento & Monasterio (1983) reviewed the phenology of savanna plants and suggested four phenological types for savanna grasses on the basis of time of

flowering: precocious, early, intermediate and late species. Seasonal partitioning is very sharp and each species takes from four to six weeks to complete its annual reproductive phase including seed dispersal. As has been suggested for savannas (Gulman *et al.* 1983) and other plant communities (Medway 1972; Frankie *et al.* 1974; Rabinowitz *et al.* 1981) this temporal segregation is probably related to niche partitioning of resources needed to complete the reproductive phase (Sarmiento 1983) although there are no direct evidences of this for savanna plants.

Several studies of savanna communities have shown that apart from flowering phenology, dominant grass species may also differ in their aboveground architecture (Sarmiento 1984; Sarmiento & Monasterio 1983; Silva 1987), and in their seasonal patterns of tillering and leafing (Silva & Ataroff 1985). This is especially important since savannas are usually burnt towards the end of the dry season, and both survival and reproduction depend on the ability of the plants to regrow their foliar surface during the rainy season. Sarmiento & Monasterio (1983) suggested that regrowth is related to the time of flowering, with early flowering species regrowing their foliage rapidly whereas late flowering species have a peak of growth late in the rainy season. These authors concluded that early growers after the passing of fire would not face any competitive pressure from other species, either for light, water or nutrients.

Based on these hypotheses we predicted that competitive interference between species would increase with phenological similarity, and that this could be detected in the seasonal regrowth of the foliage. In addition, we wanted to study to what extent plant architecture and foliage regrowth dynamics are correlated to flowering phenology. Competitive interference experiments usually imply a comparison of performance in pure and mixed cultures. However, under savanna field conditions, grass plants occur either as single tussocks or form small groups of two or three species. To study the differences between grass species under natural savanna conditions regarding the way they occupy the aerial space with their foliage during the regrowth season and the interference effects of neighbours growing close by, we compared the stratified aerial regrowth of individu-

als growing alone with individuals growing in a mixture with other species under field conditions.

Methods

The study site

The experiment was conducted under field conditions in a seasonal open savanna located near the city of Barinas in the western Llanos of Venezuela (8°38′N; 70°12′W). Average annual rainfall is 1500 mm, with a wet season between May and November and a dry season from January to March. April and December are transitional months, sometimes wet sometimes dry. Mean annual temperature is 27 °C with very little fluctuation throughout the year. These savannas are commonly burnt once a year, between February and April.

The community has a very open tree layer dominated by *Bowdichia virgilioides*; common tree species are *Palicourea rigida* and *Casearia sylvestris*. The herbaceous layer is continuous and codominated by the following grass species: *Elyonurus adustus, Trachypogon plumosus, Andropogon semiberbis, Axonopus canescens, Sporobolus cubensis* and *Leptocoryphium lanatum*.

The species

Among the dominant grass species coexisting side by side in the savanna community at the study site, we selected three perennial species with different flowering phenologies. a) *Elyonurus adustus* flowers after the annual burning at the end of the dry and beginning of the rainy season, classified as a 'precocious' species (Sarmiento 1983). It is a bunch grass with long, membranous and very narrow leaves, which grows only in very well drained savanna soils (Silva & Sarmiento 1976). b) *Leptocoryphium lanatum* flowers in May, one month after the onset of rains and is considered an 'early' species (Sarmiento 1983). It is a bunch grass as well with long, hard and scleromorphic leaves, usually involute (Sarmiento & Monasterio 1983) which grows in a wide range of savanna soils, from very well- to moderately drained

(Silva & Sarmiento 1976). c) *Andropogon semiberbis* flowers in November, at the end of the rainy season and is thus considered a 'late' species (Sarmiento 1983). It is a slender medium size grass, with rather short and membranous leaves, and is also restricted to well drained savanna soils (Silva & Sarmiento 1976).

Sampling design

In January 1985 we selected groups of these three species growing in the field as follows: a) mixtures with one individual of each of the three species growing very close together (ELA); b) mixtures with one individual of each of two species growing very close together (EL, EA, LA); c) individuals of each of the three species growing alone (E, L, A). Three replicates of each group were tagged and the surrounding area was cleared of all other plants in a 30-cm radius. Care was taken to assure that all experimental individuals selected were of similar basal area and their bases were separated by no more than 2 cm. Clearing was done mechanically by carefully removing rhizomes or stems. This was enough to kill all other plants in this area without using herbicides. This clearing was repeated when germination occurred throughout the study and was performed in such a way that damage to the experimental plants was avoided.

Sampling started in February, two weeks after a fire had destroyed all the above-ground biomass. Every month during one year we measured plant-leaf densities in each individual. We used a cubic metallic structure ($200 \times 80 \times 80$ cm) in which we could set a frame of 256 squares (5×5 cm). In order to perform the measurements we set the cubic structure on permanent reference marks in the soil and mounted and dismounted the frame successively from 10 to 200 cm above ground at 10 cm intervals (Fig. 1). This operation consisted in carefully passing iron rods 3 mm in diameter until the two dimensional frame was set. Special care was taken not to alter the natural position of leaves and culms. At each level we counted all intersections with the frame surface and that was considered as the plant-leaf density for that level. In each visit additional observations were
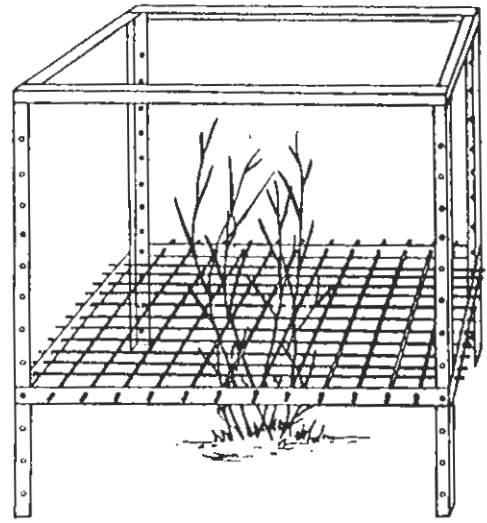

Fig. 1. Cubic metallic structure ($200 \times 80 \times 80$ cm) used to measure leaf densities. The frame formed by iron rods 3 mm in diameter was mounted and dismounted successively from 10 to 200 cm above ground at 10 cm intervals.

made to qualitatively follow the phenology of regrowth.

Results and discussion

Figure 2 shows the changes in total leaf density (the number of intersections) for each species growing alone and in mixtures of two species throughout the year. Results for the three-species mixtures are basically similar to the two-species results and are not shown (but, see Fig. 3). Variance is high in some cases, but the patterns are clear. The species differed in: a) the pattern of space occupation when growing alone; b) the magnitude of the interference effect by the companion species; c) the change in the pattern as a consequence of interference; d) their reaction to fire.

a) Regarding patterns of space occupation when growing alone: *A. semiberbis* (Fig. 2-C) showed a 4-month lag phase after the onset of rains. Leaf density increased rapidly after August to reach a plateau in November. Thus, growth peaked during a rather short period of time (August to November) which coincided with the last months of the rainy season. As mentioned before, this species flowers in Novem-
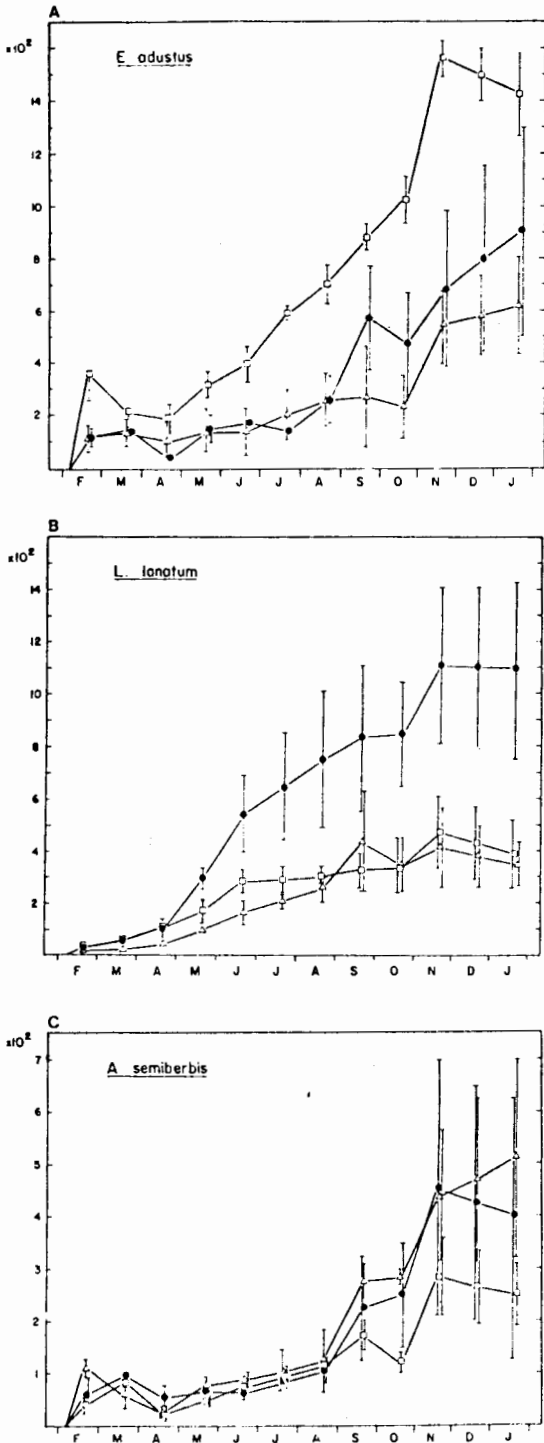
Fig. 2. Changes in mean total leaf density values (ordinate) throughout the year (abscissa) for each species growing alone or in mixtures of two species. a) *Elyonurus adustus*; b) *Leptocoryphium lanatum*; c) *Andropogon semiberbis*. □ *E. adustus*; ● *L. lanatum*; △ *A. semiberbis*.

ber. *E. adustus* is a precocious blooming species, but its leaf density kept increasing at a constant rate after the onset of rains (April) (Fig. 2-A) and showed an even higher growth rate towards November after which it reached a plateau. In *L. lanatum* (Fig. 2-B), leaf density increased very slowly after the fire, but rapidly after April, gradually reaching a final plateau at the end of the season (November).

b) The effect of interference by companion species was strong in the case of *E. adustus* and *L. lanatum*, but very low in the case of *A. semiberbis*, when growing with *L. lanatum*.

c) Interference also led to a change in the temporal patterns of seasonal growth. In *E. adustus*, the initial growth after the onset of rains was null, and the species behaved more like a late species, when growing with either of the other two species (Fig. 2-A). In *L. lanatum* under interference (Fig. 2-B), the plateau was reached very rapidly, and growth was restricted to the first two rainy months (May and June). In *A. semiberbis* (Fig. 2-C), the growth period was shortened (October to November) when growing with *E. adustus*.

d) After the fire in February, in the middle of the dry season, *E. adustus* and *A. semiberbis* showed a pulse of growth which will be discussed later. There was no pulse in reaction to fire in *L. lanatum*.

The stratification of foliage as based on the mean leaf density per height interval of each species growing alone and in mixtures is shown in Fig. 3. When growing alone the three species showed different above-ground architectural patterns. *E. adustus* reached a total height between 50 and 60 cm and 67% of the total leaf density in the first 0–10 cm. (This is a common distribution pattern, cf. Fliervoet & Werger 1985). *L. lanatum* is more evenly distributed and reaches the 60–70 cm interval, still 39% of the total leaf density is found in the 0–10 cm interval. These two species have a tussock habit, with 86% of the total leaf density of *E. adustus* in the 0–20 cm level and 80% of the total leaf density of *L. lanatum* in the 0–30 cm interval. *A. semiberbis*, on the contrary, has a slender habit with elongated aerial culms which reach 120 cm height. Its foliage is distributed rather evenly.

The effects of neighbours upon the architectural pattern of each species may also be seen in Fig. 3.
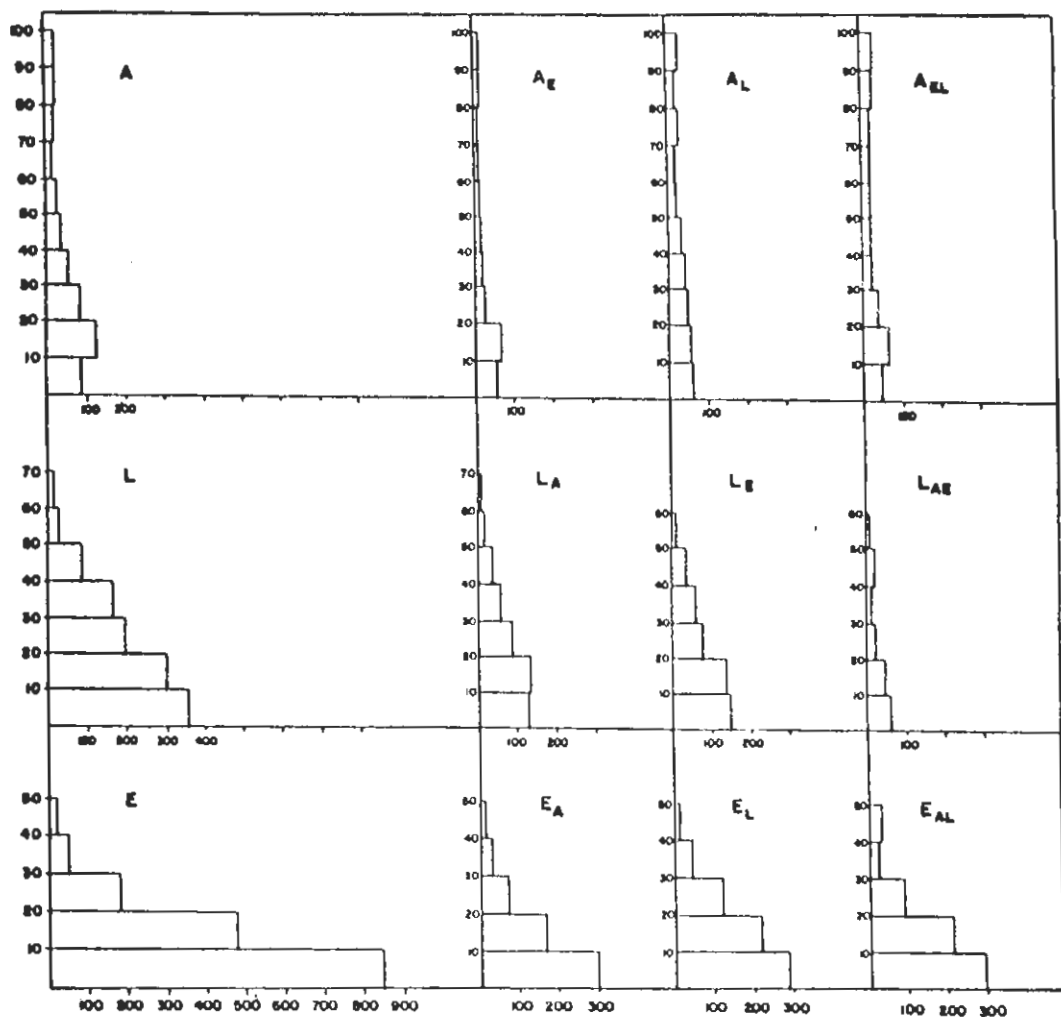
Fig. 3. Stratification of foliage for species growing alone and in mixtures of two and three species, as mean leaf density values (abscissa) for each height interval (cm) (ordinate) measured after completion of seasonal regrowth. A = *Andropogon semiberbis*; E = *Elyonurus adustus*; L = *Leptocoryphium lanatum*. Subscript letters indicate accompanying species.

The decrease in total leaf density shown by *L. lanatum* and *E. adustus* when growing in mixtures is brought about by a sharp decline in leaf density values in the first two intervals. There is only a slight change in the relative pattern of biomass allocation. The effects of interference upon *A. semiberbis* are less important than in the other two species, both on absolute and relative leaf density at each interval. However, when this species grew in mixtures the foliage density distributions are smoothed by a relative higher decline in the third and fourth height intervals. The maximum height reached by each of the three species did not change significantly, despite the changes in absolute and relative leaf density values.

In these three grass species, seasonal regrowth of above-ground biomass is the result of the following processes: a) the production of new shoots or tillers; b) the growth of culms through the elongation of the internodes of existing tillers; and, c) the production and elongation of leaves at the nodes of the culms.

Different leaf density profiles as shown in Fig. 3 have different meanings for plants of different architectural patterns, as in this case. *E. adustus* and *L. lanatum* are 'basal' grasses in the sense of Desco-

ings (1975), also called grasses with culmless vegetative shoots (Hyder 1972). In these plants the leaves are produced from very short internodes at the ground level, and the elongated culms only carry a few very small leaves and the terminal inflorescence. Therefore, in *E. adustus* and *L. lanatum* an increase of leaf density at the first level is the result of tillering and leafing, but any increase at the upper levels can only result from leafing. In 'erect' or culmed vegetative grasses (Descoings 1975; Hyder 1972) as *A. semiberbis*, which produces leaves at different heights of the elongating culm, the increase in the 0–10 cm interval is again the result of tillering and leafing, but increase in upper intervals results from both culm elongation and leafing. In both architectural types tillers are only produced at the ground level. Following these considerations, the effects of interference upon tillering, tiller growth by culm elongation and leafing could be deduced by comparing the changes in leaf density at the first level to those at upper levels.

Figure 4 allows a more detailed analysis of the temporal patterns of space occupation. Here we show the changes in leaf density in the species growing alone and in mixtures of two species for the different height intervals. The three species clearly differ in pattern.

From February to April, growth was restricted to the 0–10 cm interval. *E. adustus* (Fig. 4a, 0–10 cm) and *A. semiberbis* (Fig. 4c, 0–10 cm) showed a pulse of regrowth after the passing of fire, followed by a decrease in leaf density during the last two months of the dry season (March, April). These species do not produce new tillers before the starting of the rainy season (Silva unpubl.). Therefore the postfire pulse of growth is probably due to leafing and not to tillering. It could be a response to the sudden soil enrichment from the ash as suggested by Medina *et al.* (1978). The subsequent decrease was due to progressive desiccation and death of leaves or leaf tips. In *L. lanatum* (Fig. 4b, 0–10 cm) there was no pulse of growth after fire. Furthermore, before the onset of rains there is no apparent suppressing effect by neighbour interference at this level.

In *E. adustus* and *L. lanatum* leaf density in the 0–10 cm interval increased steadily during the rainy season, corresponding to the production of new

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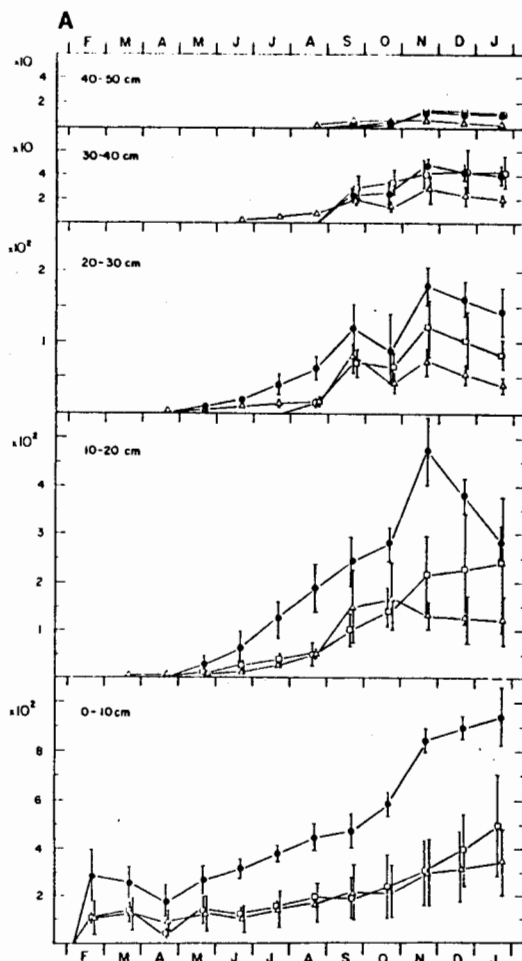
shoots and leaves. The suppressing effects of neighbours are very evident in this interval. The occupation of the 20–30 cm and 30–40 cm intervals was progressive in *E. adustus*, peaking in November and then decreasing. Leaf density values at the 30–40 cm and 40–50 cm intervals were very low. In contrast, in *L. lanatum* this occupation took place rapidly. The 10–20 cm interval reached a plateau in June, and the 30–40 cm and 40–50 cm intervals in September. Since in basal grasses the occupation of upper intervals only takes place by leaf elongation, it is apparent that *L. lanatum* leaves elongate more rapidly than those of *E. adustus*. Also, leaf elongation was suppressed by the presence of neighbours in both species, since upper interval occupation was diminished when the species were growing in mixtures. Since the proportion of leaves from the first
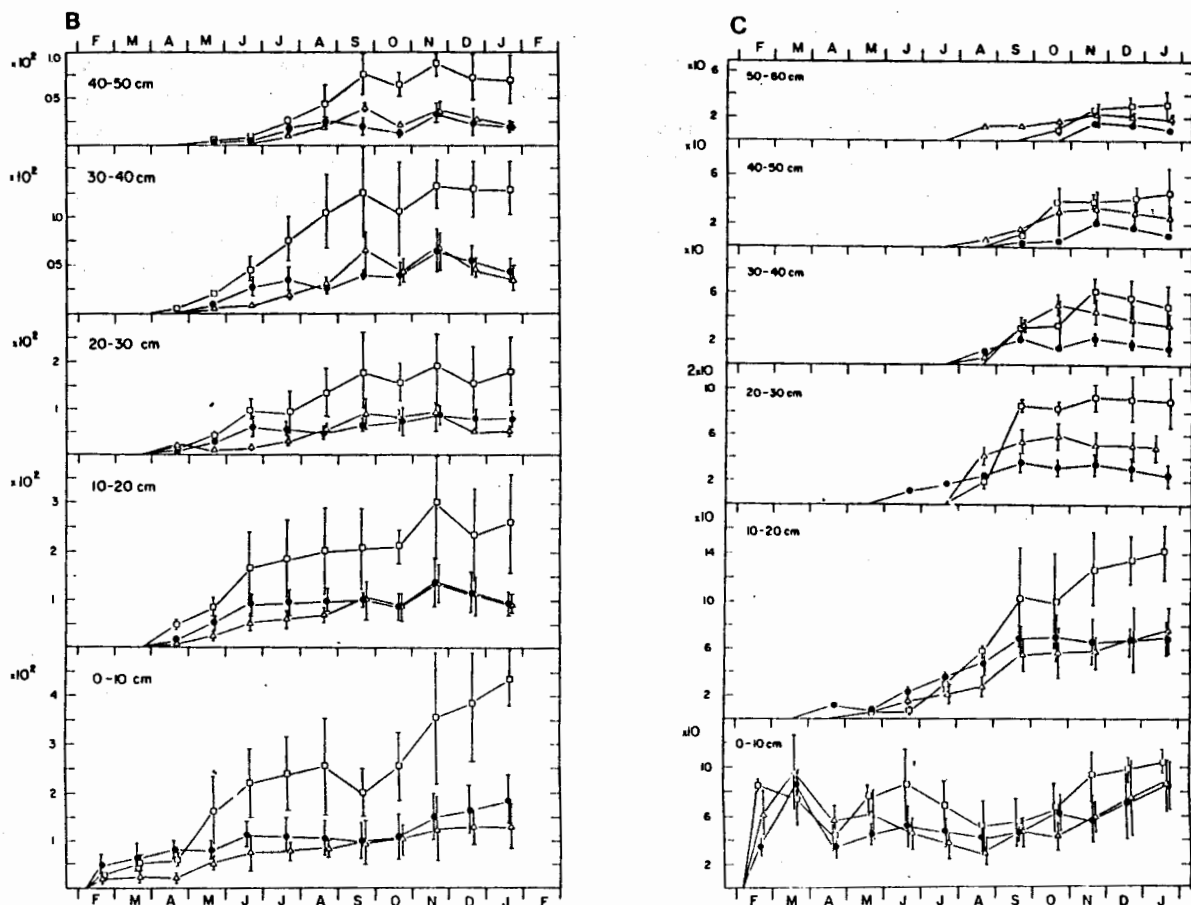
Fig. 4. Changes in mean leaf density values for each height interval throughout the year for each species growing alone or in mixtures of two species. a) *Elyonurus adustus*; b) *Leptocoryphium lanatum*; c) *Andropogon semiberbis*. Symbols as in Fig. 2 a–c.

interval reaching the upper intervals was the same in plants growing alone and in mixtures we may conclude that tiller production was also suppressed by the presence of neighbours in these two species.

In *A. semiberbis* changes in leaf density in the first 0–10 cm interval showed the same pattern for the species growing alone as well as in mixtures, with three peaks throughout the year. The first peak, after the passing of fire was already explained. The second peak occurred after two months of rain (April to June) and must correspond to leaf production and growth of the surviving tillers, since tillering only takes place during the last two months of the rainy season in this species (Silva unpubl.). The further decline was due to the progressive death of leaves at 0–10 cm during July and August. During Novem-

ber intense production of new tillers was observed, followed by leafing and leaf elongation, corresponding to the third peak. This however, had very little effect on the upper level. From June to September old tillers culms grew above this first level and new leaves were produced higher up. Leaf density in the 10–20 cm and 20–30 cm intervals increased to reach a plateau after September. Growth of older tillers continued from August to October increasing leaf densities in the 30–40 cm interval and above. In *A. semiberbis* the nature of neighbour interference appeared to be different from that in the other two species. When *A. semiberbis* grew in mixtures there seemed to be very little if any reduction in tillering but a slight reduction in culm elongation and leafing. Kirby & Faris (1972) showed that density affect-

ed culm elongation, but not tillering, in barley, and related this effect to competition for light.

Root competition probably plays an important role, as found in other grass species (Eagles 1972; Cook & Ratcliff 1984; Cook 1985) and also for interference of adults of these three species on *A. semiberbis* seedlings (Silva & Castro mscr.). Also, intensity and quality of light may have be changed under the influence of neighbour growth and may affect both tillering and elongation, as found for other grass species (Langer 1963; Casal *et al.* 1985; Deregibus *et al.* 1983, 1985).

Maximum leaf density measured in *E. adustus* and *L. lanatum* was three times as high as maximum leaf density measured in *A. semiberbis* when the species grew alone, showing that the two basal species had a higher potential for producing foliar surface during the regrowth season than the tall species. However, when growing together, the maximum values measured for each of the three species were not significantly different suggesting that asymmetric competitive interference tended to equalize their ability to grow.

Conclusions

Each of one of the three studied species showed a distinct pattern of close relationship between architecture, regrowth dynamics and reproductive phenology. As a result, the three species differ widely in their spatial and temporal patterns of occupation of the above-ground space. Contrary to what we expected, important levels of competitive interference between neighbour plants were detected. Growing close to neighbour plants of other grass species in the savanna community would impair the ability of plants of these three species to regrow their photosynthetic surface. The interference is not symmetric and it is not related to phenological similarities based on flowering season. The basal species showed a higher potential to produce leaf surface during the regrowth season than the tall species, but the stronger interference from the latter tended to equate their growth when the species grew in mixtures.

Spatial and temporal differences between the species are reflected in their responses to neighbour in-

terference. In the basal species (*E. adustus* and *L. lanatum*), the neighbour interference lead to a reduction of the period of growth. In the erect species (*A. semiberbis*), the neighbour interference also reduced the period of growth but it did not affect the lowest height intervals. We interpret this as the result of a reduction in culm elongation and leafing without any important reduction in tillering. A demographic study of tiller and leaf dynamics would be necessary to reach a conclusion on the mechanisms of this growth response.

The species also differed in their reaction to fire, *A. semiberbis* and *E. adustus* showed a pulse of regrowth after the passing of fire which is missing in *L. lanatum*. In all cases the neighbour interference affected both the intensity of growth and the length of the growing period, but it did neither affect the height of the plants, nor the reproductive phenology of these three grass species.

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